

Importance of scale in ecology biology essay



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The concept of scale in ecology is seen as increasingly important in our understanding of the functioning of ecological communities and the interaction of individual species with the environment. This has been recognised globally by the awarding of the 2011 Crafoord Prize to Ilka Hanski for his work on the concept of metapopulations (www.crafoordprize.se).

The importance of scale in ecology was only seriously recognised in the late 80's and 90's by ecologists (Krebs 1985; Wiens 1989; Levin 1992; Bissonette 1997). Krebs (1985) stated: " the importance of scale in ecology is a focal issue for the 1980's as we attempt to gain a finer understanding of how ecological systems operate in the real world". This is further highlighted by the fact that Kareiva and Anderson (cited in Wiens 1989 and Bissonette 1997) showed that about half of all studies conducted between January 1980 and January 1987 were done on plots a metre or less in diameter.

The two major types of scale are spatial scale and temporal scale. Spatial scale can be considered in terms of grain size and extent. The grain size is the resolution of the sampling. It describes the size of an individual sample. A common example for grain size in ecology would be a quadrat. The extent describes the area (or volume) within which all the samples are taken. Temporal scale can be thought of as the frequency of sampling.

The importance of scale when studying migrations was shown by Hanski and his colleagues (Hanski 1999, Hanski et al. 1994). Previous work has suggested that there are two types of butterfly populations; " open" and " closed". This is due to the mobility of different species of butterflies with some migrating long distances like the monarch butterfly and others only a

few kilometres. It was observed that the majority of species of butterflies in closed populations remained in their natal habitat patch. However, Hanski states that “ nobody had conducted extensive mark-recapture work simultaneously in many habitat patches (populations) to really establish the extent of migration. In other words he suggested that by looking at the metapopulation instead of population level, a better picture of the butterfly migration would be had (Hanski 1999). When this was done it was found that some populations were not as closed as they seemed (Hanski 1999, Hanski et al. 1994).

Insect herbivores life-history strategies

According to Bale (2002) there are six different types of life-history strategies found in insect herbivores:

Methuselah. Growth and development is dependent on climatic conditions. The life cycle can last several years. For example, the periodic cicadas have a 13 or 17-year life cycle (Williams and Simon 1995).

Stop go. Growth and development is controlled by environmental cues. It starts and stops in synchrony with seasonal changes. This can be seen in the heather psyllid *Strophingia ericae* (Miles et al. 1998).

Grab it. There is close synchrony of life cycle with host plant phenology because the duration of the availability of the plant as a food resource is limited to an interval during the growing season. There is usually only a single generation per year. For example, in the spruce bud moth (*Zieraphera canadensis*) larvae survivorship decreases significantly for those hatched 4-5 days after bud burst (Quiring, 1992).

Keep trying. The host plant allows for continuous development during a limited growing period. Two or more insect generation may occur per season depending on temperature and host plant condition. For example, the southern pine beetle *Dendroctonus frontalis* can have up to five generations per season depending on temperature (Rudinsky 1962).

Hop about. The insect changes host plant depending on suitability. An example of this strategy can be seen in the moth *Hyles lineata* (Cates 1980).

Never give up. In non-seasonal environments, continuous development occurs on a single host with several generations per year. In seasonal conditions, insects are adapted to survive unfavourable periods in any one of all stages. A seasonal synchronization mechanism may be included in the life cycle (e. g diapause and photoperiodic inhibition of development). An example of this strategy in seasonal conditions can be seen in the corn borer *Pyrausta nubilalis* (Babcock, cited in Masaki 1961) and in non-seasonal environments in the beetle *Chelobasis perplexa* (Strong and Wang 1977).

When studying any aspects linked with growth and development in insect herbivores, it is therefore important to know what type of life-history strategy the study species displays when choosing the temporal scale of the study. A species with a “ never give up” strategy can be sampled continuously throughout the year but this is not the best sampling process for a species with a “ methuselah” strategy because growth and development is dependent on climatic conditions and, to study its whole life cycle, sampling would have to take place over several years.

