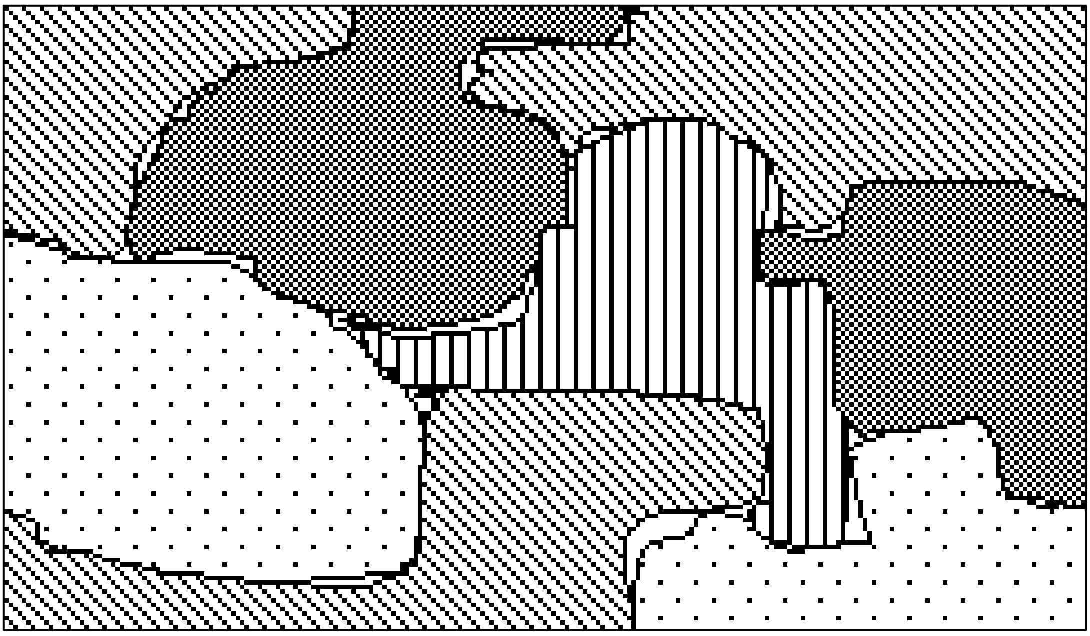
Quantification of the effects of spatial heterogeneity on animals at different spatial scales



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Content

Abstract

Landscape ecology is an ecological discipline that considers four main principles: "the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous landscapes, the influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity". Spatial heterogeneity refers to the characteristics of a landscape. A landscape can be seen as an environmental mosaic, with a pattern that can be classified at several scales, with an influence at abiotic and biotic processes, for instance at animals. Not all processes and parameters have the same effect at various scales, therefore it is important to determine the effect of spatial heterogeneity on organisms at various scales. This overview demonstrates which methods are used to determine this effect.

Differences between studies are the kind of environment, size of study area and samples, classification and number of spatial scales, kind of species and the aim of the research. The methods for dividing the area in studies used for this overview can be classified into nested or hierarchical design, a design with several circles with a range of radii, a block design or a design that depends on animals or vegetation. The spatial heterogeneity has been determined with already existing surveys, but topographic maps, aerial photographs, satellite images, and computer software are also used. Combinations of the methods are used as well. The variables measured to determine the spatial heterogeneity of the area are divers. The study area can be divided in patches with vegetation variables, with traces of animals or with other variables.

Examples of influences of spatial heterogeneity on animals are the species richness, the diversity and the species composition or community structure, the abundance, distribution and movement patterns of animals, the species survival, the locations of nests sites, size of a home range, selection of feeding sites or the size and biomass of organisms. The majority of the studies observes or counts individual animals, but there are also methods that make use of traces of the animals, such as occupied tree cavities, sounds or density of preferred food to determine the influence.

It is clear that there are many ways to measure the influence of spatial heterogeneity on animals at several spatial scales. A method to dividing a landscape into an appropriate amount of scales, with clear definitions of those scales is not established, but most of the studies emphasize the importance of research done at various spatial scales. None of the methods for dividing the area in studies used for this overview was considered useless or more useful than others and a clear definition of spatial heterogeneity, patchiness and patch makes it difficult define the heterogeneity of the area. A study should quantify the patchiness of the area first with a combination of all methods and the measure of a lot of environmental variables and then use a circle design or a block design and use one of the appropriate methods for the species where is focused on. But each study has specific circumstances and other methods may be better to use. So, choosing a method to determine the influence of the heterogeneity is difficult and complex and further research is needed to define which amount of scales should be used and to clarify the definition of the different scales and the definition of spatial heterogeneity.

Introduction

Landscape ecology is an ecological discipline that considers four main principles: "the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous landscapes, the influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity" (Turner, 1989). To describe this analysis of the effect of pattern on process on landscape scales, this branch of the ecology has developed new terms. The emphasis on the effect of pattern on process differentiates the landscape approach discipline from other ecological disciplines (Turner, 1989).

Spatial heterogeneity refers to the characteristics of a landscape. The term or concept landscape can simply be considered as "a spatially heterogeneous area" (Turner, 1989). But it can also refer to "a heterogeneous land area composes of an interacting mosaic of patches, at any scale, relevant to the phenomenon (e.g. species) under consideration" (Mcgarigal and Mccomb, 1995). Another definition that is postulated is that a landscape is "the land surface and its associated habitats at scales of hectares to many square kilometres" (Turner, 1989). So a landscape can thus be seen as an environmental mosaic, with a pattern that can be classified at several scales, with an influence at abiotic and biotic processes, for instance at animals.

The heterogeneity, or the variation in composition of the landscape, displays the temporal progression of stages in succession at each point in space. Patchiness is another term which outlines spatial heterogeneity. This term refers to the spatial scale of a system and has been seen as a factor in how a system is described (Krebs, 2001). In general a patch can be defined as a patch that covers a few square metres to a few hectares, but there is no single definition for this concept that can cover all ecological communities.

According to Wiens et. al. (Krebs, 2001) there are five different spatial scales at which ecologists work on:

1 "space occupied by one plant or sessile animal, or the home range of an individual animal"
2 "local patch, occupied by many individual plants or animals"
3 "region, occupied by many local patches or by local populations linked by dispersal"
4 "closed system, or a region large enough to be closed to immigration or emigration"
5 "biogeographical scale, including zones of different climate and different communities"

Most field studies of communities and almost all experimental manipulations of communities are conducted at the local patch scale (Krebs, 2001). Conclusions that apply to one spatial scale will not necessarily apply to others. Processes and variables at one scale can have another outcome than at another scale. For example, "oak seedling mortality at local scales decreases with increasing precipitation, whereas mortality at regional scales is lowest in the drier latitudes" (Turner, 1989).

