SELF-SUSTAINING FOREST

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Abstract. It has been recognized and discussed in the literature that values associated with forest integrity, i.e., sustainability and diversity, are relevant to the three aspects of self-organisation: resilience, health, and evolvability. However, evolvability has not yet been studied and also there is still no relevant notion of forest health. This calls for a biodynamic approach to forests and clearly addresses questions relating to scaling and self-organisation since the different levels of detail must be compatible to ensure the consistency of sustainability and diversity assessments. To support the development of a biodynamic approach to forests we review the concepts of self-organisation, criticality and resilience, and their relationship to forest integrity in the light of fractal organisation theory. An exploration of fractal connectivity behind key bioindicators and biomonitors in the avoidance of a biodiversity threshold can be suggested thus far. Forest integrity refers to empirical scaling relationships that are emergent features of biodiversity. In a forest, species as different as fungi, plants, animals and insects, and processes as disparate as disturbance, dispersal, facilitation/competition and nutrient cycling, are related through ecological interaction networks; a ‘fractal’ is the ‘collective phenomenon’ of these networks.

Keywords: biodynamic approach, forest integrity, fractal connectivity

Introduction

Cyclic processes in the biosphere are self-organised and demonstrate sustainable development that inevitably involves change (Kazansky, 2010; Kimmins et al., 2007). The most important direct driver of change in forest biodiversity and ecosystems is habitat shifts and forest loss. Nearly half of the world’s original forest cover has been lost, yet the economic potential of a large part of the global forest area is under-realised because of a lack of sustainable forest management (FAO, 2014). Even if forest loss were to end today, it would take hundreds of years for species numbers to reach a new, lower, equilibrium in response to the habitat shifts that took place in recent centuries (Millennium Ecosystem Assessment, 2005). This means that since large areas are required to conserve viable populations and that since nature reserves eventually become isolated islands in the landscape, the long-term fate of many forest-dependent organisms will depend on activities and conditions in the unreserved portions of forests (Lindenmayer and Franklin, 2002; Whittaker et al., 2001; Kemp, 1992). For this reason, the present understanding of sustainable forest management must include values associated with integrity. A significant change, compatible with economic realities, requires the intrusion of biological considerations and conservationist philosophy into modern methods of exploitation (Stern and Roche, 1974). This calls for a biodynamic approach to forests and clearly addresses questions relating to scaling and self-organisation since the different levels of detail must be compatible to ensure the consistency of sustainability and diversity assessments.
Values associated with integrity, i.e., sustainability and diversity, are in essence about maintaining the combined biospherical-societal system: humans, with their social, cultural, economic, and environmental needs, are an integral part of ecosystems. It means that the capacity to sustainably use forests rests on our understanding and interpretation of pattern and process at several scales, the recognition of thresholds, and the ability to translate knowledge into appropriate management actions in a reflexive manner (Garmestani and Benson, 2013; Thompson et al., 2009). However, there is no single underpinning model that fully meets all the requirements for evaluating the sustainability of multi-functional forest management (Rennolls et al., 2007). So, the focus of attention shifts from the value components of sustainable development projects, to the domain of existence, in that we can map and model single, or even multiple relationships, but not a total set of evolving interactions and feedbacks (Fernandez et al., 2014; Jiggins and Röling, 2002; Waldrop, 1992). Here the reflexivity makes possible to connect any aspects of reality, setting up feedback loops between them (Soros, 2010). This, in turn, makes fractal organisation theory, inspired by systems theory, fractal geometry, quantum mechanics, information dynamics, sociobiology, epigenetics, evolutionary biology and game theory, the central subject herein (Raye, 2012).

Fractal organisation theory could illuminate evolving interactions and feedbacks from the multiple perspectives of different types, so it is a means to support the development of underpinning models which are consistent, and scale appropriately across the levels of self-organisation and conceptual frameworks. Forest integrity is about three aspects of self-organisation: resilience, health, and evolvability (Freedman, 2012; Kay and Regier, 2000). Evolvability, however, has not yet been studied because it was presumed at the outset: empirical experiences with quantitative genetics and selective breeding produced a consensus that ‘phenotypic variation was effectively like a gas which could flow into any selective bottle’ (Luo, 2014; Altenberg, 2014). Also, there is still no relevant notion of forest health, as there is for humans: a set of properties that have been selected through evolution because they maximize fitness (De Leo and Levin, 1997). Resilience is ‘the capacity to change in order to maintain the same identity’ (Folke et al., 2010). Accordingly, to support the development of a biodynamic approach to forests we review the concepts of self-organisation, criticality and resilience, and their relationship to forest integrity in the light of fractal organisation theory.

