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Landscape Ecology

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<https://doi.org/10.1007/s10980-014-0136-6>

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Landscape diversity enhances the resilience of populations, ecosystems and local economy in rural areas

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Received: 8 April 2014 / Accepted: 3 December 2014 / Published online: 18 December 2014
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Abstract

Context In today's world, rapid environmental and economic developments and changes pose major threats to ecosystems and economic systems.

Objective In this context we explore if resilience can be increased by the spatial configuration of the rural landscape in an integrated ecological-genetic-economic way.

Methods We study the concept of landscape diversity from genetic, ecological and economic perspectives.

Results We show that small-scale landscapes are potentially more resilient than large-scale landscapes, provided that ecosystem patch sizes are sufficiently

large to support genetic diversity and ecosystem and economic functions. The basic premise underlying this finding is that more variation in a landscape generally leads to greater genetic and species diversity. This, in turn, stabilizes populations and strengthens the different ecosystem elements in the landscape. Greater variation in ecosystem elements provides for more varied ecosystem services, which may enhance the resilience of the local economy.

Conclusion We conclude that a resilient landscape is shaped within the context of economic and ecological possibilities and constraints, and is determined by landscape diversity and spatial organisation.

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Keywords Genetics · Ecosystem services · Ecotone · Edge · Landscape planning · Response diversity · Climate change

Introduction

Stresses, such as climate change, the recent global financial crisis or globalization, challenge the development and management of landscapes because these stresses may cause disruptions and changes, such as species loss, droughts and price variability of agricultural products. If we want to retain economic goods and ecosystem services for future generations, this requires that a landscape system is designed to tolerate disturbances and to operate under a wide variety of conditions. To do that, we need to understand the growing field of knowledge about resilience.

The concept of resilience in ecological systems was introduced by Holling (1973) and is now an important notion in modern ecology (Holling 1973, 1996; Walker et al. 2006; Fletcher and Hilbert 2007; Carpenter et al. 2009). If an ecosystem is close to a critical threshold of environmental change (e.g. in terms of climate and nutrient loads), sudden disturbances like storms, flooding and fires, might trigger switches from one ecosystem state—with a specific species composition—to another ecosystem state—with a different composition of species (Scheffer et al. 2001; Folke et al. 2004). In that way an ecosystem can shift from a

desired state to an undesired state, where “desired” and “undesired” are subjective and anthropocentric perceptions (Folke et al. 2004; Drever et al. 2006). In order to resist the effect of a disturbance and to prevent such an undesired shift, it is essential to conserve a high response diversity within a functional group that determines the desired ecosystem state (Elmqvist et al. 2003; Nystrom 2006). Response diversity is defined here as variation in sensitivity to disturbances (Elmqvist et al. 2003). An ecosystem with high response diversity can maintain crucial ecosystem functions because only some of the species within a functional group will be affected by a disturbance event. As a result, the other species of the functional group are unaffected and keep ecosystem functions intact, in that way preventing an ecosystem shift.

Resilience is conferred not only by species diversity but also by genetic diversity within species (Larsen 1995; Hughes and Stachowicz 2004; Reusch et al. 2005). As Schaberg et al. (2008) asserts, it is especially the rare alleles that ‘provide a basis for population adaptation and survival following environmental change’. Genetically diverse species within a functional group might have high response diversity at the species level; that is, different genotypes might respond differently to a certain disturbance. Genotypes that are able to cope with a disturbance can survive and prevent species extinction. Consequently, the surviving species is able to maintain its function within the ecosystem and prevent ecosystem shifts.

Interestingly, this relation between diversity, resilience and disturbance holds not only for ecological systems but also for economic systems (Kaufman 1993). So also in economy, a high response diversity of economic activities creates adaptive capacity in a region and makes a community less vulnerable to disturbances like declines in product prices (Darnhofer 2010; Zolli and Healy 2012; Abson et al. 2013). As such, economies made up of a variety of economic undertakings will likely be better able to deal with changes and potential shocks and are thus more resilient.

All in all, diversity seems to be the key to resilience in ecological and economic systems. In this paper we investigate how resilience—be it ecological or economic—can be increased by the spatial composition of the landscape. We hypothesize that diverse and smaller scaled landscapes are more resilient than larger homogeneous landscapes. This paper contributes to the literature on diversity and resilience.

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However, it deviates from most previous studies in its integrated ecological-genetic-economic approach and in its attention to the spatial dimension of resilience.