A landscape can thus be considered as a mosaic of habitat patches and interconnections (Turner, 1989). The habitat connectivity of a landscape has in some cases influence at the persistence of organisms and alterations of this connectivity can have effects on species, for example, on species survival, abundance and movement patterns. In the study of Belmaker et al., "small forest patches connected by a corridor to a nearby forest system were characterized by typical forest avifauna, whereas similar but isolated forests were not". Another example shows that the movement patterns of grizzly bear were altered due to the development of a road. "Bears used habitat within 100 m of roads significantly less than expected (Turner, 1989)". So not all processes and parameters have the same effect at various scales, therefore it is important to determine the effect of spatial heterogeneity on organisms at various scales.

This overview demonstrates which methods are used to quantify the effect of spatial heterogeneity on animals at different spatial scales. Methods are not always easy to establish because of the consideration of the various scales. The studies compared have a diversity of animal groups and methods used are also divers. First, differences between studies are described. Secondly, the methods to divide the study area are noted. Third, the methods used to determine the spatial heterogeneity of the area are noted, and fourth, methods and techniques to measure the effect on animals are described. In the discussion methods are compared and the usefulness of the methods is noted.

Differences in approach to determine the influence of patchiness

There are various ways to investigate the influence of patchiness on animals at different scales. Some differences can be noted between studies. Study area's can for example differ in the kind of environment and they can have different sizes. Spatial scales can differ in classification and the number of scales. But also the kind of species studied at and the aim of the research differ between studies.

Environment

Study areas can be divided in two groups; terrestrial and marine areas. Within these two groups there is a lot of variation. A terrestrial area can be for instance a grassland (WallisDeVries et al., 1999), a couple of islands (Borges and Brown, 2004), a forest or can even consists of forest fragments (Gutzwiller and Anderson, 1987; Mahon et al., 2007; Freemark and Merriam, 1986). Examples of marine areas are reefs (Gust et al., 2001), a harbour (Hewitt et al., 2002), a creek (Mcgarigal and Mccomb, 1995) a stream (Boyero, 2003) or a coast-to-sea transect along several islands (Galzin, 1987). The motives to select these specific sites are diverse. Sometimes the area is an already existing reserve (Zhang et al., 2009; Bailey and Thompson, 2007). This area is clearly defined and can be directly divided in smaller areas. Foord et. al (2008) chose the study area because that was the most varied part of the region. Other areas, such as reefs or a harbour, are also chosen because they function as one system. The effect of patchiness can then be determined in one relatively separate system.

To determine the influence of spatial heterogeneity on animals it is important to measure different environmental variables. These variables depend on the animal the study is focused on as well on the study site. In case of bird studies, for example, nest height and nest-entrance angle are important (Gutzwiller and Anderson, 1987). In marine research the current velocity, site depth, percentage volumes of different kinds of sediment, percent weight of organic matter is measured to get an indication of the heterogeneity and other factors that have an influence on the animals (Hewitt et al., 2002). For research in terrestrial areas, habitat types or vegetation types are determined. This classification is based on dominance and composition of plant species, size class of trees and canopy-closure class of trees (Kie et al., 2002). Other elements of the determination of the area are the measuring of the vegetation height and vegetation cover and sampling of standing crop (WallisDeVries et al., 1999; Bailey and Thompson, 2007).

Size of study areas and size of sample sites

The size of the chosen study area, or areas, is very variable. (Jimenez-Valverde and Lobo, 2007) used for instance a total study area of in 8028 km^2. And Zhang et al. (2009) has done research in a reserve of 390 km^2. These sites are relatively big areas. But smaller areas are also used; (Foord et al., 2008) has studied the micro-scale heterogeneity of spiders at an area of 'only' 4.3 km^2. This variation of size of the total study area depends on the motives to select this areas as mentioned before. Another factor that can contribute to the size is an interest in a specific scale, for example the local and regional scale (Borges and Brown, 2004). But there is no association between size of the target species and size of the total study area.

The size of the study area is not always related to which size is used as smallest sample size. (Gutzwiller and Anderson, 1987) measured along 24 and 12.1 km of two rivers, but the smallest sample area was still 30m x 30m. Zhang et al. (2009) used, as mentioned before, an area of 390 km^2. Despite the large area they looked within micro habitat at an area of 1m x 1m. Motives of the size of the sample sites can be different than the motives choosing the study area. In the studies used for this overview there were three reasons noted for the size of the sample sites. First, the target species can determine the size. For example, the feeding site of the wild giant panda, *Ailuropoda melanoleuca*, in study of Zhang et al. (2009) was 1m x 1m. A feeding site is defined as "a small area where the giant panda is assumed to reach its food items without moving on". So the size of the sample size is determined by the foraging behaviour of the target species. Secondly, the landscape or environment can determine the selected sample sites. In (Borges and Brown, 2004) "the selected pastures had continuity of management intensity for at least four years for the sown pastures and more than 15 years for the semi-natural pastures. The third cause of the sample size depends on the sample methods. In Boyero (2003) samples of invertebrates were taken with a modified sampler that samples 15 x 15 cm. So the sample method determs in this study the smallest size of the samples.

Classification of spatial scales

Another difference is the classification of the scales. Terms as 'small-', 'large-', micro-' and 'macro scale' are used to distinguish the different scales. But the dimension varies; Foord et al. (2008) defines, for example, a scale of 1km x 1km as a micro scale, but Zhang et al. (2009) defined a micro habitat plot as an area of 20m x 20m. In this study, though, this is not the smallest scale defined; the smallest scale was defined as 'feeding site'. So it doesn't mean that the micro scale is the smallest scale used.

The labels to define the different scales also deviate. Some labels depend on existing definition of such areas. Boyero (2003), for example, used the terms basin, segment, riffle, sections and samples. Basin, segment and riffle were defined earlier and have been defined as functionally relevant for ecosystems. But sections, approximately $1m^2$, and samples, 15cm x 15cm, are "arbitrarily defined spatial units." These labels to define the smallest scales were established only for this study. In other research the same labels can stand for another size or scale. So new definitions for the labels of scales are established in this study (Boyero, 2003). Another way used to determine the scales is depending on the animal species focused on. Bailey and Thompson (2007) determined habitat patches as "areas of potential habitat previously identified by The Nature Conservancy on Fort hood". This is depending on the habitat choice of black capped vireos (*Vireo atricapilla).*

Number of spatial scales

The number of spatial scales to determine the influence of patchiness or spatial heterogeneity is variable between studies. In the studies used for this overview the number of scales ranges from 1 scale (Jimenez-Valverde and Lobo, 2007) to 5 scales (Boyero, 2003; Hewitt et al., 2002). In some studies they only look at one scale, for example at the regional scale (Jimenez-Valverde and Lobo, 2007). The reason for this was that "preserving spider biodiversity, land management strategy design requires an understanding of the patterns of spider diversity on an appropriate regional scale". Mcgarigal and Mccomb (1995) studied only the relationship of landscape structure on breeding birds on landscape scale; 30 landscapes have been established that represented a range in structure of the forest area. They looked at the landscape scale because it was not clear if relationships already found at the patch scale could be extrapolated to landscape level. The landscape scale in their study was at the level of forest fragmentation. In other studies they look at more scales, for example, Bailey and Thompson (2007) looked at nest-site selection at landscape and habitat scale. However, the size of the total study area is not related with the amount of scales used. The study of Zhang et al. (2009) had a total study area of 390 km^2 and focused on two spatial scales, but Hewitt et al. (2002) had a study area of 25 km^2 and looked at five different scales.

