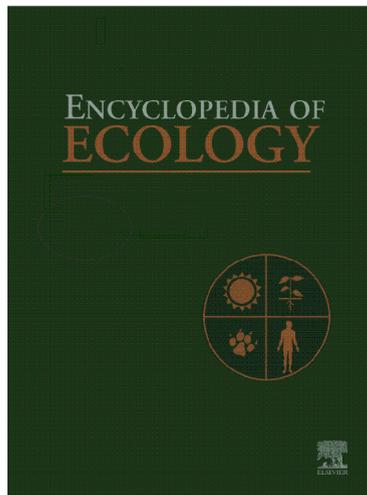


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Among them OWL is probably best known, and designed to work over the World Wide Web. So far it is yet to be seen how these ontological approaches will be accepted by the modeling community. As with other attempts to streamline and automate the modeling process, we may be compromising its most essential part, that is, the exploration and research of the system, its elements and processes, at the level of detail needed for a particular study goal. Any attempt to automate this part of the modeling process may forfeit the exploratory part of modeling and may diminish the new understanding about the system that the modeling process usually offers.

Conclusions

Conceptual diagrams are powerful modeling tools that help design models and communicate them to stakeholders in case of a collaborative, participatory modeling effort. In most cases building a conceptual diagram is the first and very important step in the modeling process.

See also: Biogeochemical Models; Forest Models.

Connectance and Connectivity

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Introduction
Measuring Connectivity
Corridors

Further Reading

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Relevant Websites

- <http://www.visual-paradigm.com> – Model-Code-Deploy Platform, UML Case Tools, Visual Paradigm.
- <http://www.likbez.com> – Modeling Course (refer to A A Voinov's homepage).
- <http://www.ento.vt.edu> – Population System, Virginia Tech's Entomology Department.
- <http://www.sparxsystems.com> – UML Tutorial, The Unified Modeling Language (UML), Sparx Systems.

Summary
Further Reading

Introduction

Several studies have reported that habitat loss and fragmentation are leading causes of imperilment for plants and animals. Very frequently, habitat loss proceeds in ways that habitat fragments are left resulting in smaller, more isolated areas of habitat. Humans also regularly erect barriers to movement in forms such as fences, roads, canals, dams, and urban areas. It is therefore almost inevitable that the capacity of many organisms to move through a landscape will be reduced. The following section reviews types of changes in habitat connectivity and their consequences. This is followed by a description of how we measure habitat connectivity, and a section on how habitat corridors are being used to attempt to reduce the effects of fragmentation.

Habitat connectivity is defined as the degree to which a landscape facilitates or impedes movement of organisms among habitat or resource patches. The term is used synonymously with habitat connectance. (This article does not review food web connectance, which refers to the density of trophic links in a food web – see Food Chains and Food Webs.) Habitat connectivity includes elements of both the physical structure of habitat and the movement ability and behavior of the organisms in question. Structural connectivity denotes the physical structure of habitat, and is evaluated using measures of habitat extent, subdivision, and contagion, or some combination of these. By contrast, functional connectivity refers to the potential for movement of organisms among habitat or resource patches, and depends on the organisms' perception of, and reaction to, their environment, as well as on their ability to move and

costs of movement. Therefore functional connectivity may vary between species or between individuals of the same species. For some species, natural currents (e.g., stream flow or oceanic currents) or winds may influence functional connectivity. Both structural and functional connectivity may vary among natural environments and as a result of human activities that alter the composition and patterning of the environment and/or an organism's movement behavior. Some studies have defined connectivity on a purely structural basis, and others have used the presence of habitat corridors as an indicator of connectivity.

Habitat connectivity can also influence the flux of materials across ecosystem boundaries, which is considered under the topic ecosystem subsidy. Here, the overlap between subsidy and habitat connectivity is considered. Ecosystem subsidy is defined as the transport of a donor-controlled resource (prey, detritus, or nutrients) from one habitat to another where it is utilized by a recipient plant or consumer. Transport here involves both physical fluxes and flows, including river flows, winds, and oceanic currents. A network of channels or rivers joining lakes or ponds fits naturally into ideas of structural connectivity. However, transport via winds and oceanic currents are not usually considered in landscape studies of structural connectivity, which usually involve the quantification of static landscape patterns. Ecosystem subsidy is therefore dependent on connectivity, but the literature for patterns with fluxes and flows is largely separate from the landscape ecology literature about habitat connectivity. Studies of ecosystem subsidy typically investigate processes at ecosystem and community levels such as fluxes of nutrients and levels of biomass at different trophic levels. By contrast, landscape ecological studies of habitat connectivity are more frequently motivated by maintaining species diversity and population persistence. Hence connectivity in a broad sense influences processes at levels from individuals up to entire ecosystems, and at the ecosystem level it is termed ecosystem subsidy.

