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The manager dilemma: Optimal management of an ecosystem service in heterogeneous exploited landscapes

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ABSTRACT

Ecosystem services are defined as benefits produced by ecological communities, supporting human welfare. Because sustainable agriculture relies on such ecosystem services, finding the optimal management – which optimizes both the surface dedicated to human activities and the delivery of ecosystem services – is particularly critical. Ecosystem services heavily depend on the presence and activity of organisms, especially ecosystem engineers. In order to find the proportion and the spatial aggregation of exploited areas that optimize an ecosystem service, we developed three complementary metapopulation models of a keystone species in an exploited landscape. We considered both anthropic and ecological constraints, by modelling the simultaneous management of two variables: the yield of human activities and the ecosystem service provided by the metapopulation. We also investigate how this optimal management can drive the metapopulation close to extinction, and how two key ecological traits of species – population growth and dispersal rates – can mitigate such extinction risks. The two spatially implicit metapopulation models show that the optimal management is a trade-off, benefits often being optimized for intermediate surfaces of exploitation. This optimal surface depends on the ecological traits and on the degree of disturbance incurred by human activities. Spatially explicit simulations suggest that optimal management is further improved when the spatial distribution of human activities is fragmented.

1. Introduction

The concept of ecosystem services arises from the need to define the relationships between human welfare and ecosystems. Ecosystem services can be defined as the goods and services that human populations derive from ecosystems (Costanza et al., 1997). Several types of ecosystem services can be distinguished: provisioning services, such as water or wood; regulating services – such as water purification; supporting services – such as biological cycles; and cultural services – like ecotourism and aesthetic value. Most of them heavily depend on organisms' presence or activity.

Some species delivering ecosystem services may be unaffected or even be favoured by human activities within an agricultural landscape (Eriksson, 2012). In such instances, economical and ecological benefits are positively correlated, and the optimal solution is to devote the whole landscape to the considered activity. However, in most situations, human exploitation of ecosystems is harmful to species delivering ecosystem services, either reducing their abundance or their biodiversity. The 2005 Millennium Ecosystem Assessment pointed out the irreversible changes humans have caused over the last fifty years on ecosystems, resulting in a threat of extinction on 10–30% of mammal, bird, and amphibian species. For instance, in intensively managed agricultural landscapes, many pollinator populations have decreased, causing large decreases in the provisioning of the pollination ecosystem service (Biesmeijer et al., 2006; Potts et al., 2010). When human activities harm species providing ecosystem services, a dilemma emerges: which surface should be exploited, considering both human welfare and species conservation? How should we organize human activity to keep it sustainable? While landscapes are increasingly disturbed by human activity, conservation of engineers appears all the more urgent.

Several constraints – biotic and abiotic – affect the outcome of this dilemma. On the abiotic side, environmental spatial heterogeneity is a key factor. Two components play an important role. First, the amplitude of the environmental alteration due to human activities, expressed as the degradation of the species ecological niche (*i.e.*, the reduction in the species growth rate). Second, the spatial aggregation of the human perturbation on the environment,

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Ecosystem services refer to the benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza et al., 1997). They are most usually provided by ecological communities embedded in a given landscape and have positive effects on human welfare.
A landscape is a mosaic of habitat patches (Dunning et al., 1992). The landscape can be either marine or terrestrial. The patch is the basic building block. A metapopulation (see below) can disperse within the landscape.
A patch is here assumed to be either exploited by human beings, either non-exploited. A patch can be occupied or not by the population of interest, which provides the ecosystem service.
Heterogeneity refers to a spatial characteristic of the landscape (Turner, 1989). Here, the landscape is an environmental mosaic, in which heterogeneity has two components: the amplitude of the environmental alteration due to human activities – compositional heterogeneity (Fahrig et al., 2011), and the spatial aggregation of the anthropized patches – configurational heterogeneity (Fahrig et al., 2011).
Fragmentation (as the reverse of spatial aggregation) is one component of spatial heterogeneity. The more fragmented the landscape, the less aggregated the exploited – or non-exploited – patches.
A metapopulation is a population of populations, connected by dispersers (Levins, 1969). Here, we assume that the metapopulation is made of local populations that live either in exploited patches or in non-exploited patches.
An ecosystem engineer species directly or indirectly modulates the availability of resources to other species by causing physical or chemical changes in biotic or abiotic materials (Jones et al., 1994).
A species niche is defined from its relationships with the biotic and abiotic elements of its environment. In other words, each species has a niche which is the intersection of all of the ranges of tolerance under which it can live (Hutchinson, 1957).
A population with a positive growth rate and which loses more emigrants than it receives immigrants is called **a source-population**. Conversely, a population with a negative growth rate, with a greater immigration than emigration is called **a true sink population** (Pulliam, 1988). It differs from **a pseudo-sink population** that has positive growth rates, but still receives more immigrants than produces emigrants due to spatial heterogeneities in environmental conditions (Watkinson and Sutherland, 1995). Here, non-exploited patches are sources and exploited patches can be either true sinks or pseudo-sinks.