Processes interact across scales in space and time, so if the aim of a research is to determine the influence of patchiness on the entire landscape, it is necessary to perceive the effect at various scales. Despite this knowledge that not all conclusions could be extrapolated to another scale, studies with the scope at only one spatial scale are still useful, because it gives the influence of patchiness at that scale.

Kind of species

In the studies used for this overview different species are focused on to determine the effect of patchiness on animals. Marine research is done on both benthic species as on pelagic species and terrestrial species used in this overview are invertebrates, herbivores and birds. Many studies have a conservation motive or mention the use for management of the study. In Freemark and Merriam (1986) for example they postulate that "to maintain a diverse forest avifauna, regional conservation strategies should maximize both size and habitat heterogeneity of forests." Also (Galli et al., 1976) have as purpose "to determine the importance of forest edge and forest interior as distinct zones for birds." So these kinds of studies contribute often important information for conservation and management strategies. These aims define in some cases which animals are focused on. If land management strategies are the reason, then a species or several species can be selected to focus on, for example spiders (Foord et al., 2008). But this choice is already made if the aim is to protect the endangered species, for instance the giant panda (Zhang et al., 2009).

The aim of the research and the animals were the focus is on are determining the methods used, because the aim determines which species is focused on and each species has their characteristics. Bird studies include for example nest site measurements, but studies with herbivores can determine the amount of bites at one feeding location. The habitat of the animal of the studies is also important in determining which method is used. Marine animal studies request for instance other methods of surveying than terrestrial animal studies.

Dividing the area

There are different designs to divide the study area. Areas of interest can for example be divided according to a nested design, where each smaller scale is nested within the bigger scale. The area can also be divided into circles with a range of radii, all with the same central point. Another division can be made by dividing the area into different sizes of blocks to make a difference in grid size. And a design can also depend on the species where the focus is on as on the vegetation (attachment).

Nested or hierarchical design

A chosen study area can be divided according to a nested design, which means that each smaller scale is nested into the scale that is one level bigger. Boyero (2003) used this design to detect patterns of variation of macro invertebrate community structure (figure 1). He used "a nested sampling design to estimate the components of variance associated with five successive spatial scales: basin, segment, riffle, section and sample". He randomly selected three segments within each basin, three riffles within each segment, three sections within each riffle, and three samples within each section. Basin, segment and riffle are chosen as scales because they are "objective spatial units that have been defined as functionally relevant for ecosystem dynamics". In contrast "sections and samples were arbitrarily defined spatial units". Sections were established within each riffle as units of approximately 1 m2 and samples were allocated randomly in each section. With this nested design the total range, from individual level to whole basin, of the environment of the macro invertebrates is covered. So the influence of environmental variables on the community characters can be detected.

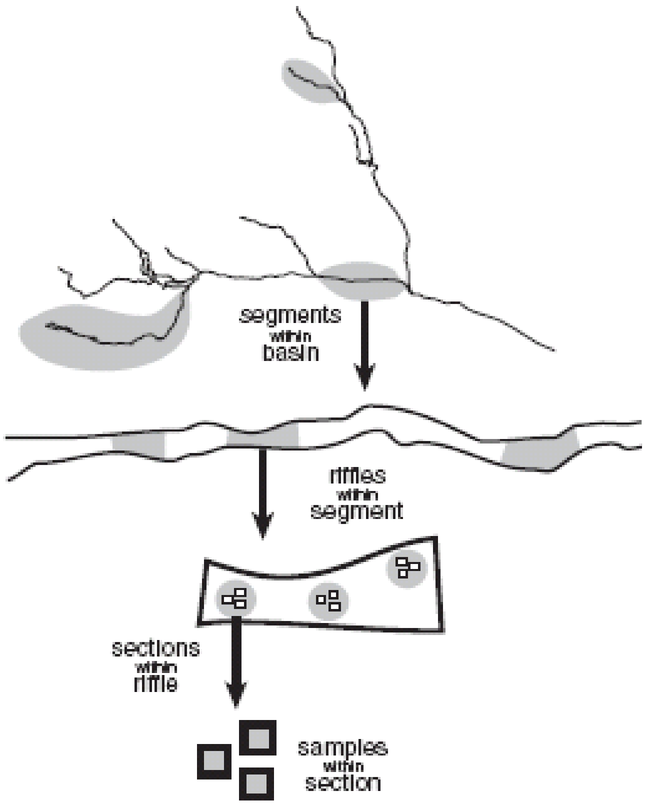

Figure 1. Sampling design for one basin, where successive nested spatial units are randomly selected: three segments, three riffles per segment, three sections per riffle and three samples per section (Boyero, 2003).

Several circles with a range of radii

Another design for dividing study areas is the use of circles with a range of radii, but with the same central point. Kie et al. (2002) have "quantified relationships between a suite of landscape metrics measured at different spatial scales and size of home ranges for female mule deer (*Odocoileus hemionus*) to test whether spatial heterogeneity played a major role in determining the distribution of deer". Landscape metrics were measured at each of the five study sites at four different spatial scales, within a range of radii (250, 500, 1000 and 2000 m) from the centre of the home range for each deer.

Pearson (1993) measured "the relative influence of within patch conditions and landscape-level variation on wintering bird populations". A landscape matrix was established at each study site with a radius varying from 100m to 500 m (figure 2). Within each band the variables were measured to determine the spatial arrangement of the habitats of the wintering birds. Each site was situated at "electrical power line and natural gas pipeline rights-of way (ROWs) that were 45 m wide and 300 m long." So each larger band represented a larger scale and the influence of the spatial heterogeneity at wintering birds could be defined.