Landscape diversity and resilience of ecosystems and economies

Landscape diversity and ecosystem resilience

As stated in our introduction, diversity of landscapes is possibly a key factor determining ecosystem and economic resilience. We define a fine-grained landscape with many small and different ecosystem elements to be a diverse landscape. A diverse landscape has more ecosystem types per unit area and therefore usually has greater species diversity (O’Farrell et al. 2010; Poggio et al. 2010). This high diversity can contribute to ecosystem stability, because species from a functional group in one ecosystem might temporarily support a functional group in a neighbouring ecosystem (Bianchi et al. 2007; Thomson and Hoffmann 2010). Additionally, a diverse and small-scale landscape has a higher cumulative edge length between ecosystem elements (Fig. 1). Edges represent ecotones, that is, gradients in environmental conditions, which facilitate high diversity. Ecotones may increase the resilience of an ecosystem because additional species can live there, contributing to both functional diversity and response diversity (Peterson et al. 1998; Elmqvist et al. 2003). Another advantage of a diverse landscape is that it facilitates the presence of animal species that need different ecosystems to survive. For example, many amphibians depend on water to reproduce, but they also need terrestrial habitats for foraging and hibernating. In addition, certain ecosystem patches in the landscape might serve to physically buffer other, neighbouring patches against disturbances. For instance, a water body might buffer a nearby terrestrial ecosystem from fires and drought, and a nearby forest might prevent strong winds from disrupting a pond.

Despite the advantages of a diverse and small-scale landscape, the metapopulation theory (Hanski 1994, 1999) predicts that large patches are generally richer in species and facilitate more stable populations than small patches. This is because large patches are associated with lower extinction probabilities and higher recolonization rates (Verboom et al. 2001; McCoy and Mushinsky 2007; Butcher et al. 2010). Furthermore, larger patches may harbour species that require a larger habitat

area (Verboom et al. 2001; Winter et al. 2006). Consequently, large landscape elements are likely to have a higher response diversity and therefore provide for more stable ecosystems (Wilson et al. 2009). Nevertheless, we expect the relationship between ecosystem area and functional diversity to follow a saturation curve, like the species-area relationship (Shen et al. 2009; Wilson et al. 2009). This means that the difference in functional diversity between a large and a very large ecosystem patch is relatively small, suggesting a rather limited advantage of very large patches over large patches. Hence, some minimum patch size threshold can be defined at which an ecosystem is sustainable and able to maintain its functions.

So, we think that a diverse landscape with varied ecosystem elements is generally more resilient with respect to ecosystem stability than a homogeneous and uniform large-scale landscape. The ecosystem elements, however, should have a certain minimum size, to provide room for sustainable ecosystem functioning. It is thus essential to define some minimum threshold at which an ecosystem is able to maintain its function and endure.

Landscape diversity, genetic diversity and population resilience

In the same way the variation in species determines the resilience within a functional group at the ecosystem level, the genetic variation within a species determines the population’s adaptive potential in response to a disturbance (Fig. 2). This means that a population of a species with high genetic diversity is likely to be more robust in the face of various kinds of disturbances, because different genotypes may respond differently to disturbances (Hughes and Stachowicz 2004; Reusch et al. 2005; Hughes et al. 2008). These robust populations in turn stabilize the response diversity within a functional group and therefore also increase ecosystem resilience.

The study of mechanisms for maintaining genetic variation has a longstanding tradition in theoretical population genetics. Explicit consideration has been given to the conditions for polymorphisms under both spatial and temporal heterogeneity (Hedrick 2005). For spatial heterogeneity, Levins (1968) put forward the classical distinction of “coarse-grained” and “fine-grained” environments. In short, large scaled landscapes give rise to specialist genotypes, increased genotype-environment interactions and reduced

genetic variation within the ecosystem type. In contrast, a finer grained environment with many ecosystem types and ecotones has a high genetic diversity because of all the gradual transitions from one environment to another. Very fine-grained environments, conversely, select for generalist genotypes with low genetic diversity. So, analogous to species diversity, a small-scale landscape with many ecosystems and ecotones within a certain area provides for high genetic diversity derived from the ecosystem variation and from all of the gradual transitions from one environment to another (Johansson et al. 2005). In turn, this high genetic diversity will induce relatively resilient populations that increase the ecosystem's stability and resilience. However, also from a genetic viewpoint, we need a certain minimum population size to maintain genetic diversity; otherwise genetic drift causes genetic diversity to decline (Rousset 2004). This indicate that landscapes must not be over-fragmented.

Landscape diversity, diversity of economic activities and economic resilience

It can be argued that diversity of economic activities strengthens resilience (Zolli and Healy 2012). For instance, looking at agriculture, Danhofer (2010)