The prime importance of the movement of organisms to biodiversity is revealed by a variety of ecological and evolutionary studies. Below we briefly review the importance of island biogeography studies of species diversity, metapopulation studies of the population dynamics of one or a few species, and studies of inbreeding in relation to isolation.

MacArthur and Wilson's equilibrium theory of island biogeography theorizes that the level of species diversity on habitat islands arises as a balance between the processes of colonization and extinction of species. Colonization is related to distance from a large mainland area of habitat such that more isolated habitat islands should contain fewer species than islands that are closer to a large mainland area of habitat. Extinction of species is related to island size, such that smaller islands can hold

fewer species than large islands. Hence, smaller more remote islands should contain fewer species than larger and more connected islands. Furthermore, there is a turnover of species and colonization is required to maintain species diversity. There is a broad range of empirical evidence supporting this theory in a diverse array of taxa. These ideas were brought to the attention of conservation biologists by Wilson and Willis, who in 1975 published a figure laying out the idea that islands closer together and those connected by habitat corridors support more species than islands that are less connected. The ideas both from the equilibrium theory of island biogeography and from Wilson and Willis' figure have been broadly applied to habitat islands of many kinds, both aquatic and terrestrial, and have been influential in perpetuating the importance of habitat connectivity.

Instead of exploring the effects of colonization and extinction on species diversity, metapopulation theory relates these processes to the regional population dynamics of one or a few species. Metapopulation studies show how reduced connectivity increases extinction rates of local populations and reduces rates of recolonization of vacant habitat patches. The net effects of such dynamics depend on whether species have their own independent dynamics, as represented in single species models, or whether species can be driven locally extinct by predators or competitors. As shown in **Figure 1**, the isolation of increasingly small habitat patches can only reduce the likelihood of regional persistence for single or noninteracting species, whereas interacting species can actually benefit from moderate reductions in connectivity. For example, in predator and prey metapopulation models, a voracious predator might drive its prey species extinct

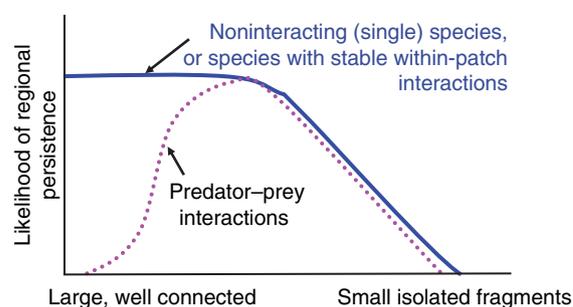


Figure 1 The influence of habitat subdivision on single species and interacting species where one species can drive another extinct within a habitat patch (e.g., a predator and prey, or a dominant and subordinate competitor species). In highly connected habitat patches, the predator is capable of driving the prey species regionally extinct whereas a single species can persist. At extremely low levels of connectivity in small habitat fragments, all species go extinct regardless of their interactions. Overall, the figure illustrates that the degree to which species interact may alter how they are influenced by changes in connectivity and habitat patch size.

from large well-connected areas of habitat. Reduced connectivity might reduce the ability of predators to reach areas containing prey, thereby weakening the net effect of predators on prey by providing prey with a refuge from predation. If connectivity is reduced too much, prey may be hindered from reaching habitat areas from which they have been driven extinct, so that local extinction rate exceeds the recolonization rate and eventually prey are driven extinct and predators would starve to death. In predator and prey metapopulation models, the dynamics of prey at extremely low levels of connectivity are similar to those of single species. There is a moderate amount of evidence supporting such dynamics for predators and prey, but mostly from microcosms and other highly manipulable systems. Metacommunity models of many competing species show similar effects of reduced connectivity, with the added prediction that species that are the worst at dispersing should be least able to withstand reductions in connectivity even if they are strong competitors in local communities.