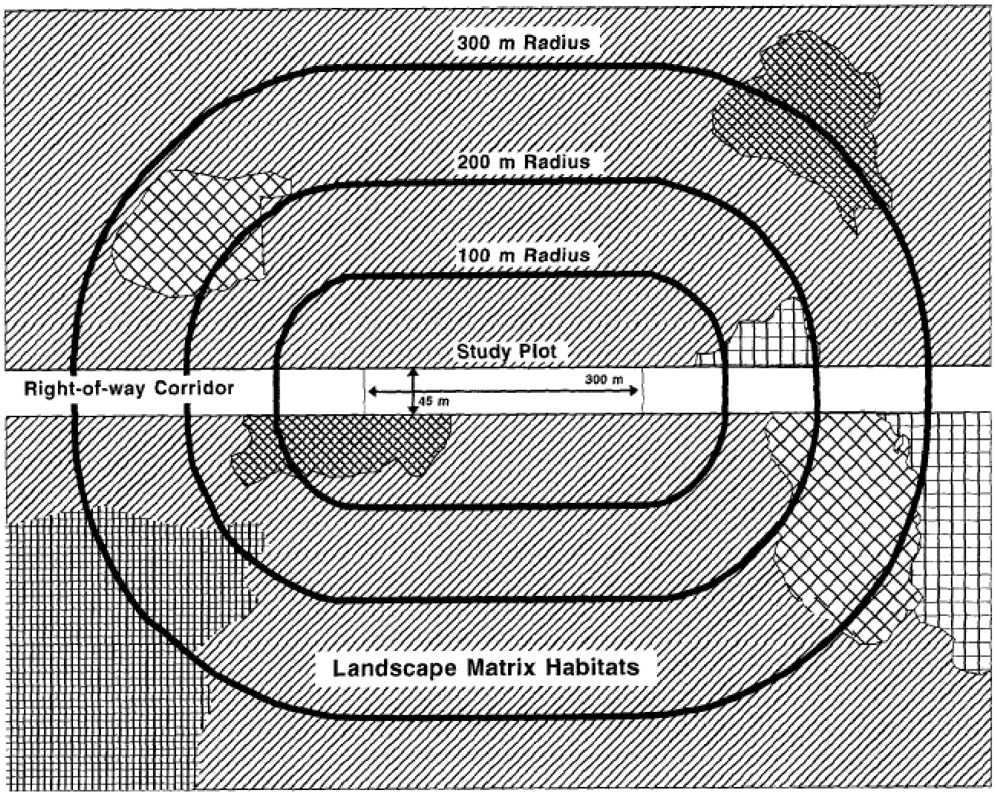

Figure 2. Schematic diagram of utility right-of-way study plot and surrounding landscape matrix. The number and proportion of area of habitats in each 100 m-radius band were calculated from habitat map of each study site. Though only three are shown here, five 100 m bands were used on the actual maps (Pearson, 1993).

Block design

Dividing the area into blocks is also used to detect spatial scale effects. WallisDeVries (1999) for example has used a block design for dividing an irrigated grassland to "test the effects of scale of patchiness on movements and selectivity of a large grazer in a controlled field experiment". Random mosaics of short/high-quality and tall/low-quality grass patches were created at equal proportion. Two grid sizes were made, patches of 2m x2m (coarse grid) and patches of 5m x5m (fine grid), to reflect two different scales.

Borges (2004) used two spatial scales, divided with a block design, to examine the relationship between local and regional species richness. Two different habitat types were examined at three islands within a plot of 900 m^2, which reflected the regional scale. Each plot was divided into 20 blocks of 3m x 3m, this was referred as the local scale.

Depending on animal or vegetation

Designs are also adjusted to the species the research is focused on. The different spatial scales are for example established from a nest (Bailey and Thompson, 2007; Gutzwiller and Anderson, 1987). If the design is established from a nest, the nest is the smallest scale and the bigger scales can be the nest sites, the vegetation around the nest site (Gutzwiller and Anderson, 1987), or a nest patch, "a distinct clump of interlocking leafy vegetation, usually a patch of shrubs" (Bailey and Thompson, 2007). Density of the species can also be a reason to base a design on. Hewitt et al. (2002) based the sampling sites on the density of *Atrina zelandica*, to represent the extreme variability of distributions (figure 3). In another study the feeding sites and traces of fresh feces are used to establish the different spatial scales (Zhang et al., 2009).

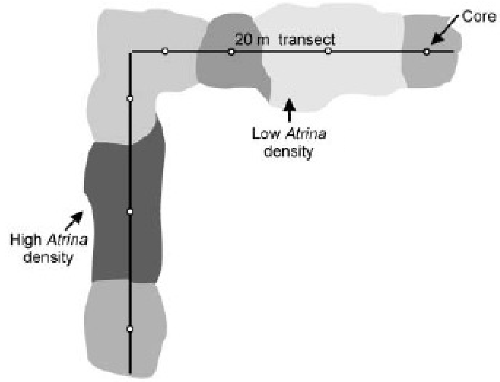

Figure 3. Diagrammatic representations of the macrofaunal sampling design. Cores were taken along the transect in positions that represented the variability of distributions of *Atrina zelandica.* Hewitt et al. (2002)

The variation in vegetation can also be the factor to divide the area. Freemark and Merriam (1986) determined, for instance the importance of habitat heterogeneity for assemblages in birds with this method. Birds were counted at points which were distributed to sample the heterogeneity in canopy species. So the heterogeneity was measured first to determine where the sampling points could be established and thus how the area was divided.

Quantify patchiness

Habin Li et al. (1994) discussed the fact that there is no single clear definition of spatial heterogeneity, which makes it more difficult to quantify patchiness and the influence of it. In this study they find that the five components: (1) number of patch types, (2) proportion of each type, (3) spatial arrangement of patches, (4) patch shape, and (5) contrast between neighbouring patches, contribute to spatial heterogeneity. But "their results signal a warning that any method to quantify spatial heterogeneity must be examined theoretically and tested under controlled conditions before it can be properly used in practice." In the studies used for this overview, there is a range of methods to determine the patchiness or spatial heterogeneity of the environment, but all studies have in common that the area is divided into a kind of map. To determine the spatial heterogeneity of a landscape it is necessary to map the study area. Variables of the environment are used to establish the quantification. But which variables are measured to quantify the patchiness depend mostly on the method used. Examples of variables measured are both vegetation parameters, such as vegetation type, as traces of animals.

The quantification of patchiness has been established with different methods. The spatial heterogeneity has been determined with already existing surveys (table 1) (Hughes et al., 2008; Pearson, 1993; Borges and Brown, 2004), but topographic maps, aerial photographs (figure 4) (Kie et al., 2002; Freemark and Merriam, 1986; Pearson, 1993; Mcgarigal and Mccomb, 1995; Gutzwiller and Anderson, 1987; Bailey and Thompson, 2007), satellite images (Vanbergen et al., 2007), and computer software (Vanbergen et al., 2007) are also used. Combinations of the methods are used as well. Vegetation types are established with existing surveys, for example 'a river habitat survey' (RHS) (Hughes et al., 2008) or with 'British Columbia's Biogeoclimatic Ecosystem Classification' (BEC) (Thompson and Gergel, 2008), or they are established by others (Pearson, 1993). But often the patchiness is measured with 'standard' measures as cover abundance, height (Borges and Brown, 2004), 'amount of woody cover' (Bailey and Thompson, 2007). An example of the use of topographic maps is the study of Boyero (2003). In this study topographic maps were used to record environmental variables of the two biggest scales. Aerial photography is mostly used in bird studies, also in herbivores studies, but not much in marine animal studies. Aerial photography is used to classify the area into habitat types (Kie et al., 2002) or to delineate the boundaries of each habitat type (Pearson, 1993). Bailey and Thompson (2007) used aerial photographs to define the landscape scale. And (Gutzwiller and Anderson, 1987) discovered the amount of canopy-covering classes within their habitat fragments. An