Scaling laws

Pattern integrity or self-similarity – the retention of distorted copies of itself across scales – is a typical property of fractals, a concept introduced by Benoît Mandelbrot (1924-2010) and one of the fundamental mathematical results of the 20th century (Satija, 2016; Raye, 2012; Rozenfeld et al., 2009). Fractals are often considered the ‘fingerprints of chaos’: the term ‘fractal’ is based on the Latin frāctus, derived from frangere which signifies to break, to create irregular fragments (Mandelbrot, 1983). Also, a fractal is known as expanding symmetry or evolving symmetry (Kumar et al., 2017). Self-similarity is symmetry across scale. The manner, in which a fern leaf’s overall shape is replicated in each of its leaflets, and again in the subleaflets of each leaflet, is a familiar illustration of fractal relationship (Mosko, 2010). However, fractals are not extrapolated from a geometric logic based on units. Rather, we can think of

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Fractals as processes, possessing a self-replicating basis, which lead to a non-integer dimensionality (Fielder and King, 2014). Let’s take, for example, the branching structures of resource distribution networks, such as the xylem that transport water through plants. According to West et al. (2009), “the entire forest is, in a very real sense, a hierarchically branching resource supply network that can be described mathematically and behaves structurally and functionally like a scaled version of the branching network of the trees it contains”: the analysis of the branching size distribution reveals an exponent which is essentially identical to the tree size distribution within a forest. So, a ‘fractal’ is what ‘emerges’ from these networks; it’s the ‘emergent property’ of the network’s memory. The analysis of fractality can provide a new strategy for studying cellular, organismal and community differentiation since fractal dimension is a good quantitative measure of the degree of morphological differentiation; it is also a useful measure for comparative studies across and among species, as they relate to cellular evolution (Smith and Behar, 1994). It should be noted, however, that the existence of changes in fractal dimension when shifting between scales implies that in place of true pattern integrity, we observe only partial self-similarity over a limited range of scales separated by transition zones. Fortunately, tests carried out using multifractals, which are objects that need a continuous spectrum of exponents to be described, may disclose the properties encoded in the data relating to the relationships on different scales; the basic graphic tools here are known as multifractal spectra or spectra of singularity (Drożdż and Oświęcimka, 2015). On the other hand, real fractals are, in fact, multifractals: the measure is not the same in every subset, and each of them has a different fractal dimension and a different associated diverging exponent (Solé and Manrubia, 1995). Several good introductions to multifractal methods applied to ecology can be found in Scheuring and Riedi (1994) and Borda-de-Água et al. (2007) (Saravia, 2014). Multifractals have been applied to vegetal communities (Scheuring and Riedi, 1994), tropical rainforest (Manrubia and Solé, 1996), and to the characterisation of species-area relationships (Laurie and Perrier, 2011; Yakimov et al., 2008; Borda-de-Água et al., 2002). Borda-de-Água et al. (2007) used the so-called multifractal approach to show that models which assume symmetric neutral dynamics and use realistic dispersal kernels predict scaling patterns of diversity and distribution very similar to those observed by Hubbell and Foster (1983) in the Barro Colorado Island rainforest, in Panama. Solé and Manrubia (1995) constructed a simple cellular automata model in order to simulate the gap dynamics of the Barro Colorado Island rainforest as well as the observed macroscopic spatial regularities. The observed and simulated fractal behaviour was shown to be related to self-similar dynamics of biomass.