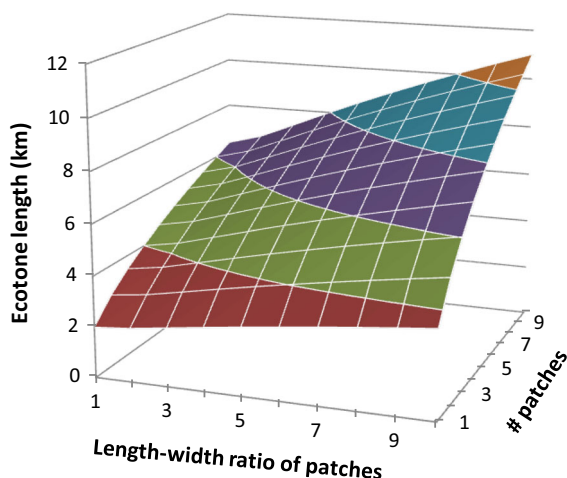


Fig. 1 The effect of the fragmentation of a landscape of 1 km² into a number of rectangular patches with various length–width ratio on ecotone (ecosystem edge) length within the landscape. The landscape is completely filled with patches, so with increasing patch number the patch size is decreasing. The figure is derived from the formula: $L = N(r + 1)\text{SQRT}(A/(N \cdot r))$ in which N = number of different landscape patches, r = the length with ratio of a patch, A = the landscape area considered

concludes that within the European Union crop farmers are diversifying their activities to be not entirely dependent upon production of a single crop. This makes them less vulnerable to the fluctuating prices of the global food market. Goldman et al. (2007) show that landscape design and the configuration of landscape elements are essential for enhancing the provision of ecosystem services and therefore for sustaining and maintaining economic activities that depend upon these services. A diverse landscape may enhance the diversity of ecosystem services (MEA 2005; Steingröver et al. 2010), which in turn enhance the diversity of economic activities (Fig. 2). Landscape configurations that include various ecosystem types, like agricultural fields, orchards, grasslands, forests, and water bodies, stimulate locally and regionally supplied ecosystem services, such as biological pest control, pollination, water-purification, flood-control services, recreation, wood production, carbon sequestration and food production. Farmers enhance the local economic resilience by using the various ecosystem services that rural areas provide (Schouten et al. 2012).

But also from a non-agricultural viewpoint, there are many plausible reasons for the realization of small-scale and diverse landscapes. For example, people in general, have greater appreciation for small-scale rural areas than for large-scale ones, which might enhance the economic activities with respect to recreation and tourism (Van Elsen et al. 2006).

So, a small-scaled landscape with various ecosystem services may improve the local economic resilience. However, here again, a certain minimum scale is necessary to provide room for sustainable ecosystem services and economic activities (Goldman et al. 2007; O'Farrell et al. 2010). For instance, a farm smaller than a certain area is economically unsustainable, while wood harvesting is only profitable above a certain stand size, additionally, ecosystem services such as water storage and purification or tourism often need a certain scale to be effective (Goldman et al. 2007).

Discussion

The preceding sections show that genetic and species diversity will enhance ecosystem resilience, and that landscapes with a certain level of fragmentation will enhance the genetic and species diversity (Fig. 2).

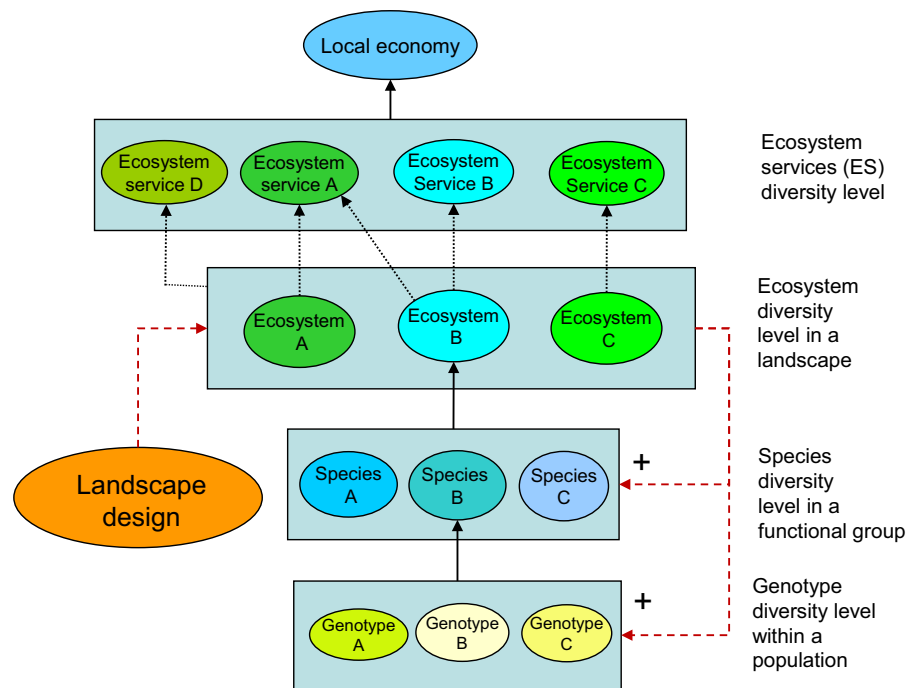


Fig. 2 Relations between landscape design, genotype diversity in a population, diversity in a functional group, ecosystem diversity in a landscape, ecosystem service diversity in a landscape and local economy. High genetic diversity within a population stabilizes (= black plain arrows) a species in a functional group. The species response diversity in ecosystem group stabilizes a certain ecosystem in the landscape. Various ecosystems in the landscape facilitate (= black dotted arrows) a

variety of ecosystem services. A variation of ecosystem services stabilizes the local economy. High ecosystem diversity in the landscape positively affects (= red dashed arrows) species and genetic diversity if the ecosystem patches are not too small. Note, that landscape design that opts for relatively high ecosystem diversity creates a resilient ecological and economic system that can cope with disturbances