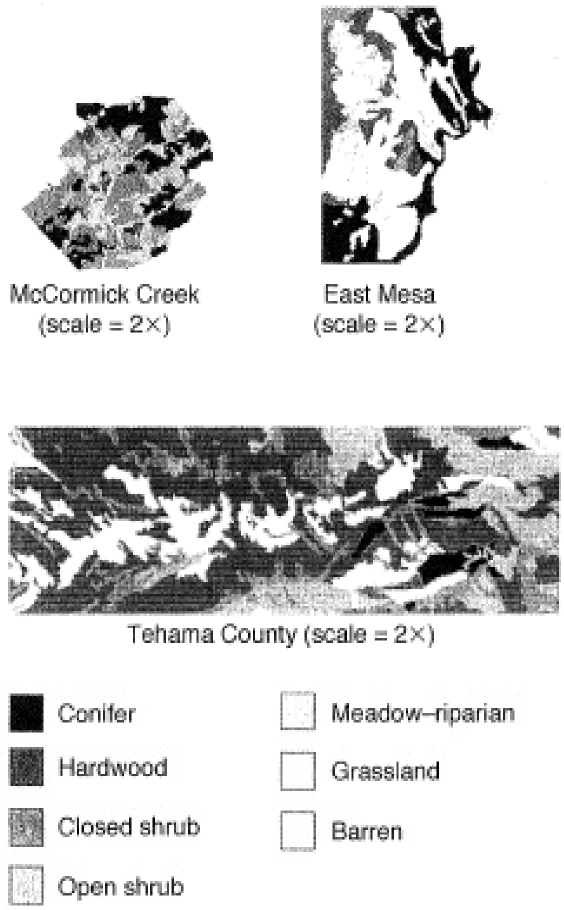

Figure 4. Aerial photographs are used to quantify the spatial heterogeneity of the area (Kie et al., 2002).

example of the use of satellite image is the study of Vanbergen et al. (2007). To interpret the satellite images a hierarchic classification system based on a biotopes database was defined. "The reliability of this land-cover classification was checked against personal knowledge of the study area and, where required, ground visits." So satellite images are used to map the area in different biotopes. Computer software is used, for example to quantify patterns of land covering of the area, with the classification done with satellite images or aerial photographs (Vanbergen et al., 2007).

A combination of all methods is used in Hughes et al. (2008). They used an already existing survey, an own survey, worked with computer software and used photographs as well as an aerial photograph. "Habitat structure, diversity and quality were assessed using an adapted version of the UK River Habitat Survey (RHS) method (table 1), with the addition of land-use categories and plant species typical of the Iberian Peninsula" and "extensive field surveys of riparian vegetation and land use were taken." The "RHS software was used to calculate the Habitat Quality Assessment index (HQA) and the Habitat Modification Score (HMS)" and "at least two photographs of each site were taken." Further "a geographical information system of land use and the quality, conservation and continuity of the riparian corridor was created from the survey data and aerial photography of the study area." This method was used to "assess the primary environmental and human factors that drive change in the benthic macro invertebrate assemblages of the Odelouca, and the spatial scale at which they occur".

Recorded feature	Basis for attribution of HQA score
Flow type	Diversity of flow types
Substrate (river bed)	Predominant natural substrate types
Channel features	Presence and extent of recorded 'natural' features, e.g. exposed bedrock and boulders, vegetated rock
Bank features	Presence and extent of recorded 'natural' features, e.g. eroding cliff, point and side bars
Bank vegetation	Presence and complexity of vegetation
Point bars	Count of total number of point bars along reach
Instream vegetation	Number of types of vegetation present in the stream (filamentous algae do not score)
Land use within 50 m	Broadleaf woodland, native pinewood, moorland/heath and wetlands
Trees and associated features	Tree density and continuity; presence of associated features (hanging boughs, exposed bank-side roots, coarse woody debris, fallen trees)
Special features	Waterfall > 5 m high, braided or side channel, debris dams, natural open water
Recorded feature	**Basis for attribution of HMS score**
Reinforcement	Presence: bank or bed, partial or whole
Resectioning	Presence: bank or bed, partial or whole
Two-stage bank modification	Presence
Embankment	Presence
Poaching of bank	Presence (livestock or humans)
Set-back embankment	Presence
Two-stage channel	Presence
Plant management	Evidence of weed-cutting or bank-mowing
Culvert	Presence (major)
Dam, weir, ford	Presence (minor, intermediate or major)
Bridges	Presence (minor, intermediate or major)
Enhancements	E.g. presence of groynes (minor, intermediate or major)
Flow control	Site partially (<33%) or extensively (> 33%) affected
Realignment of channel	Site partially (<33%) or extensively (> 33%) affected

Table 1. List of the recorded RHS features (Hughes et al., 2008)

Another method to determine the influence of patchiness on animals is to set up a controlled field experiment, thus to create patchiness. (WallisDeVries et al., 1999) and (WallisDeVries et al., 1998) "created random mosaics of short/high-quality and tall/low-quality grass patches in equal proportion at grid sizes of 2m x 2m and 5m x 5m."

The variables measured to determine the spatial heterogeneity of the area are divers. The study area can be divided in patches with vegetation variables, with traces of animals or with other variables. Vegetation type or habitat type of the area are often determined. For example, the study of Foord et al. (2008) established "five representative vegetation types, based on broad-scale structural classification." They related the differences in family and species composition and levels of endemicity of spiders between these vegetation structures. The study of Kie et al. (2002) is an example of the utility of habitat types. They compared the habitat use by mule deer. In the study of Hewitt et al. (2002) the variation in occurring and other aspects of *Atrina zelandica* was a measure of the heterogeneity. They measured: "*A. zelandica* shell width (size), total density of *A. zelandica*, minimum nearest-neighbour distance between *A. zelandica* and maximum clear distance between individual *A. zelandica.* So also traces of other animals are used to determine the spatial heterogeneity. In marine research other environmental variables are measured. Examples of variables are wave motion, substratum temperature (Pech et al., 2007) or water depth, current velocity, altitude, the heterogeneity of stone size and surface area of those stones (Boyero, 2003).

Influences on animals and methods to detect them

The spatial heterogeneity of an area can influence organisms living or depending on that area. This influence varies at different spatial scales. Examples of influences are the species richness, the diversity and the species composition or community structure. The patchiness also influences the abundance, distribution and movement patterns of animals and the species survival, the locations of nests sites, size of a home range, selection of feeding sites or the size and biomass of organisms. Some influences are species specific, such as nest site selection. But others are independent of a specific organism, for example community structure or species composition. Research on fish species examines mostly the abundance and distribution of the animals, whereas nest site selection obviously is investigated in bird studies. The majority of the studies observe or count individual animals, but there are also methods that make use of traces of the animals, such as occupied tree cavities (Gutzwiller and Anderson, 1987), sounds (Bailey and Thompson, 2007) or density of preferred food (Zhang et al., 2009) to determine the influence. Zhang et al. (2009) used the density of preferred bamboo shoots and bamboo trees as measure, because direct observations were difficult due to the dense forest where the giant panda lives.