‘From a wildlife perspective, each organism scales the environment differently, and thus there is no absolute size for a landscape’ (Sun and Southworth, 2013). As scale changes, new patterns and processes may emerge and controlling factors may shift even for the same phenomena (Wu and Li, 2006). Fortunately, the fractal hierarchy is a method which can be used to unify different scaling phenomena and rules in complex systems (Seuront, 2009). ‘The hierarchy always follows a pair of exponential laws and a power law’ (Chen, 2012). Power laws describe empirical scaling relationships that are emergent quantitative features of biodiversity (Brown et al., 2002). A power law is obtained when one observes a straight line in a plot of ‘the number of events’ versus ‘how often they occur’; in other words, the probability \( f(x) \) of an event of magnitude \( x \) occurring is inversely proportional to \( x \): \( f(x) \sim x^{-\alpha} \) (Rhodes and Anderson, 1996).
\( x^{-1} \) – a critical dependence – is often associated with ‘self-organised criticality’ which provides a general mechanism for the emergence of scale-free networks with the characteristic power-law distribution of links (Graham, 2014; Nottale, 2013; Laurienti et al., 2011; Messier and Puettmann, 2011; Turcotte, 1999; Bak et al., 1989). ‘Scale-free model’ incorporates two generic mechanisms thought to be common to many real-world networks: growth of the network by addition of nodes and links at each time step and preferential attachment of new nodes to certain highly connected hubs – the existing nodes with a high number of links. In other words, ‘A scale-free topology automatically emerges whenever new species (nodes) add preferentially to pre-existing ones with a probability proportional to the number of pairwise interactions (links) of the target species’ (Jordano et al., 2003). However, most ecological interaction networks examined so far have cut-off numbers of pairwise interactions per species giving rise to a gradient of variation from scale-free to broad-scale and to single-scale distributions; these distributions depart in most cases from the power-law beyond cut-off values. Constraints in the addition of links such as morphological mismatching or phenological uncoupling between mutualistic partners restrict the number of plant-animal interactions established, causing deviations from scale invariance, which is solely described by a power-law function, \( f(x) = kx^\alpha \), where the power-law exponent, \( \alpha \), is a measure of scale-invariance, and \( k \) is a constant (Katz, 2016). In food webs, the distribution of links changes from (partial) power-law to exponential to uniform as the level of connectance increases (Dunne et al., 2002).

**Self-organised phenomena**

Nothing happens directly in this indirectly ordered universe (Schauberger, 1936). Unlike the action of seasons and natural disasters, long-term change in the composition of communities is brought about by the activities of living organisms which themselves inhabit the environment. Over a period of time, the environment is modified by these organisms so it becomes suitable for colonization by another species and less suitable for those already there (Rose, 2005). For example, after a stand-replacing disturbance, shade-intolerant species colonize and grow into a dominant canopy, but due to their shade-intolerance they are unable to regenerate under their own canopy, so the understory (composed of shade-tolerant species) gradually replaces the canopy (Kotar, 1997). Thus, all elements of any developing living system co-determine each other, whether it is the coevolution of biological species, a behavioural act or an immune response (Kazansky, 2015). Any living organism has relatively autonomous organisation of metabolic processes and, at the same time, all living creatures are fundamentally dependent on each other via trophic, behavioural or sexual relationships, and also indirectly, via the environment (Levchenko et al., 2012). A forest exists by virtue of all the fungi, trees, other plants, insects, birds and other animals, and they are fully what they are by virtue of dwelling in that forest; neither can ‘exist’, at least not fully, without the other.

‘Self-organisation is basically the spontaneous creation of a globally coherent pattern out of the local interactions between initially independent components’ (Heylighen, 2001). ‘In the optic of biological research, the common meaning of self-organisation is defined by the global emergence of a particular behaviour or feature that cannot be reduced to the properties of individual system’s components such as molecules, agents and cells’ (Camazine et al., 2003 as cited in Di Marzo Serugendo et al., 2011).
Physiological interactions among molecules, cells, tissues, organs do not simply sum each other up: they are “entangled”, “non-local”, “non-separable” . . . they are “superposed” (Longo and Montévil, 2011). Therefore, despite its intuitive simplicity as a concept, self-organisation has proven notoriously difficult to define and pin down formally or mathematically, and it is entirely possible that any precise definition might not include all the phenomena to which the label has been applied. One of the objectives of the present article was, therefore, to give prominence to the concepts of self-organised criticality and resilience because they are of relevance to forest integrity. As a result, forest integrity could be understood in terms of attractors as defined by conceptual inferences related to self-organised criticality and resilience (Table 1). The explanatory power of self-organised criticality stretches so far as to assume that a given scale-free phenomenon is caused by the system which organises its critical state by itself (Pruessner, 2012). This critical state acts as an attractor. The fractal patterns may be a fingerprint of a system close to a critical point (Manrubia and Solé, 1996). To substantiate such a viewpoint, Manrubia and Solé (1996) performed an extensive study of a real rainforest in Barro Colorado Island, Panama. They found the strong evidence of self-organised critical state in the power laws that the magnitudes of the system follow, both in space (fractality, correlation function, clearings and tree sizes distributions) and time (biomass fluctuations). Moreover, self-organised critical models of extinction have been used to explain power-law distributions of species’ life span and extinction events in statistical evidence from the fossil record (Solé et al., 1997; Solé and Bascompte, 1996; Sneppen et al., 1995; Bak and Sneppen, 1993).
**Table 1. System integrity in terms of attractors by conceptual inferences related to self-organised criticality and resilience**