Temporal and spatial influence on community ecology

Krebs (1985) recognised five traditional characteristics of communities that have been measured or studied; species diversity, growth form (e. g. trees, shrubs, herbs, and mosses) and structure, dominance amongst species, relative abundance of species, and trophic structure. Temporal changes to these characteristics are known as successions and lead to a stable climax community “ A climax is the final or stable community in a successional series. It is self-perpetuating and in equilibrium with the physical and biotic environment” (Krebs 1985). Krebs describes the floral development of abandoned farmland in Oklahoma as example of plant succession. Booth (1941) analysed the different plant stages and their duration in the succession. His findings are tabled below.

Table 1. Plant succession stage and its duration. (After Krebs 1985)

Stage

Duration of Stage

Weeds

2 years

Annual Grass (*Aristida oligantha*)

9-13 years

Bunchgrass (*Andropogon scoparius*)

25+ years

Tall grass prairie

Climax vegetation

The replacement of weeds by annual grass can be explained to be due to weed species producing chemical inhibitors that affected themselves but not the annual grass. *A. oligantha* can survive in a low nitrogen environment and nitrogen levels are low after crop abandonment. As the soil improves, the bunchgrass replaces the annual grass and in turn is replaced by the prairie grass.

Temporal changes that occur in a stable community are known as cyclic changes. An example of this type of change can be seen in the population of lemmings in Greenland (Gilg et al. 2003). The collared lemming (*Dicrostonyx groenlandicus*) in Greenland is preyed upon by four species of predators; the arctic fox (*Alopex lagopus*), the stoat (*Mustela ermine*), the snowy owl (*Nyctea scandiaca*), and the long tailed skua (*Stercorarius longicaudus*). Gilg et al. were able to show that there is a 4-year cycle in lemming and stoat numbers. They were also able to predict this 4-year periodicity in lemming dynamics by constructing a predator-prey model. This and the Gilg et al. observations of the 4-year cycle were graphed and can be seen in Fig. 1 below.

Fig. 1. The top graph is a visual demonstration of the lemming (black squares) and the stoat (grey circles) 4-year cycle based on field observations. The bottom graph demonstrates the cycle predicted by a model. (Gilg et al. 2003)

They also highlight that there is a similar cycle in the arctic fox in Greenland. Using data from trapping records, they demonstrated that arctic fox numbers

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between 1935 and 1960 peaked at intervals of 4, 5, 4, 4, and 4 years. Like the changes in stoat numbers, they suggest that this cycle is due to changes in lemming densities.

Spatial influence on community ecology is especially obvious when considering the theory of island biogeography put forward by MacArthur and Wilson (1967). This theory states that on an island, the number of species is proportional to the size of the island and its distance from the source population (usually the mainland). This theory does not work solely on island populations. It has been adapted to work on fragmented forests, lakes and ponds, caves, and mountaintops (Harris 1984, Lassen 1975, Culver et al. 1973, Riebesell 1982).

Communities can have different species diversity depending on their latitude. Simpson (1964) recognised a north-south gradient in the abundance of mammals in North America. He identified a clear but irregular gradient with a minimum number of 13 species in a quadrat (240 km²) in one of the northernmost areas (latitude 70°) and a maximum number of 163 species in one of the southernmost areas (latitude 10°). This gradient can be explained due to the warm temperatures found in the tropics which favour the diversification of the biota (Krebs 1985, Jacobsen et al. 1997). Krebs (1985) states that the increase in species diversity towards the tropics could be due to an increase in spatial heterogeneity. This influence has been recognised in forest ecosystems by Burnett et al. (1996) and in bird species diversity by Roth (1976). Another factor to this gradient might be that towards the equator diversity in species is greater because the area is greater and

species richness is scale dependent; it increases with area (Willig et al. 2003).

How communities are structured/evolve

A community is formed from processes which occur at very large spatial and temporal scales such as speciation, vicariance, and dispersal (Holt 1993).

