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Heterogeneity and the trade-off between ecological and productive functions of agro-landscapes: A model of cattle–bird interactions in a grassland agroecosystem

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ABSTRACT

There is empirical evidence that the proportions of different land uses or management regimes and their spatial arrangements can affect the long-term dynamics of bird species in agro-landscapes. The aim of our study was to assess the extent to which biodiversity can be enhanced by altering landscape structure without reducing agricultural production. We focused on a wader bird, the Northern Lapwing (*Vanellus vanellus*), in grassland landscapes in the Marais Poitevin area (France). For the purposes of our study, we developed a spatially explicit, dynamic model linking grass dynamics in grazed and mowed fields to lapwing population dynamics on a landscape scale. We then computed contrasting landscapes composed of fields with different management regimes that compensated for or complemented each other. The mechanism of compensation corresponded to the case where one management regime is favorable to a species, and the other is less so. The mechanism of complementation corresponded to the case where each of two management regimes is partially favorable to a species. Our results showed that the relative share of different management regimes was the main driver of Northern Lapwing dynamics in landscapes characterized by compensatory management regimes. In landscapes characterized by complementary management regimes, the spatial arrangement of the management regimes was also an important, albeit secondary, driver of bird population dynamics. Managing the spatial arrangement of management regimes is a way to improve the trade-off between ecological and agricultural performances on a landscape scale by improving ecological performances without altering the level of production. Landscape heterogeneity appears to be a promising way to reconcile the agricultural and ecological functions of agriculture, although it raises several issues concerning collective management.

1. Introduction

Agricultural intensification in Europe has resulted in a substantial decline in biodiversity, with farmland bird specialists being particularly at risk (Julliard et al., 2003; Donald et al., 2006). It has entailed changes in farming practices such as increased mechanization and the broad use of chemical inputs on a field scale, as well as landscape-scale changes such as field enlargement, the standardization of practices, and the loss of semi-natural elements. This homogenization of agro-landscapes has reduced the availability and diversity of resources (e.g., food and shelter) and is one of the main drivers of biodiversity loss (Tscharntke et al., 2005).

Recent reviews highlight the importance of heterogeneity in reversing the decline of biodiversity in agricultural landscapes (Benton et al., 2003; Tscharntke et al., 2005). Heterogeneity is a complex notion and has been defined in different ways (Sparrow, 1999). The term synthesizes two landscape characteristics: first, the proportions of different agricultural land uses or management regimes; and second, their spatial arrangement (i.e., the composition and structure of the landscape) (Burel and Baudry, 1999). Benton et al. (2003) and Tscharntke et al. (2005) point out the importance of landscape heterogeneity and complexity to hosting a diversity of species but provide few details on the underlying mechanisms. More recently, Fahrig et al. (2011) went further by describing the different aspects of the functional dimension of heterogeneity. This functional dimension of heterogeneity is very much in line with former theoretical and empirical studies that analyzed the interactions between habitats and proposed various hypotheses linking landscape composition to biodiversity (Dunning et al., 1992; Andren et al., 1997). They distinguish two types of mechanisms (compensation and complementation), depending on the nature of the various habitats generated by each

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management regime and on the way they interact on the ecological point of view. These two types of mechanisms have been synthesized by Brotons et al. (2005). The mechanism of compensation corresponds to the situation where one land-use type is favorable to a given species and a second is of lower quality (Andren et al., 1997). The mechanism of complementation corresponds to the case where each of the two management regimes is partially favorable to a species, and both management regimes are required for the species to complete its life cycle; e.g., one habitat provides shelter, while another provides forage (Dunning et al., 1992). The proportion of the different management regimes is then a strong driver of the mechanism of complementation. However, it is also likely that the spatial arrangement of the landscape interacts with the mechanism of complementation and modifies its outcome.

Many studies and policies focussing on the ecological functions of agro-landscapes implicitly posit that a favorable habitat (e.g., a field under an agri-environment scheme) compensates for the effects of an unfavorable one (e.g., a field with conventional management). This approach is embodied in the model of Green et al. (2005) contrasting intensive land use, which is detrimental to biodiversity, to extensive land use, which is favorable to biodiversity. The compensatory view also prevailed for a long time in conservation policies for agro-ecosystems. For example, Swiss agricultural policy imposes a minimum threshold of 7% compensatory areas in agricultural landscapes (Albrecht et al., 2007). But along with the composition of landscapes, landscape structure is increasingly considered a major driver of biodiversity, and the heterogeneity of landscapes is starting to be taken into account in conservation policies. These include introducing measures of the mosaic management of habitats in the Netherlands (Melman et al., 2010) to protect the Black-Tailed Godwit (*Limosa limosa*).