Therefore, landscape scale is an important aspect determining ecosystem resilience. So, intermediate scaled landscapes with ecosystem patch sizes that are sufficiently large to support genetic diversity and ecosystem functions are likely to be more resilient than very small or very large scaled landscapes. These intermediate scaled landscapes with relative large ecosystem diversity allow a wider variation in ecosystem services and economic activities. These may in turn induce a more resilient local economy (Fig. 2).

Minimum patch size

We suggest that each ecosystem element in a landscape has a minimum patch area requirement. It should be sufficiently large to support genetic diversity and ecosystem functions necessary to maintain its stability and ecosystem services. This implies that there is a certain threshold, below which an ecosystem

cannot fully function from all of the various perspectives. Looking only at the individual ecosystem elements we expect a saturation function, with larger sized ecosystems functioning better (Kallimanis et al. 2008; Dengler 2009). The minimum sufficient patch size, however, depends on the desired targets. From a resilience point of view, sufficiently large is large enough to stay in the current ecosystem state. If we consider a forest in which insectivorous birds are crucial for controlling herbivorous insect plagues that might kill the trees, the size should be sufficiently large to allow a viable population of these birds (Vos et al. 2001). If large herbivores are necessary to have a full ecosystem functioning of a forest patch, the patch should be larger allowing a viable herbivore population (Pe'er et al. 2014; Schippers et al. 2014). If top predators are crucial to control large herbivore populations that eat all the tree seedlings at high-density levels, the forest site should be even larger to

accommodate a viable population of these top predators (Pe'er et al. 2014). Consequently, the minimum size of e.g. a forest patch is dependent on the kind of ecosystem element, the level of ecological ambition and the ecosystem definition. Criteria for the minimum size can be estimated from population genetic and population survival standards of functional key species (Verboom et al. 2001; Vos et al. 2001; Gotmark and Thorell 2003; Rousset 2004). Additionally, we can estimate the minimum area size based on cost-benefit analysis in relation to area size see e.g. (Potts and Vincent 2008; Savastano and Scandizzo 2009; Jenkins and Sutherland 2014). To stay on the safe side, we may use the maximum of these three criteria as the minimum sufficient patch size. By analysing all ecosystem types in this way a blueprint of the optimal landscape fragmentation level can be made.

Our approach challenges the “bigger is better” idea originating from the island theory and metapopulation theory (MacArthur and Wilson 1967; Schippers et al. 2009). There is growing evidence from experimental studies that report higher or equal diversity per area in smaller patches (McNeill 1993; McCoy and Mushinsky 1994; Baz and GarciaBoyer 1996; Fukamachi et al. 1996; Oertli et al. 2002; Tschardt et al. 2002; Hoyle and Harborne 2005). These studies, therefore, support our observation that habitat fragmentation does not necessarily affect diversity, provided that it is not too drastic.

Disturbance and changing conditions

We have defined resilience in terms of the capacity of a system to absorb disturbances. Disturbances are infrequent events that occur within a limited time-frame and that may or may not trigger a shift in the system state. But there is another component necessary to considering the theory of alternative stable states and that are the system conditions (Scheffer et al. 2001). A system can only collapse when the relation between system state and system conditions is catastrophic (Fig. 3). By definition, existing ecological and economic systems developed out of the past. It is likely that the system conditions of ecological and economic systems are growing out of their stable range and might become subjected to alternative attractors over time (Scheffer 2009). Here, a relatively small disturbance might trigger a system shift, not because of the disturbance itself, but because system

conditions are no longer globally stable for the current state.

Our focus in this paper has been on mitigating the impact of disturbances on ecosystems and local economies. This is because we live in a world of rapidly changing economic and ecological conditions (MEA 2005; Cavelaars 2006). Indeed, many developed countries are witnessing a collapse of their rural economies, and ecosystems suffer under a change in system conditions like climate change, land degradation, eutrophication and landscape fragmentation (Opdam and Wascher 2004; Omann et al. 2009; Scheffer 2009). Nature and economies are often unable to cope with the fast pace of change. So, not only reducing the impact of disturbances is important, but it is equally vital to mitigate the change in system conditions, in order to protect ecosystems and economic systems from deterioration.