Species richness and community structure is mainly studied at invertebrates species, as well at terrestrial as marine species. To determine these influences, sampling of individual invertebrates has been done with different methods. The individuals have been trapped by nets (Hughes et al., 2008; Foord et al., 2008; Jimenez-Valverde and Lobo, 2007), pitfall traps, as a result of beating or trapped by active searching (Foord et al., 2008; Jimenez-Valverde and Lobo, 2007). Studies with herbivores are more focused on the size of the home range (Kie et al., 2002), habitat and feeding site selectivity (Kie et al., 2002; WallisDeVries et al., 1999; Zhang et al., 2009; Jiang and Hudson, 1993) and movement patterns (WallisDeVries et al., 1999). Information is received by observing the animals, for example the grazing location (WallisDeVries et al., 1999) or the occurrence at specific spots (Jiang and Hudson, 1993). Another technique which is used for herbivores is radio telemetry. Kie et al. (2002) obtained information about the size of the home range of female mule deer based on radio telemetry techniques. Further, data are obtained with video and sound recordings of grazing herbivores. These records were used to determine for instance the amounts of bites, chews and steps at one location (WallisDeVries et al., 1999). In studies with the focus on fish species the community structure is an influence which is examined. But also abundance (Gust et al., 2001; Russ, 1984), distribution (Gust et al., 2001; Galzin, 1987; Russ, 1984; Belmaker et al., 2009) and even the size (Gust et al., 2001) of the species are considered. In most of these studies, data are collected with underwater visual censusing (UVC) techniques (table 2). A scuba diver estimates with this method the densities of the fish species. Other methods are to collect dead fish, killed with poison or plastic explosives. Galzin (1987) defined, besides visual surveys, single coral patches within each sampling station which were poisoned. In the study of (Williams and Hatcher, 1983) plastic explosives were used to collect fish species. Direct after detonating the explosives divers and men in a boat collected the dead and stunned fish with hand nets. Also in bird studies the influence of patchiness on community structure (Pearson, 1993) or the bird assemblage (Freemark and Merriam, 1986) is studied. And besides the focus on nest site selection (Bailey and Thompson, 2007; Gutzwiller and Anderson, 1987; Mahon et al., 2007), there is a focus on the selectivity of foraging sites of birds (Milesi et al., 2008). The nest sites are determined by keying in on breeding or territorial behavioral cues, such as alarm call or singing birds or by searching possible nest locations (Bailey and Thompson, 2007; Mahon et al., 2007). Another method is, as mentioned before, searching for occupied tree cavities (Gutzwiller and Anderson, 1987) and in the study of Milesi et al., (2008) the birds were observed with binoculars. Birds were observed as well in the whole study area (Bailey and Thompson, 2007) as spotted by point counts (Freemark and Merriam, 1986). Point counts were established to sample the heterogeneity of the area.

Abundance category	Number of fishes
1	1
2	2–3
3	4–9
4	10–27
5	28–81
6	82–243
7	244–729

Table 2. Numbers of individual fishes contained within each abundance category (Russ, 1984).

Discussion and conclusion

It is clear that there are many ways to measure the influence of spatial heterogeneity on animals at several spatial scales. In this overview I compared different studies with varying species focused on, different aims and various methods. Differences between studies are the kind of environment, size of study area and samples, classification and number of spatial scales, kind of species and the aim. Most of the studies emphasize in their discussion the importance of research done at various spatial scales (WallisDeVries et al., 1999; Borges and Brown, 2004; Pech et al., 2007; Hewitt et al., 2002; Galzin, 1987; Bailey and Thompson, 2007; Gutzwiller and Anderson, 1987; Mcgarigal and Mccomb, 1995; WallisDeVries et al., 1998; Hughes et al., 2008; Milesi et al., 2008; Thompson and Gergel, 2008). Borges and Brown (2004) recommend that there should be an investment to standardize sampling at other scales, the region scale in their research. And they argue about using bigger scales in next studies (WallisDeVries et al., 1999). Although the study of (Gutzwiller and Anderson, 1987) also discusses the importance of the use of more spatial scales, it also states that research can be done at one scale if there are no interdependencies between scales. But those can not be known without research at different spatial scales and therefore the influence of spatial heterogeneity should always be studied at varying scales, even though each establishment of scales gives upper and lower limits. The classification of spatial scales is very divers, the terms ‘micro-’ or ‘macro scales’, for instance, have not the same meaning. There is no established method of dividing a landscape into appropriate amount of scales, with clear definitions of those scales. Research could have more value if these definitions would be clear. Establishing such a method would be a difficult, if not impossible, job, because of the enormous variation between studies, such as environment and the kind of species the study is focused on.

The methods for dividing the area in studies used for this overview can be classified into nested or hierarchical design, a design with several circles with a range of radii, a block design or a design that depends on animals or vegetation. Boyero (2003) noted the usefulness of the nested design for examining scales of variation, although the number of scales was constrained in this study for practical reasons. Pearson (1993) used a design with several circles with varying radii. He discusses the fact that the factors at landscape level and at lower levels should be separable to distinguish the effects, which was debatable in this study. He also concludes that the vegetation patches were larger than the established 100 m wide bands, which resulted in correlation between some of the bands. In a block design used by (WallisDeVries et al., 1999), patchiness was created by a controlled field experiment. There were no differences in the exploitation of the steers per feeding station and because each patch was larger than a feeding station, the scale of patchiness may have been too large. Hewitt et al. (2002) used a method depending on the density of *A. zelandica*. They tried to maximize the extent and resolution of the survey with the collection of a minimum of core samples, but this resulted in a low sampling intensity. Despite this, the dividing is considered as a good method, because the benthic macro fauna were related to the spatial distribution of *A. zelandica.* Thus, none of these methods were discouraged for further use, but in each design were some constraints, such as number of scales, correlation between scales, scale of patchiness and a low sampling intensity.

The nested or hierarchical method covers the total range of an area, so varying spatial scales can be established from small to large scales, which is an important factor to measure the influence of patchiness (table 3). But the way Boyero (2003) established the spatial scales is not easy to establish in another study area, because “the objective spatial units have been defined as functionally relevant for ecosystem dynamics”. These units may not be defined in all study areas. Therefore this method is useful if the spatial scales can be established. The method with establishing circles can also cover the total range of an area. Furthermore, the scales are easy to establish if the patchiness of the environment is known. Pearson (1993) used this design, but the patches of the vegetation were larger than the established circles and were therefore not separable. This study used only one centre, but the result would have been more valuable if more matrices at random points in the area would be established. So dividing the area with circles can be a good method if the patchiness is known, if the data of the circles are separable and if more matrices are established at random points. However, I think it is a better method than the nested method, because patchiness is measured in these studies anyway, so the scales are easier to establish. In the block design the spatial scales are the best to establish, because the area can easily be divided in different grid sizes and the total range of the area is always covered. Despite the various scales which could be established with this method, Borges (2004) only used two spatial scales. So the block design is a good method if more scales are used. The use of animals to divide the area is less useful, because I think it may not be clear if the measured heterogeneity and the influence of animals at those places is due to the spatial heterogeneity of the area or it is created by the animal itself. Furthermore, an unstrained amount of scales is not possible, because these depend on the animal. For example, the studies of Gutzwiller and Anderson (1987) and Bailey and Thompson (2007) used the scales nest sites, the vegetation around the nest site or a nest patch, but larger scales depending on birds are hard to establish. And if the heterogeneity is measured within these scales, the variables can be influenced by the occurrence of birds. If the area is divided in scales by vegetation the total diversity of the area can be covered (Freemark and Merriam, 1986), but the influence on animals is only detected in that, for example, vegetation types, while other environmental variables of patchiness can also have an effect on animals. So dividing the area depending on animals or vegetation is debatable.