Two types of community structures are the physical structure and the biological structure (Krebs 1985). The physical structure refers to the structures within which species distribute themselves, for example, trees and shrubs. Krebs (1985) recognised three components to the physical structure of communities; growth forms, vertical stratification and seasonality which will be discussed in the next section. The growth form refers to the architecture of a plant in terms of its form, method of branching and arrangement of its shoot system, and underground system if possible (Gimingham 1951). They can be classified into six major growth forms:

Trees

Lianas

Shrubs

Epiphytes

Herbs

Thallophytes

All communities have a vertical structure. This stratification is associated with a decrease in light (Krebs 1985).

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“ Biological structure involves species composition and abundance, temporal changes in communities, and relationships between species in a community” (Krebs 1985). Examples of temporal changes and relationships between species in communities were given in the previous section. All these characteristics of the community structure are interlinked. This is best shown in Fig. 2.

Fig. 2. The relationships between factors that influence the structure of a community. (After Krebs 1985)

The evolution of a community is not dependant on individual biological components but of the pattern of interaction expressed in the community structure (Olson 1966). Although, it could be argued that changes in a species can change an interaction in the community structure (Brooks and McLennan 2002). Changes in one of the factors in Fig. 2. can contribute to the evolution of a community. The evolution of a community can also be thought of in terms of succession as a community changes until it reaches a stable climax community. The extent to which a community can evolve is dependent on species density. A community which has a number of species that is below equilibrium numbers has a greater chance of evolving than a community in equilibrium (Brooks and McLennan 2002).

Factors influencing the structure and longevity of communities

Seasonality is a major component of the physical structure of communities. The structure of all communities is affected by seasons, and seasonal events are important to the functioning of communities (Krebs 1985, Wiens 1974). It

can also be considered as affecting the biological structure since the physical structure of a community affects its biological structure (Krebs 1985, Wiens 1974). Wiens (1974) states that the highly seasonal distribution of precipitation and production found in grassland habitats can influence the species abundance or the size of the resident population. He also describes how climatic irregularities can limit the number of species in a community, especially in large unfragmented grasslands where there are few places for opportunistic species to reside. He argues that in grassland which covers a small area, populations of species can take refuge in a different habitat type until conditions are favourable for them. Also, natural hazards (e. g. fires and floods) and anthropogenic influences can affect community structure (Zimmerman 1992, Dale et al. 2001).

The longevity of a community is dependent on its resilience. Resilience indicates how fast a community can return to an equilibrium state after a perturbation (Pimm 1984). If a community is resilient it does not mean that it is unstable. In fact, Holling (1973) states that the spruce budworm forest community is highly unstable and because of this it is very resilient. Measurements of resilience are specific to a type of perturbation. A community can be resilient to one type of perturbation (e. g. low temperatures) but not at all resilient to another (e. g. increased nutrients) (Krebs 1985). Two factors that can affect the resilience of a community are patchiness and dispersal (Krebs 1985, Holling 1973). Some communities are resilient because they reside in a patchy environment. When a perturbation occurs in one patch, species can disperse to another patch until conditions are favourable again (Krebs 1985, Wiens 1974). Species composition and

biodiversity can also affect resilience (Allison 2004, Griffiths et al. 2000).

According to Pfisterer and Schmid (2002) “ greater number of species can express a greater range of responses to environmental perturbations”.

Differences in immigration/emigration between guilds, species, and kingdoms

Different organisms have different success in migrating. For example, Walsh and Kay (1995) showed that when eucalyptus trees were introduced to New Zealand from the Australia, woodborers, sapsuckers and defoliators species immigrated to New Zealand to colonise the eucalyptus number of species being roughly equally distributed amongst the three guilds. At around the same time, pine trees from the North America were introduced to New Zealand. Half the amount of woodborer species that colonised the eucalyptus emigrated to colonise the pines while only a quarter of the numbers of sapsuckers that colonised the eucalyptus colonised the pines and no defoliators managed to establish in the pines. The success of the insects, considered to be pests to trees, is due to the distance of their source population from New Zealand (Fig. 3). The insect that colonised the eucalyptus trees came from Australia and had no problem in immigrating. However, the insect pests to the pines originate from North America and would have had to travel a long distance to reach introduced pines. The defoliators could not emigrate and synchronise their life history with the introduced pines. The woodborers are well-adapted to travelling long distances because their life history is isolated from their environment. Sapsuckers are not as well adapted to travelling long distances but only one

female need to arrive at the destination to colonise because of their parthenogenesis capability.