In this paper we have reasoned that system shifts should be avoided and that improving the resilience of ecosystems and local economies should prevent such shifts. Whether a shift is good or bad is of course an anthropogenic issue. Because current systems are a result of the past, we have learned to appreciate and work within them. Protecting the current system state from change is in fact conservation. Nonetheless, system shifts might sometimes be inevitable and could be regarded as natural or necessary if system conditions change (Holling 2001). A different system might evolve from a collapsed system. This new system might be as valuable as the old in terms of ecosystem services and species diversity. Rigid conservation therefore becomes superfluous, especially when change is small in scale. So, we do not propose trying to prevent every system change. Rather, we want to prevent system change to undesired or degraded states in terms of ecosystem value and ecosystem services.

Panarchy

Our approach is related to the panarchy concept (Gunderson and Holling 2002). This concept discloses that many smaller adaptive cycles with shorter time scales and smaller spatial scales “carry” a system on a higher scale which also has its own adaptive cycle as an emergent property. Within these adaptive cycles we can distinguish four phases: exploitation, conservation, release and reorganisation (Holling 2004). In ecosystem terms, the exploitation deals with the

succession towards a climax ecosystem, the conservation phase is the climax ecosystem state that can exist for a long time, the release phase is actually the collapsing of the system to a degraded state and the reorganisation phase refers to a period of change into a new exploitation state that results in the same or another conservation state. Like in our approach, the panarchy concept discloses that a system needs a certain size to function because faster cycles that carry a system need a certain spatial dimension to function (Holling 2001). Another similarity is the hierarchical structure. The hierarchy in the panarchy concept is exclusively organised along spatial and temporal scales. For instance, the dynamics of a forest ecosystem can be described by the adaptive cycles of leaves, crowns and patches (Holling 2001). We propose, however, a hierarchical functional diversity approach, in which we maximize the diversity of genotypes, species, ecosystems and ecosystem services to create a resilient landscape which is in fact a mixture of ecosystems. In our approach, the spatial requirements of genetic, species and ecosystem service diversity does not necessary follow the hierarchical lines. Furthermore, our approach does not consider the

whole panarchy cycle but focuses on transition from the conservation phase to the release phase.

Local specialization in economic systems

A region with a concentration of one core business might be economically strong because of the advantages of the economy of scale. For example, in a locality focused on dairy farming the transport of milk, cattle, fodder and machines might be quite efficient. This means that dairy farms situated there might be more competitive than multifunctional farms that are scattered across the landscape. But if we take product distribution (de Souza et al. 2008) and the sensitivity to cattle diseases into account the efficiency gain might be much less pronounced. Nevertheless, scale advantages could still be an argument against our approach. Separation of functions and specialization in the landscape might, however, be profitable in a relatively stable economic environment with controlled prices and governments that are willing to pay for disturbances, like animals diseases. In a more liberal market, however, the occurrence of variable prices and disturbances may dislocate the local economy in a highly specialized area. In such a context, a more diverse economic system could turn out to be more sustainable. Framed in the words of Walker and Salt (2006): any attempt at a sustainable economic system that does not explicitly acknowledge the resilience of this system, leads to a malfunctioning system that does not provide the goods and services that are expected (Walker et al. 2006).

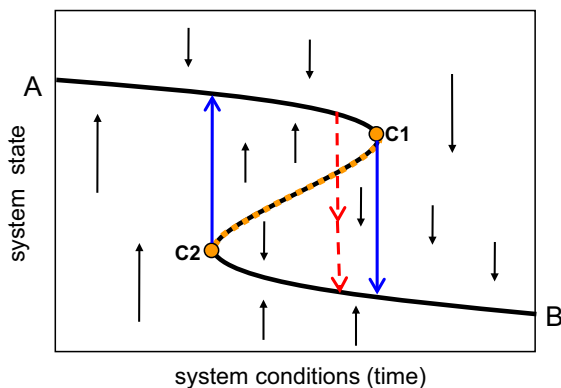


Fig. 3 Catastrophic ecosystem transitions and the effect of disturbance on the system state. Small black arrows indicate the direction of change in system state under constant system conditions, the black lines indicate locally stable equilibria, the orange-black dashed line represents an unstable equilibrium. C1 and C2 are critical thresholds where a change in system conditions triggers a fast switch between system states, blue arrows. An accidental disturbance that pushes the system state below the orange-black line, causes a switch from state A to state B (dashed red arrows). Note that because of environmental and/or economic change in system conditions, the system state A, that developed in the past, is no longer globally stable and becomes susceptible to a catastrophic shift to state B

Climate change

Climate change has two aspects: (1) temperature and CO_2 are gradually increasing causing a change in system conditions (IPPC 2007) and (2) climate change is expected to cause an increase in the frequency of extreme weather events which can be regarded as disturbances (Verboom et al. 2010). The change of system conditions may drive ecosystems closer to their critical limits (point C1, Fig. 3). This in combination with increased environmental variability increases the risk of a catastrophic shift to a degraded stage. We think that diverse landscapes are better able to deal with disturbances and therefore will be less sensitive to these shifts.