The isolation of a habitat patch refers to the rate of immigration into that habitat patch. Hence, isolation and connectivity are inversely related. Mortality during dispersal may add to isolation. In the absence of immigration, populations are expected to suffer from several effects. Small populations are likely to have reduced genetic variability as a result of the small number of individuals present. This may be compounded by the accumulation of deleterious mutations through inbreeding, leading to mortality and reduced reproductive capacity in a population. Small populations are also more likely to go extinct, such that a metapopulation with lots of small populations in a region may experience a regional reduction in genetic diversity, which may exasperate the effects of small population size through reducing the potential for gene flow. Populations with low heterozygosity may have a reduced potential for future evolution. A meta-analysis (quantitative review) by Derek Spielman, Barry Brook, and Richard Frankham of over 170 threatened taxa from the IUCN (World Conservation Union) Red List showed that on an average, threatened taxa had a 35% reduction in heterozygosity compared to nonthreatened relatives. Several empirical studies indicate that the loss of heterozygosity is frequently associated with a reduction in reproductive rates through inbreeding. Furthermore, computer simulation models that involve reasonable assumptions suggest that this 35% level of loss of heterozygosity could cause 24–78% reductions in the median time to population extinction because of reduced reproduction (estimates vary depending on assumptions about the extent of juvenile mortality caused by inbreeding). Habitat loss and fragmentation are the prime causes for imperilment of taxa (at least in the US), and therefore reductions in connectivity are likely to be involved in

these effects. It is important to realize that in severe cases reduced connectivity likely produces genetic changes that can impact populations before purely demographic processes cause these populations (or species) to go extinct. Hence, both demographic and genetic changes are important to understanding the effects of habitat fragmentation and reduced habitat connectivity.

Implicit in the idea of measuring connectedness is that there is a sharp demarcation between habitat and nonhabitat. By contrast, many organisms are not strict habitat specialists and may use different landscape elements to different extents. A step toward recognizing that species may not sharply demarcate habitat from nonhabitat while still simplifying the landscape is to recognize the matrix that lies between habitat patches. Differentiating between species that use the matrix and those that do not may improve the predictability of analyses that look at species diversity in relation to connectivity because connectivity is only relevant to species that do not use the matrix as habitat. The same is true of metapopulation studies that investigate patch occupancy in relation to connectivity.

Measuring Connectivity

There are a variety of ways of quantifying the structural and functional connectivity of a landscape. Structural connectivity is usually quantified from aerial photographs, maps, or remote sensing data (geographic information systems (GIS) data, satellite imagery). Many metrics require that an image is rasterized by overlaying a grid of cells, with each cell having a defined size or grain. The impression of structural connectivity may vary with the grain size that is chosen, with coarser grains making it more likely that small gaps between habitat areas will be overlooked because large cells average across the gaps. Similarly, organisms may have a particular spatial scale at which they sample the environment and make decisions about movement. The grain of our sampling a landscape to measure connectivity should be sufficiently fine that it is congruent with the scale selected by the study organism. However, this is often not known prior to commencing a connectivity analysis and therefore analyses at multiple scales are of value to identify the grains that have the highest ability to describe the movement or occupancy patterns of a species across a landscape.

There is a distinction between connectivity measured between pairs or landscape elements, or other portions of a landscape, and connectivity across an entire landscape. Often movement is measured between pairs of points, or along particular paths (e.g., for radio-tracked animals), and this data is then analyzed in relation to

habitat type or the occurrence of particular landscape elements (rivers, roads, etc.). A typical approach is to start with pairwise measures of connectivity between two points and then repeat such measurements across a landscape. However, there are no general guidelines available to set the spatial scale at which connectivity should be measured.

It is useful to further consider functional connectivity, which can either be based on potential or actual measurements. Potential connectivity comes from combining structural connectivity with information about the movement behavior, distance, and costs in the organism in question. Actual connectivity is that which is actually measured. Be it potential or actual, functional connectivity might be based on strict adjacency (touching) of habitat, a threshold maximum dispersal distance, a decreasing function of distance which reflects that movement frequency (or potential) is inversely related to distance, or a resistance-weighted distance function that incorporates the different costs of traversing various paths.

A useful framework for classifying connectivity metrics was presented by Justin Calabrese and Bill Fagan in 2004, and this framework is used here to organize connectivity measures. Furthermore, the description of the advantages and disadvantages of different metrics, as well as the data requirements to estimate them, draw heavily on their work. Six classes of metrics can be distinguished.