<table>
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<tr>
<th>Concept</th>
<th>Inference</th>
<th>Connection</th>
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<td>Self-organisation</td>
<td>'The basic mechanism underlying self-organisation is the variation which explores different regions in the system’s state space until it enters an attractor' (Heylighen, 2001). ‘Standard examples of attractors are stable equilibrium and stable limit cycle’ (Fradkov and Chen, 2009). A limit cycle of infinite period is sometimes referred to as a chaotic state (Li and Yorke, 1975). An attractor – a region in state space that a system can enter but not leave – is a mathematical model of causal closure. ‘Closure usually results from the nonlinear, feedback nature of interactions’ (Heylighen, 2001). Therefore, it seems that reflexivity can act as an attractor when attempting to predict the outcome of a self-organising system at work (see Schiavello, 2013; Sandywell, 1996).</td>
<td>Reflexivity as an attractor</td>
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<td>Criticality</td>
<td>'Dynamical criticality, a central property for the functioning of a living organism, naturally emerges as a consequence of evolution that favours evolvability' (Torres-Sosa et al., 2012). Also, it is a property of (classes of) dynamical systems that have a critical point as an attractor (Aschwanden, 2011; Bak and Creutz, 1994). Actually, many slowly driven open non-equilibrium systems self-organise to a critical point where everything can happen within well-defined statistical laws (Jensen, 1998; Bak, 1996; Bak et al., 1989). Moreover, as a system parameter changes through a critical value, a symmetry-broken attractor can be born (Lai, 1997). Lastly, when the symmetry is lost, it can be said that it is replaced by a collective mode.</td>
<td>Symmetry-broken attractor</td>
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<td>Resilience</td>
<td>An ecosystem is resilient if it remains in the same domain of attraction and returns to the same state after a disturbance (Rietkerk and van de Koppel 2008). However, it may exist almost continuously in a transient state if there is frequent disturbance. So, it turns out that the final attractor toward which the system will converge (e.g., successional pattern, community type, etc.) usually depends on the initial conditions involving several attractors, leading to difficult issues related to the ability to predict which attractor a given trajectory will asymptote from (Freire et al., 2008; McDonald et al., 1985). Hypothetically, intransitivity, i.e., coexistence of attractors, is a peculiar characteristic of meta-communities without strict competitive hierarchies (Freire et al., 2008; Kerr et al., 2002).</td>
<td>Intransitivity of attraction</td>
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The basic assumption of resilience thinking is that systems are most resilient in their natural (evolved) states (Hopkin's, 2009). Over the long run resilience is needed to maintain organismal fitness, however, the dynamics of organismal fitness remain poorly understood over long time scales (Wiser et al., 2013). Although researchers such as Kauffman (1993) have started exploring the structure of fitness landscapes for various formally defined systems by computer simulation, examples of individual adaptation via plasticity by temporal variation of fitness-related traits observed during the lifetime of forest organisms are very seldom documented at this time (see Lindner et al., 2008; Heylighen, 2001; Durzan, 1993). This leads to a reconsideration of the traditional approach to forests focused on long-term dynamics in favour of biodynamic approach. ‘The commonly accepted fact is that the cell/organism (any living organisation, in fact) is an open nonequilibrium system, which exists and functions only because of the incessant flow of energy/matter passing through it’ (Kurakin, 2011). For that reason, one of the most fascinating and mould-breaking findings has been the discovery of self-organised spiral/loop patterns, occurring commonly in nonliving and living nature (Luo and Zhan, 2008; Hill, 2006; Heylighen, 2001; Bascompte and Solé, 1998; Jean, 1994). Spirals exist in formations such as weather patterns because the interplay between physical forces and matter tend towards that shape, while they also exist in formations such as forests. Fractal hierarchy underlies these formations in all growth processes (Hill, 2006; Selvam, 1998). For example, a positive feedback loop that results in periodic organ formation has been recently uncovered behind the spiral patterns of leaves on a stem by Bhatia et al. (2016). According to Selvam (1998), such patterns are the clearest examples of self-organised criticality in the plant kingdom.