affecting the ecological dynamics at landscape scales. Based on this idea, some theoretical bioeconomics models take into account as many abiotic constraints as possible in order to optimize the human exploitation of a given resource (Sanchirico and Wilen, 1999).

Many empirical studies illustrate the critical role of spatial heterogeneities in the management of ecosystem services. Fragmentation has for instance been shown to increase extinction risks in disturbed landscapes (Fahrig and Merriam, 1994). Landscape structure also strongly affects the spatial distribution of wild populations. For instance, the abundance and structure of vole populations widely change depending on landscape type – from a village to an open field (Delattre et al., 1996). Landscape heterogeneity management is therefore at the heart of agricultural practice issues, as exemplified by the land sharing *vs.* land sparing debate (Green et al., 2005). This debate tackles the future food security. It discusses how management option trades-off exploitation and species conservation in space, by opposing farming the entire surface with wildlife friendly techniques – *i.e.*, land sharing – *vs.* farming intensively some land whilst other land remains as a nature reserve – *i.e.*, land sparing. Such options indirectly question the issue of landscape heterogeneity: is it optimal to reduce such heterogeneities (by exploiting a large group of homogeneous nature-friendly patches) or to strongly exploit fewer patches?

Biological aspects inherent to the ecosystem engineer species are equally important. Variation in dispersal capacities or reproduction rates modulates the consequences of human modifications for the persistence and functioning of such populations. Metapopulation (Hanski, 1991) and metacommunity (Leibold et al., 2004) models incorporate such aspects, and offer good opportunities to determine suitable strategies for a sustainable management of ecosystem services accounting for both conservation and economic issues. The role of non-exploited patches is highlighted when it comes to agricultural landscapes (Burel and Baudry, 2005) because the spatial variations in habitat quality may increase extinction risks for many species (Hanski, 1991) but also provide adjacent ecosystems with services due to population spillovers (Tylianakis et al., 2007; Loeuille et al., 2013). Dispersal, combined with environmental autocorrelation, defines the environmental "grain" under which the species demography, evolution and management should be considered (MacArthur and Levins, 1967). Adapting spatial models also requires considering how the ecosystem service is delivered by populations. Ecosystem services can be due to the presence of the species, independently of its density (presence-dependent ecosystem service: *e.g.*, Byers et al., 2006) or proportional to the species density (density-dependent ecosystem service: *e.g.*, Hodgson et al., 2010).

Several models tackle the issue of the optimal exploited proportion of a landscape. This is for instance a classical topic concerning the design of marine reserves, to improve the fishing efficiency and preserve wild populations (Baskett et al., 2007; Gaines et al., 2010; White et al., 2008). Pollination services can be similarly modelled, integrating ecological and economic constraints to define the optimal design of a landscape (Brosi et al., 2008). Such previous studies have often focused on specific situations with a detailed description of a particular ecosystem service with its inner constraints. Here, we intend to develop models that are more general in order to focus on the two constraints we view as key in determining ecosystem service management: species dispersal and spatial environmental heterogeneity. Particularly, we aim at understanding how these two constraints interact.

We consider a species in a heterogeneous landscape made of two different types of patches: exploited and non-exploited. Individuals disperse throughout the landscape, and provide an ecosystem service which positively affects human activities. The exploitation activity has a negative impact on the species survival. We take the point of view of a landscape manager who wishes to optimize his welfare or landscape utility. This welfare depends on two factors: the economic yield of the landscape exploitation, and the ecosystem service provided by the studied species. Using three complementary metapopulation models, we tackle the following questions:

1. What range of exploitation intensity allows the survival of the metapopulation?
2. What proportion of the landscape should the manager exploit to optimize both his yield and the ecosystem service?
3. Can this optimal management be dangerous for the metapopulation in terms of extinction probability?
4. What is the optimal spatial aggregation of non-exploited patches within the landscape?

Model (1) is spatially implicit and considers a "presence-dependent" ecosystem service. Model (2) is a two-patch model that investigates the consequences of density-dependence for ecosystem service management ("density-dependent" ecosystem