Nearest-Neighbor Distance Metrics Using Patch Occupancy Data and Interpatch Distances

The crudest measures of connectivity are based on the distance from a given habitat patch to other occupied habitat patches, which might provide immigrants. This is an index of isolation, and is turned into an index of connectivity by taking its inverse. Indices of this type use only the distance to the nearest habitat patch, ignoring all other patches that might provide immigrants, and variation in the size of source populations in different patches. Meta-analyses and simulations both confirm that nearest-neighbor metrics are crude estimates of connectivity and that they have lower predictive ability than the more sophisticated measures discussed below. Measures could be converted from structural measures to potential connectivity by converting links from distances to binary presences or absences, or probabilities using known movement distances and a dispersal kernel (describing the probability of dispersal as a function of distance), respectively. Nearest-neighbor distances are the most widely used of the different kinds of connectivity metrics, despite their low predictive ability.

Spatial Pattern Indices Using Spatially Explicit Habitat Data

A variety of metrics can be calculated from a map portraying the spatially explicit layout of habitat areas. These include things like the number of patches, patch sizes, patch perimeter-to-area ratios, fractal dimension, contagion, and indices of patch shape. Such indices are readily calculated with software packages such as FRAGSTATS and reflect the popularity of analyzing GIS data. However, simulated analyses of the ability of these indices to predict connectivity suggest that they are inconsistent when the characteristics of a landscape are varied. Empirical work is needed to establish relationship between actual connectivity and structural connectivity measured using spatial pattern indices.

Scale–Area Slope Indices Using Spatially Incomplete Data

Records of individuals at either random locations on a landscape or from a systematic survey of points on a landscape can be used to quantify the occurrence of a species across a landscape and how this varies with spatial scale. Specifically a grid can be overlaid and the presence and absence of the species in each cell recorded. As grid cells are made larger (or adjacent grid cells summed), the number of records can be plotted as a function of cell size; specifically, the map area occupied by a species can be plotted against the size of the cells sampled and a power function can be fitted using regression. Such plots will have shallow slopes if species are uniformly distributed across space, which is taken as an indicator of highly connected landscapes. Conversely, steep slopes are likely to result from aggregated distributions and these are presumed to arise because of limited movement. The slope is called the scale–area slope and is a measure of connectivity. Such approaches cannot distinguish whether steep slopes are because habitat is aggregated in its distribution across the landscape or whether habitat is uniformly distributed and the organisms are restricted in their movement for some reason other than habitat connectivity. The approach also assumes that proximity is the major determinant of connectivity, an assumption that had predictive power for the long-term dynamics of populations of fishes in desert springs and streams in the southwestern US. The validity of the approach for other study systems requires evaluation.

Graph–Theoretic Measures Using Dispersal Data and Spatially Explicit Habitat Data

Graph–theoretic measures of connectivity use spatially explicit habitat data and known biological information

about dispersal to estimate potential connectivity. The approach consists of using a habitat graph that summarizes habitat patch arrangement and patch information in a concise way. The graph is then converted to measures of potential connectivity either using fixed dispersal distances to create links if the metric is less than the maximum dispersal distance or this is done probabilistically if a dispersal kernel is available. A dispersal kernel is a function describing the probability of dispersal as a function of distance, and can be combined with structural landscape data by using random draws to decide whether a patch is connected or not depending on the appropriate probability of dispersal for the distance in question. Pairwise metrics such as the maximum distance able to be traveled in a random direction are then scaled up to the entire landscape. Two main approaches are in use, based on percolation theory and the correlation length of spanning clusters, which are both described below.

Percolation is most easily understood for a rasterized grid of habitat and nonhabitat cells and is a measure of the probability that habitat cells are contiguous. Percolation theory comes from mathematics and was developed in physics before being applied to landscape ecology. The main concept is the existence of a percolation threshold, defined in the following way. Suppose p is a parameter that defines the average degree of connectivity between cells (in a grid) of a landscape classified into habitat and nonhabitat. When $p=0$, all patches are totally isolated from every other subunit. When $p=1$, all habitat cells are connected to (touching) their neighbors. At this point, the landscape is connected from one side to the other, since there are paths that go completely across the system, through spanning clusters. Now suppose, starting at $p=1$, habitat cells are randomly removed, so that p , the measure of average connectivity, decreases. The percolation threshold is that value of p , usually denoted p_c , at which there is no longer an unbroken path from one side of the system to the other. Measures of structural connectivity based on percolation can be changed into functional connectivity by allowing gaps between habitat cells of certain distances, corresponding to the organism's maximum movement distance across nonhabitat.