Resilience, or the stabilizing effect of feedback loops, is defined as the ability of an adaptive system to absorb impacts before a threshold between attractors is reached where the system changes into a different state altogether (Messier and Puettmann, 2011; Thompson et al., 2009; Heylighen, 2001). Since the reaching of an attractor is an automatic process it can be viewed as a general model of self-organisation. Most modelled systems with just one stable attractor (e.g., successional pattern, community type, etc.) tend to return to this attractor when perturbed in their dynamics. When the dynamical system has more than one coexisting attractor, it often turns out that the fractal boundaries of the basins of attraction are leading to difficult issues related to the ability to predict which attractor will a given trajectory asymptote to (McDonald et al., 1985). ‘An observer might see one kind of behaviour over a very long time, yet a completely different kind of behaviour could be just as natural for the system’ (Gleick, 2008). This implies intransitivity – a major factor stimulating emergence of chaotic dynamics (Klimenko, 2015; Lorenz, 1990; Crutchfield et al., 1986). Stone and Ezrati (1996) argued that chaos theory may be particularly useful in modelling vegetation change, where nonequilibrium dynamics (e.g., disturbance, natural mosaic cycling, and habitat fragmentation) often prevail (Kenkel and Walker, 1996). Nevertheless, emphasis on a broader understanding of possible system behaviours and the effects of human intervention has contributed to a significant shift toward resilience thinking, away from the mathematics of chaos.

Self-organisation of a self-sustainable ecological community is a highly-ordered non-random process based on information written in the genomes of participating species. ‘The genetic program of species constitutes the informational basis for the compensatory environmental processes initiated by the biota when challenged by an environmental change’ (Gorshkov et al., 2004). In a forest, species as different as fungi,
plants, animals and insects, and processes as disparate as disturbance, dispersal, facilitation/competition and nutrient cycling, are related through ecological interaction networks; a ‘fractal’ is the ‘collective phenomenon’ of these networks. Not coincidentally, loss of fractal dimension by a system implies loss of collectivity, i.e., capability of the interconnected components to interact in a common mode (Waliszewski et al., 1999). Moreover, if fractal space, in which a dynamic process takes place, becomes a classic, i.e., Euclidean, space with integer dimension, this means that the process has left its strange attractor, and tends towards, or already is in, the state with a lower number of possible directions of further evolution (Devaney, 1986). To sum up, in the light of fractal organisation theory, forest integrity refers to empirical scaling relationships that are emergent features of biodiversity (see Messier et al., 2015; Simard et al., 2013; Chen, 2012; Marks-Tarloow, 2012; Raye, 2012; Willerslev and Pedersen, 2010; Gorshkov et al., 2004; Brown et al., 2002; Turcotte and Rundle, 2002; Kirilyuk, 2002; Sandywell, 1996).

General suggestions

What is sustainability in the context of forest integrity? It is maintaining scaling relationships inherent to self-organisation (see Graham, 2014; Simard et al., 2013; Rozenfeld et al., 2009; Rickles et al., 2007; Sandywell, 1996). In the presence of intransitivity, the forces driving self-organisation can be analysed with game theory (the analysis of group interaction). However, intransitivity implies that every alternative is dominated by another alternative, so no one pure strategy can be argued to be any better than another (see Ficici and Pollack, 2003; Cooter, 2000). Therefore, sustainable forest management guided by the principles of self-organisation is to be based on a collective of strategies (see Graham, 2014; Cornett and White, 2013; Schütz, 2011; Willerslev and Pedersen, 2010; Li and Bowerman, 2010; Rennolls et al., 2007; Rickles et al., 2007; Millennium Ecosystem Assessment, 2005; Ficici and Pollack, 2003; Lindenmayer and Franklin, 2002; Lorenz, 1990). The two principles of the self-organisation are nature automation, like self-regeneration of a forest, self-differentiation of a stand, self-structuration of a community, etc., and concentration on essential, such as on a protecting key response traits and ecosystem legacies that are critical in the avoidance of a biodiversity threshold, i.e., an abrupt decline in species richness, with habitat loss (see Mackey et al., 2015; Estavillo et al., 2013; Simard et al., 2013; Holt and Miller, 2011; Thompson et al., 2009; Rickles et al., 2007; Schütz, 2006; Diaci, 2006; Kotar, 2006; Kerr et al., 2002; Cody, 1985). In this context, ‘A critical management target is conservation of genetic legacies for the system memory and adaptive capacity they provide’ (Simard et al., 2013). Unfortunately, ‘the vital requirements of clarity, simplicity and practicality do not appear to have been seriously considered in the formulation of many of the genetic criteria and indicators developed to date for the management and monitoring of forest resources’ (Boshier and Amaral, 2004; Table 2).