In response to climatic warming, we also expect species to move northwards (Spies et al. 2010). Smaller-scaled landscapes generally have significantly smaller inter-patch distances (Schippers et al. 2011). In these situations many relatively immobile plants and animals, may more successfully find their way to suitable patches in line with climate change (Travis 2003; Opdam and Wascher 2004; Vos et al. 2008). Here small-scale landscapes may also be superior, as they provide ways for such species to escape from areas that have become unsuitable under climate change. Diverse landscapes might therefore be more “climate proof” than large-scale monotone landscapes.

Ecotones and edges

Linear elements have gained increased attention as important landscape components for biodiversity conservation. Linear elements offer habitat for various species, connection zones or corridors between ecosystems, and add variation in ecosystem services, like wood production, fencing, shading, a nectar source for pollinators, pest control and aesthetics. In many landscapes, therefore, hedgerows, field margins and ditch banks are being established or conserved (Thomas and Kevan 1993; Tischendorf and Wissel 1997; Grashof-Bokdam et al. 2009; Schippers et al. 2009). Although ecotones and edges are generally considered as beneficial for species diversity they can sometimes be used by invasive species which may have the opposite effect (van Rensburg et al. 2013; Vicente et al. 2014).

Conclusion

The general idea, originated from the island and metapopulation theory, is that bigger ecosystem patches are better for maintaining and protecting biodiversity (MacArthur and Wilson 1967; Schippers et al. 2009). We argue that more ecosystem variation in a landscape generally leads to greater genetic diversity within species and higher species diversity within functional groups. This, in turn, stabilizes and strengthens the different ecosystem elements in the landscape and increases the resilience. So, we expect that smaller-scale landscapes are potentially more resilient than larger-scale landscapes, provided that

ecosystem patch sizes are sufficiently large to support genetic diversity and ecosystem and economic functions. Greater variation in ecosystem elements, in turn, provides for more varied ecosystem services, which may enhance the resilience of the local economy. This idea could be especially important in today’s world in which fast economic development and environmental changes pose major threats to ecosystem and economic functioning.

Acknowledgments This study was supported by Ecological Resilience (project no. KB-01-007-004) of the Knowledge Base of the Dutch Ministry of Agriculture, Nature and Food Quality. We thank three anonymous reviewers for their helpful comments.

References

- Abson DJ, Fraser EDG, Benton TG (2013) Landscape diversity and the resilience of agricultural returns: a portfolio analysis of land-use patterns and economic returns from low-land agriculture. *Agric Food Secur* 2(2):1–15
- Baz A, GarciaBoyer A (1996) The SLOSS dilemma: a butterfly case study. *Biodivers Conserv* 5(4):493–502
- Bianchi F, Honek A, van der Werf W (2007) Changes in agricultural land use can explain population decline in a ladybeetle species in the Czech Republic: evidence from a process-based spatially explicit model. *Landsc Ecol* 22:1541–1554
- Butcher JA, Morrison ML, Ransom D Jr, Slack RD, Wilkins RN (2010) Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *J Wildl Manag* 74(1):133–139
- Carpenter SR, Folke C, Scheffer M, Westley F (2009) Resilience: accounting for the noncomputable. *Ecol Soc* 14(1):13
- Cavelaars P (2006) Output and price effects of enhancing services sector competition in a large open economy. *Eur Econ Rev* 50(5):1131–1149
- Darnhofer I Strategies of family farms to strengthen tier resilience. In: 8th International Conference of the European Society for Ecological Economics, Ljubljana 2010
- de Souza JL, Casali VWD, Santos RHS, Cecon PR (2008) Energetic balance and sustainability analysis in the organic production of vegetable crops. *Horti Bras* 26(4):433–440
- Dengler J (2009) Which function describes the species-area relationship best? A review and empirical evaluation. *J Biogeogr* 36(4):728–744
- Drever CR, Peterson G, Messier C, Bergeron Y, Flannigan M (2006) Can forest management based on natural disturbances maintain ecological resilience? *Can J For Res-Rev Can De Rech For* 36(9):2285–2299
- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Env* 1(9):488–494
- Fletcher CS, Hilbert DW (2007) Resilience in landscape exploitation systems. *Ecol Model* 201(3–4):440–452

- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Syst* 35:557–581
- Fukamachi K, Iida S, Nakashizuka T (1996) Landscape patterns and plant species diversity of forest reserves in the Kanto region. *Jpn Veg* 124(1):107–114
- Goldman RL, Thompson BH, Daily GC (2007) Institutional incentives for managing the landscape: inducing cooperation for the production of ecosystem services. *Ecol Econ* 64(2):333–343
- Gotmark F, Thorell M (2003) Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. *Biodivers Conserv* 12(6):1271–1285
- Grashof-Bokdam CJ, Chardon JP, Vos CC, Foppen RP, WallisDeVries M, van der Veen M, Meeuwsen HA (2009) The synergistic effect of combining woodlands and green veining for biodiversity. *Landsc Ecol* 24(8):1105–1121
- Gunderson LH, Holling HCS (2002) *Panarchy: understanding the transformations in human and natural systems*. Island Press, Washington
- Hanski I (1994) Spatial scale, patchiness and population-dynamics on land. *Philos Trans Royal Soc Lond Ser B-Biol Sci* 343(1303):19–25
- Hanski I (1999) *Metapopulation ecology*. Oxford University Press, Oxford
- Hedrick P (2005) *Genetics of Populations*. Jones & Bartlett, Sudbury
- Holling CS (1973) Resilience and the stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23
- Holling CS (1996) Surprise for science, resilience for ecosystems, and incentives for people. *Ecol Appl* 6(3):733–735
- Holling CS (2001) Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4(5):390–405
- Holling CS (2004) From complex regions to complex worlds. *Ecol Soc* 9(1):11
- Hoyle M, Harborne AR (2005) Mixed effects of habitat fragmentation on species richness and community structure in a microarthropod microecosystem. *Ecol Entomol* 30(6):684–691
- Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc Natl Acad Sci USA* 101(24):8998–9002
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M (2008) Ecological consequences of genetic diversity. *Ecol Lett* 11(6):609–623
- IPPC (2007) *Climate change 2007: synthesis report*. International governmental panel on climate change, Geneva, p 73
- Jenkins TL, Sutherland JW (2014) A cost model for forest-based biofuel production and its application to optimal facility size determination. *Forest Policy Econ* 38:32–39
- Johansson M, Primmer CR, Sahlsten J, Merila J (2005) The influence of landscape structure on occurrence, abundance and genetic diversity of the common frog *Rana temporaria*. *Glob Chang Biol* 11(10):1664–1679
- Kallimanis AS, Mazaris AD, Tzanopoulos J, Halley JM, Pantis JD, Sgardelis SP (2008) How does habitat diversity affect the species-area relationship? *Glob Ecol Biogeogr* 17(4):532–538
- Kaufman RK (1993) An empirical exploration of the relation among diversity, stability, and performance in ecosystem systems. *Struct Chang Econ Dyn* 4:299–313
- Larsen JB (1995) Ecological stability of forest and sustainable silviculture. *For Ecol Manage* 73(1–3):85–96
- Levins R (1968) *Evolution in changing environments*. Princeton University Press, Princeton
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton
- McCoy ED, Mushinsky HR (1994) Effects of fragmentation on the richness of vertebrates in the Florida shrub habitat. *Ecology* 75(2):446–457
- McCoy ED, Mushinsky HR (2007) Estimates of minimum patch size depend on the method of estimation and the condition of the habitat. *Ecology* 88(6):1401–1407
- McNeill SE (1993) Fairweather PG (1993) Single large or several small marine reserves? An experimental approach with seagrass fauna. *J Biogeogr* 20:429–440
- MEA (2005) *Ecosystem and human Well-being: synthesis*. Island Press, Washington
- Nystrom M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* 35(1):30–35
- Oertli B, Auderset Joye D, Castella E, Juge R, Cambin D, Lachavanne JB (2002) Does size matter? The relationship between pond area and biodiversity. *Biol Conserv* 104(1):59–70
- O'Farrell PJ, Reyers B, Le Maitre DC et al (2010) Multi-functional landscapes in semi arid environments: implications for biodiversity and ecosystem services. *Landsc Ecol* 25(8):1231–1246
- Omann I, Stocker A, Jager J (2009) Climate change as a threat to biodiversity: an application of the DPSIR approach. *Ecol Econ* 69(1):24–31
- Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol Conserv* 117(3):285–297
- Pe'er G, Tsianou MA, Franz KW, Matsinos YG, Mazaris AD, Storch D, Kopsova L, Verboom J, Bagueette M, Stevens VM, Henle K (2014) Toward better application of minimum area requirements in conservation planning. *Biol Conserv* 170:92–102
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1(1):6–18
- Poggio SL, Chaneton EJ, Ghersa CM (2010) Landscape complexity differentially affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields. *Biol Conserv* 143(11):2477–2486
- Potts MD, Vincent JR (2008) Spatial distribution of species populations, relative economic values, and the optimal size and number of reserves. *Environ. Resour. Econ.* 39(2):91–112
- Reusch TBH, Ehlers A, Hammerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc Natl Acad Sci USA* 102(8):2826–2831
- Rousset F (2004) *Genetic structure and selection in subdivided populations*. Princeton University Press, Princeton
- Savastano S, Scandizzo PL (2009) Optimal farm size in an uncertain land market: the case of Kyrgyz Republic. *Agric Econ* 40(6):745–758
- Schaberg PG, DeHayes DH, Hawley GJ, Nijensohn SE (2008) Anthropogenic alterations of genetic diversity within tree populations: implications for forest ecosystem resilience. *For Ecol Manage* 256(5):855–862