The correlation length for a rasterized habitat patch map is based on the average extensiveness of connected cells. The correlation length is the average distance one might traverse across a landscape without leaving what is defined as habitat from a random starting point and moving in a random direction.

An advantage of graph-theoretic approaches is that they can be used to calculate how an individual patch contributes to landscape-scale connectivity. However, such approaches are data intensive, requiring both movement data (maximum dispersal distance or a dispersal kernel) and spatially explicit landscape data representing habitat and nonhabitat areas.

Buffer Radius and Incidence Function Metrics Using Spatially Explicit Patch Occupancy Data, Patch Area, and Dispersal Data

Building on the idea of nearest-neighbor distances, a buffer radius calculates the number of occupied habitat patches or total number of individuals of a species within a given distance. The metric uses more information than nearest-neighbor distances, potentially improving its accuracy, and it can also be calculated at multiple spatial scales. The spatial scale of relevance will depend on typical movement distances and consequently movement data could greatly improve the utility of buffer radius connectivity metrics. A related idea is captured in Ilkka Hanski's incidence function model approach, which includes an explicit function of the number of individuals in habitat patches at different distances and these are weighted by distance in a power function. The approach can also be adapted to use information just on patch occupancy, or patch area as a surrogate measure, if the number of individuals per patch is not known. The approach has been tried and tested with a variety of taxa and appears to work well when organisms occur in discrete patches and are limited in their dispersal ability. As a minimum, information on patch occupancy or colonization is required and this needs to be complete spatially, without missing (uncensused) habitat patches in the study area. Such approaches are mainly limited by the high data requirements and limited areas that can be censused.

Observed Movement Rates Requiring Individual Movement Data

A broad range of metrics of movement are collected by ecologists and biologists. Common forms of measurement are tracking individuals using radio-telemetry, satellite tagging, or other methods, mark-release-recapture, mass mark-recapture, observations of colonization of habitat patches over some period of time, and indirect estimates from genetic data. Using genetic data requires making assumptions about effective population size and the equilibrium of dynamics, and the neutrality of genetic markers. Rolf Ims and Nigel Yoccoz reviewed the different measures of measuring movement and discussed the advantages and disadvantages of different metric. The most accurate measures are those that are most labor intensive to collect and these will necessarily be spatially limited.

Measuring Connectivity: Putting It All Together

The preceding discussion should have highlighted that connectivity metrics differ in their ease of measurement and the amount and type of data required to use them. There is a tradeoff between the ease of measurement of

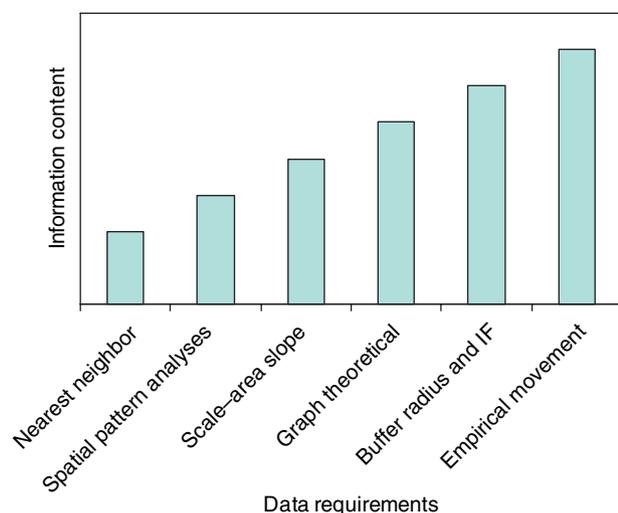


Figure 2 A representation of the information contained in different metrics of connectivity as a function of the amount of data required for their measurement. IF = incidence function model approaches. Modified from Calabrese JM and Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment* 2: 529–536.

connectivity metrics and the amount of detail they capture. This is illustrated in [Figure 2](#). Hence, we face a choice between metrics in which we are uncertain about their utility or accuracy and investing the time and resources to measure metrics that are more information rich. The choice of metric is likely to depend on the spatial scale of the problem which we are attempting to solve, be it a conservation strategy for a region, or the need for a migration route for deer across a highway, and so on. It should be noted that the metrics that have been discussed can often be improved by including additional information. Most commonly, information about the number of individuals within patches is used, or patch size is taken as a surrogate for information about local population size. Alternatively, immigration and emigration may scale differently with patch size, such that individuals are more likely to remain in or colonize smaller or larger habitat patches. Movement can also be adjusted for variation in the type of habitat being crossed or landscape features present in the area traversed. Such modifications to metrics have been shown to improve the accuracy in specific studies, but their general utility is unknown.