How can geneticists help forest biodiversity adapt to changing ecoclimates? First, there should be an effort to complete vulnerability assessments and action plans for forest tree species. For example, in the U.S. Pacific Northwest and Southern Appalachian regions the Forest Tree Genetic Risk Assessment System (ForGRAS) was used to rank forest tree species for a number of primary risk factors: population structure, rarity, regeneration capacity, dispersal ability, habitat affinity, genetic variation, pest and pathogen threats, and climate change pressure (Erickson et al.,
Second, the conservation of biodiversity implies that the biotic verifiers, such as habitat shifts (*Table 2*), should necessarily be used by auditors and managers to derive an objective decision on the quality of the forest management under assessment. If wild organisms are extracted from their habitats and placed under artificial conditions never encountered in their natural environment, a decay of the genetic information will be manifested as an increase in genetic polymorphism of the populations and appearance of organisms with various defective properties not encountered in the wild type (Gorshkov and Makarieva, 1997; Gorshkov et al., 2004). Nevertheless, studies simulating the impact of forest exploitation, other silvicultural practices and forest fragmentation on genetic diversity are uncommon, and those that exist usually contain oversimplified representations of biological processes (Degen et al., 2004; Gorshkov et al., 2004).

An exploration of fractal connectivity behind key bioindicators and biomonitors in the avoidance of a biodiversity threshold can be suggested thus far. According to Holt and Miller (2011), bioindicators or biomonitors rely upon the complicated intricacies of ecosystems and use a representative or aggregated response to convey a dynamic picture of the condition of the environment. For instance, lichen diversity is commonly used as a general indicator of forest health and 'ecological function', as lichens are key primary producers with important linkages to nutrient cycling and forest food webs: high or low lichen diversity can result from certain types of air pollution, changes to forest management or stand structure, diversity of plant substrates available for colonization, favourability of forest climate, return interval of disturbances like fire, and so on (Jovan, 2008).
Table 2. Proposed indicators and verifiers of the maintenance of genetic diversity in sustainable forest management at interspecific, species and infraspecific levels. Sources: Déri et al. (2010), Rodriguez et al. (2009), Magura et al. (2006), Gorshkov et al. (2004), Boshier and Amaral (2004), Namkoong et al. (2002), Legendre and Legendre (1998)

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<tr>
<th>Indicator</th>
<th>Biotic verifiers</th>
<th>Demographic verifiers</th>
<th>Genetic verifiers</th>
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<td>Levels of variation</td>
<td>Species' site specificity</td>
<td>Census number of sexually mature individuals</td>
<td>Number of alleles</td>
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<td>Species' site fidelity</td>
<td>Census number of reproducing individuals</td>
<td>Gene diversity</td>
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<td>Habitat affinity index</td>
<td>Coefficient of phenotypic variation</td>
<td>Genetic variation</td>
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<td>Directional change in allele or</td>
<td>Habitat shifts</td>
<td>Phenotypic shifts</td>
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<td>Age/size class shifts</td>
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<td>Environmental shifts</td>
<td>Genetic mean shifts</td>
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<td>Migration among populations</td>
<td>Forest removal</td>
<td>Physical isolation</td>
<td>Gene flow</td>
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<td>Propagule removal</td>
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<td>Reproductive processes/mating</td>
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<td>Parental pool size</td>
<td>Outcrossing rate</td>
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<td>system</td>
<td>Symbiotic regulation</td>
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REFERENCES


