Spatially heterogeneous populations with mixed negative and positive local density dependence

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A B S T R A C T

Identifying the steady states of a population is a key issue in theoretical ecology, that includes the study of spatially heterogeneous populations. There are several examples of real ecosystems in patchy environments where the habitats are heterogeneous in their local density dependence. We investigate a multi-patch model of a single species with spatial dispersal, where the growth of the local population is logistic in some localities (negative density dependence) while other patches exhibit a strong Allee effect (positive density dependence). When the local dynamics is logistic in each patch and the habitats are interconnected by dispersal then the total population has only the extinction steady state and a componentwise positive equilibrium, corresponding to persistence in each patch. We show that animal populations in patchy environments can have a large number of steady states if local density dependence varies over the locations. It is demonstrated that, depending on the network topology of migration routes between the patches, the interaction of spatial dispersal and local density dependence can create a variety of coexisting stable positive equilibria. We give a detailed description of the multiple ways dispersal can rescue local populations from extinction.

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Population dynamics studies the changes over time in the size (density) of a group of individuals who share the same habitat. Since there are so many interactions between individuals and the environment, describing how populations grow or shrink is often a complex task. Mathematical growth models are frequently used to better understand these dynamics in real populations. In simplest terms, the change in the size of the population can be expressed by the difference of births and deaths. If environmental conditions are favourable (that is, food, space, etc. are abundant), then the population is able to grow. Growth is said to be exponential when the growth rate is proportional to the total population size. However, when resources are limited, an intraspecific competition of the individuals can occur which results in a slowdown of the exponential growth as competition for the resources increases.

Eventually, population growth decreases nearly to zero as the population reaches the carrying capacity of the environment. This way, the growth of the population is described by an S-shaped curve, known as the logistic curve.

Numerous examples illustrate that in real ecosystems the growth of populations can exhibit another type of dynamics, the Allee effect, which is very different from that of exponential and logistic growth. Animal populations are often subject to the Allee effect, that is, they are better able to grow at higher densities. The concept was first described by Warder Clyde Allee, who studied the growth of goldfish. While classical population dynamics modelling approaches – including the concepts of exponential and logistic growth – assume negative density dependence of per capita growth rate, Allee's experiments showed that goldfish were better able to survive on higher densities. It has been observed that certain aquatic species can affect the chemistry of the water by releasing protective chemicals that could enhance their survival. In a tank, goldfish better manage to render the water closer to their optimal chemical requirements when there are several of them (Allee and Bowen, 1932). Based on his experiments and observations, Allee arrived to the conclusion that

the evolution of social structures is not only driven by competition (which classically implies negative density dependence), but that cooperation is another fundamental principle in animal species (Allee, 1931). The individuals of many species cooperate in various ways: they join forces to hunt or to escape predators, they forage together, they use cooperative strategies to survive unfavourable conditions, or they seek partners for reproduction.

The phenomenon of the Allee effect, often referred to as positive density dependence in population growth, has been studied comprehensively in the literature. Both in the direction of theoretical works with mathematical models and empirical works with the unveiling of Allee dynamics in natural populations, a large number of studies have been published (Dennis, 1989; Courchamp et al., 1999; Berec et al., 2007; Stephens and Sutherland, 1999). We also refer to the excellent book of Courchamp et al. (2008) which details the history and recent developments of the topic, and also provides a thorough overview of the relevant literature. We distinguish two types of Allee effect: the strong and the weak Allee effects. The strong Allee effect includes a population threshold that is often referred to as the Allee threshold: the population goes extinct when rare (per capita growth rate is negative), and it is able to grow at densities higher than the threshold (Dennis, 1989; Lewis and Kareiva, 1993; Odum and Barrett, 2004). In case when a weak Allee effect occurs in the population, the per capita population growth rate is lower (however, still positive) at low densities than at higher densities.