- Scheffer M (2009) *Critical Transitions in Nature and Society*. Princeton University Press, Princeton
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413(6856): 591–596
- Schippers P, Grashof-Bokdam CJ, Verboom J, Schippers P, Grashof-Bokdam CJ, Verboom J, Baveco JM, Jochem R, Meeuwsen HA, Van Adrichem MH (2009) Sacrificing patches for linear habitat elements enhances metapopulation performance of woodland birds in fragmented landscapes. *Landsc Ecol* 24(8):1123–1133
- Schippers P, Verboom J, Vos CC, Jochem R (2011) Metapopulation shift and survival of woodland birds under climate change: will species be able to track? *Ecography* 34(6): 909–919
- Schippers P, van Teeffelen AJA, Verboom J, Vos CC, Kramer K, WallisDeVries MF (2014) The impact of large herbivores on woodland-grassland dynamics in fragmented landscapes: the role of spatial configuration and disturbance. *Ecol Complex* 17:20–31
- Schouten MAH, van der Heide CM, Heijman WJM, Opdam PFM (2012) A resilience-based policy evaluation framework: application to European rural development policies. *Ecol Econ* 81:165–175
- Shen GC, Yu MJ, Hu XS, Mi X, Ren H, sun IF, Ma K (2009) Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology* 90(11):3033–3041
- Spies TA, Giesen TW, Swanson FJ, Franklin JF, Lach D, Johnson KN (2010) Climate change adaptation strategies for federal forests of the Pacific Northwest, USA: ecological, policy, and socio-economic perspectives. *Landscape Ecol* 25(8):1185–1199
- Steingrover EG, Geertsema W, van Wingerden WKRE (2010) Designing agricultural landscapes for natural pest control: a transdisciplinary approach in the Hoeksche Waard (The Netherlands). *Landsc Ecol* 25(6):825–838
- Thomas VG, Kevan PG (1993) Basic principles of agroecology and sustainable agriculture. *J Agric Env Ethics* 6(1):1–19
- Thomson LJ, Hoffmann AA (2010) Natural enemy responses and pest control: importance of local vegetation. *Biol Control* 52(2):160–166
- Tischendorf L, Wissel C (1997) Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. *Oikos* 79(3):603–611
- Travis MJM (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc Royal Soc Lond Ser B-Biol Sci* 270(1514):467–473
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol Appl* 12(2):354–363
- Van Elsen T, Van Günther A, Pedrolí B (2006) The contribution of care farms to landscapes of the future. In: Hassink J, Van Dijk M (eds) *Farming for health; green care farming across Europe and the United States of America*. Springer, Dordrecht
- Van Rensburg BJ, Hugo S, Levin N, Kark S (2013) Are environmental transitions more prone to biological invasions? *Divers Distrib* 19(3):341–351
- Verboom J, Foppen R, Chardon P, Opdam P, Luttikhuisen P (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biol Conserv* 100(1):89–101
- Verboom J, Schippers P, Cormont A, Sterk M, Vos CC, Opdam PFM (2010) Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. *Landsc Ecol* 25(8): 1289–1298
- Vicente JR, Pereira HM, Randin CF, Goncalves J, Lomba A, Alves P, Metzger J, Cezar M, Guisan A, Honrado J (2014) Environment and dispersal paths override life strategies and residence time in determining regional patterns of invasion by alien plants. *Perspect Plant Ecol Evol Syst* 16(1):1–10
- Vos CC, Verboom J, Opdam PFM, Ter Braak CJF (2001) Toward ecologically scaled landscape indices. *Am Nat* 157(1):24–41
- Vos CC, Berry P, Opdam P, Baveco H, Nijhof B, O’Hanley J, Bell C, Kuipers H (2008) Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *J Appl Ecol* 45(6):1722–1731
- Walker B, Salt D (2006) *Resilience thinking: Sustaining ecosystems and people in a changing world*. Island Press, Washington
- Walker B, Gunderson L, Kinzig A, Folke C, Carpenter S, Schultz L (2006) A handful of heuristics and some propositions for understanding resilience in social-ecological systems. *Ecol Soc* 11(1):13
- Wilson TL, Johnson EJ, Bissonette JA (2009) Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. *Landsc Ecol* 24(3):351–360
- Winter M, Johnson DH, Shaffer JA, Donovan TM, Svedarsky WD (2006) Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management* 70(1):158–172
- Zolli A, Healy AM (2012) *Resilience: why things bounce back*. Free Press, New York