method	**advantage**	**disadvantage**	**usefulness**
nested/hierarchical	covers total range of the area	hard to establish the different scales	good method if scales can be established and separable
circle	covers total range of the area	factors at each level are not easy separable	good method if scales are separable
block	easy to establish	only two scales are used	good method if more scales are used
animal	scales are easy to establish	not clear if measured variation is created by the animal or reflects the spatial heterogeneity and an unstrained amount of scales is not possible	debatable measure of area
vegetation	all heterogeneity of the vegetation is measured	other environmental variables are not measured	debatable method

Table 3. Divide the area

To quantify the spatial heterogeneity different methods has been used. The patchiness is measured with already existing surveys (Hughes et al. 2008; Pearson, 1993; Borges and Brown, 2004), topographic maps, aerial photographs (Kie et al., 2002; Freemark and Merriam, 1986; Pearson, 1993; Mcgarigal and Mccomb, 1995; Gutzwiller and Anderson, 1987; Bailey and Thompson, 2007), satellite images (Vanbergen et al., 2007), and computer software (Vanbergen et al., 2007), but combinations of the methods are used as well. The variables measured to determine this are vegetation variables, traces of animals or other variables. Mcgarigal and Mccomb (1995) classified habitat from a community-centered perspective, but argued that other variables not measured in this simple scheme also could be important. But Hughes et al. (2008) can conclude that the 'River Habitat Survey' (RHS), used to determine the heterogeneity of the environment, was a good survey in their study.

The use of surveys is only useful at small scales, because it demands a lot of work and time, so large areas can not be easily quantified with this method (table 4). Aerial photographs and satellite images are good methods for large scales, but they have to be available. Computer software is a good method to combine information from surveys, aerial photographs and satellite images. So I think that each study should quantify the patchiness of the area with a combination of all methods and the measure of a lot of environmental variables, as in the study of Hughes et al. (2008), even though this gives a lot of data.

method	**advantage**	**disadvantage**	**usefulness**
survey	useful for small scales	influence of interpretation, demands lots of work and time	good method as basic method
topographic map	useful for large scales	not useful for small scales	only useful for large areas
aerial photograph	useful for large scales	not useful for small scales	only useful for large scales
satellite image	useful for large scales	not useful for small scales	good method for large scales if available
computer software	easy to map the area		good method to combine information from survey, aerial photographs and satellite images

Table 4. Quantify patchiness

Spatial heterogeneity is a term with no single clear definition, as is the term patchiness and patch. That makes it difficult to define the heterogeneity of the area. It seems that all methods deal with the issue 'measured heterogeneity' vs. 'functional heterogeneity' (Mcgarigal and Mccomb, 1995). The scheme to classify landscapes, the scale of the research and the manner of analysis determine the 'measured heterogeneity'. But this corresponds not necessarily with the 'functional heterogeneity', thus the heterogeneity important for the animal (Mcgarigal and Mccomb, 1995). Thus there are many methods and variables to measure the heterogeneity, where the unclear definitions and the variations in studies, environment and which species focused on, could be the cause. So a clear definition of spatial heterogeneity, patchiness and patch would give the studies more value. But establish such definitions would be difficult, like the establishing of a method to dividing a landscape into the right amount of scales with clear definitions, as mentioned before.

Which method used to detect the influences on animals depends on the focus animal and the method used to divide the area. All comments about this method were made about the sampling design. Methods to detect the influence on animals are species specific. Some methods can be used for various species, but others are only useful for a specific species (table 5). For herbivores observing, radio telemetry, video/sound, active searching, behavioural cues and looking for traces of animals are good methods. For fish and marine studies observing, nets and active searching would be appropriate methods. Nets, pitfall traps/beating and active searching are useful methods for invertebrates. Methods with behavioural cues, sound/video, looking for traces of animals and observing are useful methods for birds. All those methods are useful because they can be applied to those species.

method	**advantage**	**disadvantage**	**usefulness**
observe	good method if animals can easily be observed	animals are not always visible (invertebrates)	useful if animals can be observed, less useful for invertebrates
with traces of animals	good method if animals can not be observed	less reliable data due to estimations of traces	only useful if animals can not be observed
radio telemetry	for herbivores a good method and maybe for birds	not useful for invertebrates and fish	useful for herbivores, maybe for birds, not for invertebrates and fish
video/sound	good method for herbivores and maybe for birds	not useful for invertebrates and fish, difficult with wild animals	useful for herbivores and maybe for birds, not for invertebrates and fish
nets	good method for invertebrates and maybe for fish	not useful for birds and herbivores	useful for invertebrates and maybe for fish, not for birds and herbivores
pitfall traps/ beating	good method for invertebrates	not useful for herbivores, fish and birds	only useful for invertebrates
active searching	useful for herbivores, birds, fish and invertebrates	demands a lot of time	useful for all species used for this overview
underwater visual censusing	useful for fish and other marine studies	not useful for herbivores, bird and invertebrates	only useful for marine research
poison	useful for fish and maybe for herbivores, birds and invertebrates	harmful for the environment, kills animals	harmful method, but useful for fish and maybe for herbivores, birds and invertebrates
explosives	useful for fish	harmful for environment , not useful for herbivores, birds and invertebrates	useful for fish, but harmful method and not useful for herbivores, birds and invertebrates
behavioural cues	useful for birds, herbivores and maybe for fish	not useful for invertebrates, demands a lot of time	only useful for birds, herbivores and maybe for fish

Table 5. Detect influence on animals

So, landscape configuration is complex as is determining the influence of spatial heterogeneity on animals at different spatial scales. But, most of the studies emphasize the importance of research done at various spatial scales. I think that a study should quantify the patchiness of the area first with a combination of all methods and the measure of a lot of environmental variables and use a circle design or a block design with several spatial scales and use one of the appropriate methods for the species where is focused on. But each study has specific circumstances and other methods may then be better to use. Further research is needed to define which amount of scales should be used and to clarify the definition of the different scales and the definition of spatial heterogeneity.