An Allee effect can arise from a large variety of different ecological mechanisms. There are several types of reproductive Allee effects, as fertilization efficiency in sessile organisms, mate finding in mobile organisms or cooperative breeding. Examples also include mechanisms related to survival, like environmental conditioning and predation. Comprehensive description of the various mechanisms with appropriate ecological examples can be found in Berec et al. (2007), Stephens and Sutherland (1999), Courchamp et al. (2008). Predation can generate a strong Allee effect in prey. An example for this mechanism is the case of the island fox (prey) and the golden eagle (predator) on the California Channel Islands (Angulo et al., 2007). Foxes are consumed by eagles as secondary prey, since feral pigs are the main prey for eagles. If pigs are not present on an island, then eagles will not sustain a permanent population on that habitat, as the fox population by itself cannot provide enough prey. If, on the other hand, there are sufficient pigs around to maintain the eagle population then the eagles establish residence on the island. This way, eagle population dynamics do not depend on fox density, and unlike in the classical predator–prey models, eagles can deplete the fox population without negative feedback on the predator population. If the eagle kill rate follows a Holling type II functional response then this phenomenon reveals an Allee effect in the fox population, since the lower the fox density, the higher the individual risk of eagle predation (Angulo et al., 2007). Clutton-Brock et al. (1999) also compared survival between prey populations living in sites where predators are abundant and sites where predators have been reduced or removed as a result of human interference. They find that suricates in Kalahari Gemsbok Park – an area of high predator density – were subject to a strong Allee effect whilst those living in the neighbouring ranchland where predator density is relatively low, could survive even in small groups.

If the mechanism that triggers the Allee effect depends on ecological circumstances (e.g., presence of particular predators), then the Allee effect may be present in some areas or time periods, and absent in others. Sinclair et al. (1998) investigates the impact of reintroducing endangered predators on the prey. Since predation causes an Allee effect in the prey population which is not the primary food supply for the predator, it might be necessary to apply predator control to allow the escape of the prey population.

In Australia, several indigenous mammals – the black-footed rock wallaby and the quokka for instance – have been reduced to a fraction of their former range, so for their conservation some sensitive prey species are now confined to outer islands where exotic predators (feral cats and red foxes) are absent. Sometimes different habitats support different colony sizes, and it depends on their density whether the population is subject to an Allee effect or grows logistically. Pollock apply two types of strategies for protection from predators. Fish who live in structured habitats (such as algal beds) disperse to reduce detection by predators, so predation triggers a negative density dependence in fish. On the other hand, in open intertidal habitats the fish shoal, which means that their risk-dilution effect is positively density dependent (Stephens and Sutherland, 1999).

The term "metapopulation" was introduced in the works of Levins (1969, 1970), referring to a collection of local populations that are connected by migration (Levins, 1970). The metapopulation concept, though it has undergone some paradigm shift, has been firmly established in population ecology and conservation biology since the work of Hanksi and Gilpin (1991), and the topic is also receiving increasing attention in mathematical modelling of ecological processes. The classical metapopulation theory (Levins, 1969) rests on the assumptions that dynamics of local populations occur on a fast time scale in comparison with metapopulation dynamics. This way, the classical metapopulation theory is concerned with the number of local populations but changes in their sizes is ignored. The dynamic theory of island biogeography (Macarthur and Wilson, 1963, 1967), models the changes in the size of local population in the discrete habitat fragments (patches). In a mathematical model that rests on the island theory approach the dynamic variable is the number of individuals on a particular patch, while in the classical approach the dynamic variable is the number of habitat fragments occupied by the species. Hanski (2001) explains how the two metapopulation approaches can be integrated by providing a theoretical framework that explicitly unites the two theories.

In this paper we focus on the approach where the size of local populations is modelled. Most literature with this approach assume negatively density-dependent (typically, logistic) growth in the local populations (Levins, 1969, 1970; Levin, 1974; Holt, 1985; Hastings, 1993; Doebeli, 1995; Allen et al., 1993; Ruxton, 1993, 1994; Poethke and Hovestadt, 2002; Yakubu and Castillo-Chavez, 2002). Besides, spatial theory for the case when the local dynamics is governed by the Allee effect is also relatively well developed (Dennis, 1989; Courchamp et al., 2008; Lewis and Kareiva, 1993; Amarasekare, 1998; Gyllenberg et al., 1999; Keitt et al., 2001; Boukal and Berec, 2002; Kang and Lanchier, 2011). However, an interesting question – that has not been studied yet – is how dispersal and spatial heterogeneity influence metapopulation dynamics when the nature of local density-dependence is negative in some patches but positive in others. Throughout the above discussion we provided examples for real animal metapopulations where in some habitats local populations grow logistically while different locations exhibit an Allee effect. Such difference in the local dynamics can arise when some ecological circumstances (e.g., presence of particular predators) vary over the localities.

We consider an animal population distributed over several discrete geographical patches that are interconnected by dispersal. If a local population is subject to a strong Allee effect then typically it has three steady states: the extinction (zero) equilibrium attracts every solution started below a positive equilibrium (Allee threshold, unstable), and all solutions converge to the population carrying capacity (another positive, stable equilibrium) if the initial population size is larger than the Allee threshold. On the other hand, in a local population that follows logistic growth there exist