Fig. 3. An adaptation of the MacArthur and Wilson (1967) model for the prediction of the number of pests that can colonise a host. (Walsh and Kay, 1995)

Insects have more success in establishing themselves in a new environment if they migrate on an east-west axis as opposed to a north-south (Kay, 2005). This is because there is more of a chance of phenological synchrony of pests and host in east-west dispersal because season reversal is encountered when travelling north-south.

How does this assist our understanding of ecology on a local and global scale?

When choosing scale one must be aware of the characteristics of the processes that might influence your study (if they are not the subject of the study themselves) and the characteristic of organisms in the study. For example, if we are studying the potential threat of an invasive herbivore insect to a community, it is not enough to study the community structure to see if it can accommodate the insect but the distance of the source population must be known as well and also the life-history strategy of the insect. Although spatial and temporal scales are usually positively correlated to achieve high predictability in a study (Wiens, 1989) this is not the case when looking at the evolution of a community. When studying succession, a later sequence can survive longer than the investigator (Connell and Slayter,

1977). This means that you could be looking at the succession of a local community in a small area using years of data.

Hanski (1999) makes an argument of not restricting to a local scale when studying a local population. By looking at a more global scale you can make an inference on a local population.

It is important to note that even when a community is in a stable condition, temporal changes can still occur and lead to population dynamics. These cyclic changes could affect data and therefore the temporal scale of a study done on species in a stable climax community would have to take this into consideration. For example, if one were looking at the stoat population in Greenland between 1996 and 1999 (Fig. 1.) one would assume that there is a pattern with number of individuals gently rising, unaware of the cyclic changes in their population.

Since when we look at evolution we look at changes against time it is safe to say that time is the main process influencing the evolution of a community. This is visually demonstrated in Fig. 2. where time is on top of the diagram showing the factors that influence community structure. However, there is a spatial influence on the evolution of a community as well. Spatial heterogeneity, as previously discussed, can dictate the species diversity. Also, the species density (amount of species per area) affects the ability of a community to change.

The theory of island biogeography can be applied on a local and global scale. The Culver et al. (1973) study on cave-limited species in the Greenbrier valley in West Virginia can be considered to be done on a local scale

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compared to the MacArthur and Wilson (1967) study on amphibians and reptiles in the West Indies using data collected by Preston (1962).

On a global scale, we see that species diversity increases on a gradient from one of the poles to the equator. This can be attributed to the change climate, spatial heterogeneity, or simply because of the greater amount of space available towards the equator.

Seasonality can have an ecological effect on global as well as local scale. On a local scale, it can effect species abundance and population density in a community. Seasonl irregularities can affect species diversities in spatially homogenous communities. On a global scale, seasonality can lead a community to be species specific. Some herbivorous insect cannot colonise certain areas because they are unable to synchronise their life cycle with the potential host plant phenology due to change in seasons.

A community's longevity is not dependent on how stable it is but on its resilience. A community's resilience is influenced by how patchy is the environment it occupies. If its environment is heterogenous, species can disperse between habitat types to avoid perturbations. Biodiversity is also important for resilience and , as already mentioned, is affected by spatial and temporal forces.

Success of migration in species is dependent on the scale of the migration. Walsh and Kay (1994) showed that woodborers, sapsuckers and defoliators had much more success in immigrating to New Zealand from Australia than from North America. There was also variation in successes to the emigration

of the three guilds from North America due to the different influences that seasonality has on the guilds.

In brief, the main conclusion of this review is that a study should not be restricted to one scale. When possible, different observations should be done on different scale. For example, when studying species diversity we know that it can be affected by spatial heterogeneity (local scale) and latitude (global scale). We have already established that different processes work on different scale but it is important to note that some processes work on multiple scales.