Corridors

Corridors are continuous strips of habitat connecting areas of habitat that would otherwise not be connected. They are one of the major ways in which we attempt to improve habitat connectivity. However, corridors serve many purposes that are related to connectivity, from

facilitating the movement of individuals, enhancing social structure (e.g., for primates), population viability (e.g., for spotted owls in the Pacific Northwest of the US), and community structure to improving ecosystem properties. Furthermore, corridors can be natural (e.g., riverine vegetation) or constructed (e.g., wildlife crossings on roads), deliberate or inadvertent (e.g., road verges), and vary in scale from highway crossings to ambitious international projects such as connecting the Greater Yellowstone area in Montana and Idaho to the Yukon and Alaska with a forest corridor to facilitate the movement of large mammals. Constructed corridors are often greenbelts or greenways in urban and suburban areas that serve recreational purposes, enhance ecosystem functioning (e.g., groundwater infiltration), or are low-value areas, such as those subject to flooding.

When first conceived of, corridors were viewed as being nonselective pathways that facilitate movement. The reality is that certain species may benefit from corridors of a particular type, depending on width, length, and habitat composition within them, the surrounding habitat matrix, and what they are connecting; all of these things are measured relative to the requirement of the species and individuals in question. Corridors may also be selective in terms of factors like the ages, social status, or other traits of the individuals dispersing. Increasing connectivity through the use of corridors is not always good. For example, weedy plants are often spread along highway corridors, introducing non-native invasive species that are selected for factors like rapid generation times, high movement capacity, being able to benefit from disturbance (e.g., open ground for germination), and high competitive ability. The spread of a disease, pathogen, predator, dominant competitor, or non-native invasive species may also occur and impact either particular species or whole communities and ecosystems. Nonetheless, the negative effects of isolation on population viability, genetic diversity, species diversity, and community structure are generally severe so that the weight of evidence suggests that improving connectivity is usually desirable. It is clear that long-term studies of the community-wide effects of altering habitat connectivity are especially desirable. [Figure 3](#) shows an aerial view of a long-term ecological experiment where Nick Haddad and colleagues manipulated the connectivity of pairs of habitat patches consisting of clearings within a pine forest in South Carolina. The experiment controls for the amount of habitat edge and the increase in habitat area caused by having corridors by using winged patches that are of similar area to patches connected by corridors except that the corridors do not connect to other patches. Nick Haddad and colleagues showed that connecting patches using corridors increased the interpatch movement rate of a diverse



Figure 3 False color aerial photograph showing a large-scale habitat fragmentation experiment conducted by Nick Haddad and colleagues. Three treatments are shown: pairs of patches connected by a habitat corridor (100 m by 100 m patches connected by a 25 m by 150 m corridor); an unconnected patch (of 137.5 m by 100 m) and winged patches that have the same total habitat area (100 m by 100 m, with two 25 m by 75 m wings). The amount of edge habitat is also broadly similar in a connected patch and a winged patch.

suite of taxa, including butterflies, small mammals, and bird-dispersed plants. In the same study system, Ellen Damschen and colleagues demonstrated that by the end of a 5-year period after initiating the experiment the connected patches contained an average of 20 more plant species than unconnected patches.

Summary

Connectivity has important links to a broad range of population processes, genetic variability (and evolutionary potential), species diversity, and community structure. Connectivity can be defined through structural

and functional means, and functional connectivity can be further subdivided into potential and actual measurements. Connectivity can be measured between pairs of patches or across entire landscapes and many scales between. A complex diversity of metrics has been used to measure connectivity, with different metrics exhibiting different degrees of reliability, to the extent that this is known. Different metrics also differ in whether they require movement data or not, and spatially explicit landscape data or information on neighboring patches only. A key idea is that connectivity can be manipulated using habitat corridors, although such corridors are often constructed and their long-term consequences are less-often explored.

See also: Abiotic and Biotic Diversity in The Biosphere; Biodiversity; Island Biogeography; Landscape Modeling; Metapopulation Models; Neutral Theory; Spatial Subsidy.

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