The proportion of different management regimes in the total cultivated area of a farm is an important driver of ecological performance (Jouven and Baumont, 2008; Tichit et al., 2011). However, converting some intensively managed fields into extensive ones often involves a trade-off in production (Sabatier, 2010). In this context, acting on the spatial arrangement of management regimes to increase the heterogeneity of landscapes without altering the proportions of different management regimes could be an important lever for reconciling productive and ecological functions of agro-landscapes, because it promotes mechanisms of complementation.

The objective of this study was to assess the extent to which biodiversity can be enhanced by altering landscape structure without reducing agricultural production. The following two hypotheses were successively tested:

1. In a landscape composed of complementary management regimes, the spatial structure of the landscape influences the ecological performance (Fig. 1a).
2. Increasing the complexity of the landscape structure makes it possible to offset the trade-off between agricultural and ecological performances (Fig. 1b).

Testing such hypotheses in the field would mean monitoring several landscapes with different land-use proportions and different spatial structures (all other things being equal) and recording data on ecological and agricultural performances. A simple way to have a first overview is to use a modeling approach. In this study, we developed a model that formalizes the interactions between agricultural management regimes and the dynamics of a bird population (Northern Lapwing) in a landscape consisting of permanent grasslands. Our aim was to build a theoretical model, still as realistic as possible, to reveal through simulations how the spatial arrangements of management regimes can impact a target species. The model simulates how Lapwing populations are affected by the proportions of different management regimes and the complexity of the spatial arrangement. Each landscape is characterized by its performances: ecological (population size at time horizon) and agricultural (average grazed-grassland production). We successively simulated series of landscapes composed of two complementary management regimes, two compensatory management regimes, or three management regimes leading to both complementary and compensatory mechanisms.

2. Material and methods

2.1. Description of the case study

The case study was focussed on the population dynamics of the Northern Lapwing (*Vanellus vanellus*) in a wet-grassland landscape on the French Atlantic coast (Marais Poitevin, 46°22′N, 1°25′W). These grasslands are anthropomorphic agro-ecosystems. Whereas, on the one hand, their maintenance depends on livestock farming, on the other hand, over-intensive management of grasslands is detrimental to biodiversity (Durant et al., 2008b; Vickery et al., 2001; Sabatier et al., 2010). Waders reproduce in grasslands, and their life cycle is closely linked to the management practices and characteristics of landscapes (reviewed in Durant et al., 2008b). A large part of their life cycle depends on the direct and indirect effects of management practices on the field scale (Sabatier et al., 2010). The direct effect of management occurs before hatching, when eggs are exposed to trampling by cattle (Beintema and Muskens, 1987). Indirect effects linked to habitat quality, such as predation risks or food availability, occur after hatching, as juveniles leave the nest in their first month of life and disperse to a neighboring area, where they remain quite sedentary (Redfern, 1982; Johansson and Blomqvist, 1996; Kruk et al., 1997). Since they collect food by themselves and do not depend on their parents for foraging, they are highly sensitive to habitat quality at this time in the life cycle. This habitat quality depends on grass height and structure (review in Durant et al., 2008b). Therefore, their dispersal through fields of different grass heights just after hatching is an important mechanism in their population dynamics in addition to the direct and indirect effects on a field scale. After the first month, juveniles strongly increase their mobility by starting to fly. Due to this dispersal behavior, waders are good model species for a multi-scale analysis of interactions between agricultural management regimes and ecological dynamics. Of the different wader species nesting in our study area, the Northern Lapwing (hereafter simply referred to as the Lapwing) was by far the most common and best studied. We therefore focussed our study on this species.

2.2. Model overview

We developed a spatially explicit model that represents a grassland landscape, consisting of fields with different grassland-management practices, exploited for beef-cattle farming. This agro-ecosystem is seen both as a feeding resource for cattle and as the habitat of the Lapwing. The landscape is composed of $K = 64$ fields represented in a lattice grid of 64 square pixels of 4 ha. Given the high geometric regularity of the real landscape shaped by rills and canals, this lattice grid can be considered to be a reasonable approximation. The dynamics are discrete in time with a time step of 1 month and a time horizon of 2 years ($T = 24$ months). The model links the dynamics of the grass biomass of a set of fields to the dynamics of a population of Lapwings (Fig. 2). Both dynamics are adapted from Tichit et al. (2007) and Sabatier et al. (2010). The grassland sub-model simulates grass growth controlled by grazing or mowing in each field. The Lapwing sub-model simulates the dynamics of a Lapwing population in relation to the direct and indirect effects of grazing and mowing