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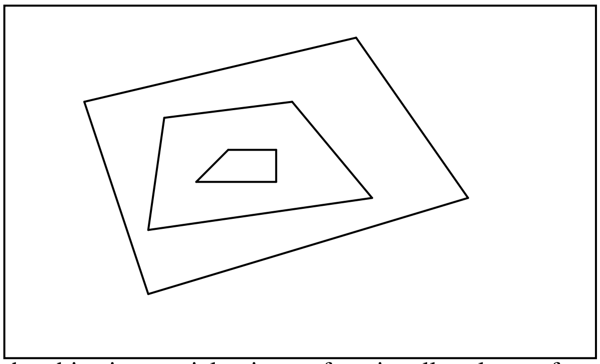
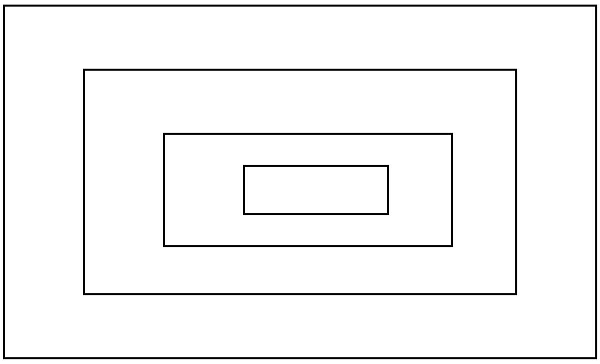
Attachment: methods to divide the area

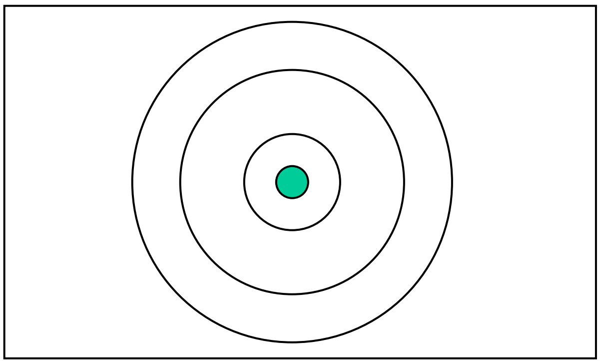
Nested/hierarchical design



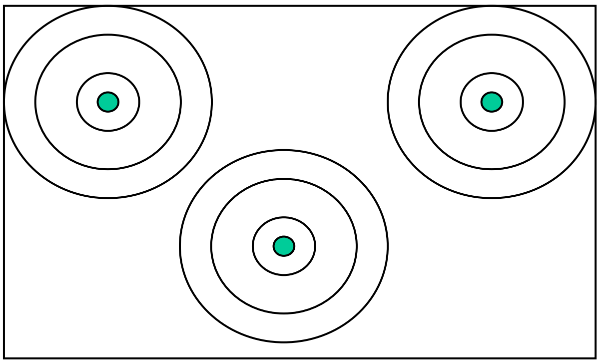


the objective spatial units are functionally relevant for ecosystem dynamics

Circle design

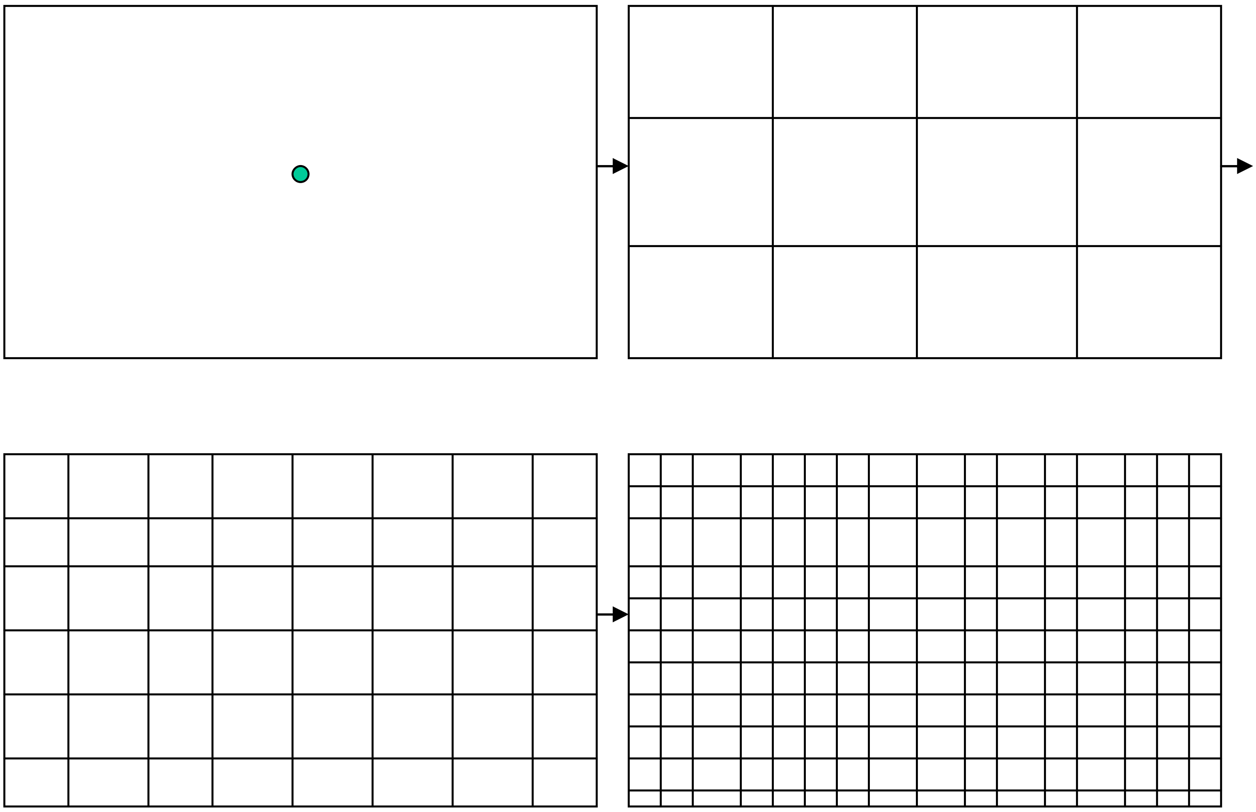


design with one centre



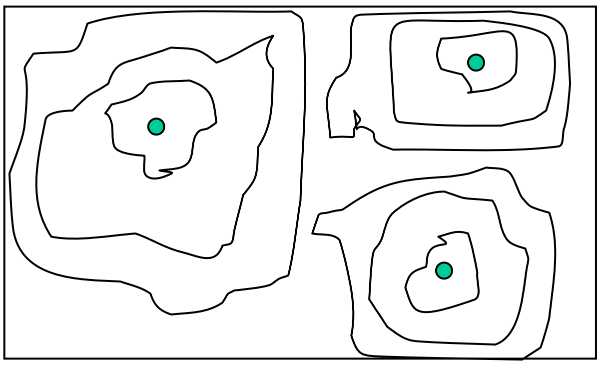
design with more centres

Block design

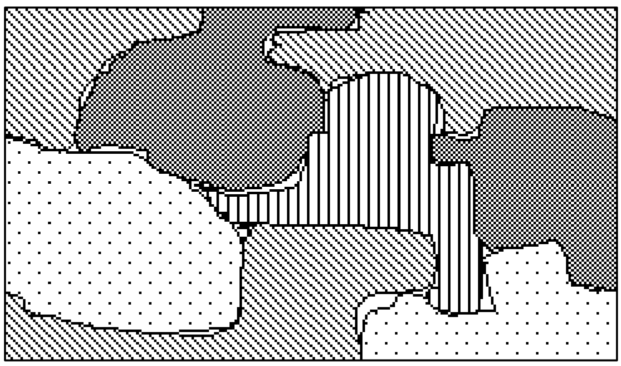


different grid sizes

Depending on animal and vegetation



a nest site is for example taken as centre



area is divide into different vegetation types