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Does landscape heterogeneity modulate the trade-off between production and biodiversity?

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Introduction

There is empirical evidence that the proportion of land uses and their spatial arrangement can affect the long-term dynamics of bird species in agro-landscapes (Benton et al. 2003). Modifying the proportion of land uses, through the conversion of some intensive land uses into extensive ones often involves a trade-off for production (Sabatier et al. 2010). Acting on the spatial arrangement of land uses to increase the heterogeneity of landscapes without altering the proportion of land uses, could help to reconcile production and biodiversity in agro-landscapes. Theoretical and empirical studies propose various hypotheses linking landscape characteristics to biodiversity (Brotons et al. 2005). They distinguish between compensatory and complementary land uses, depending on the nature of the various habitats generated by each land use. The mechanism of compensation occurs when one land use only provides a part of the resources to the species considered, e.g.. The mechanism of complementation occurs when each of the two land uses is partially favourable to a species, i.e. each of them favours a single stage in the life cycle. Several land uses are then necessary in the landscape to provide all the resources to a species. In such a context, it is likely that along with the proportion of land uses, their spatial arrangement, and thus the landscape structure, strongly affects the mechanisms of complementation. The objective of this study was to assess to what extent biodiversity can be enhanced by altering landscape structure, without reducing agricultural production.

Materials and Methods

We developed a spatially explicit model that represents a grassland landscape made of different types of fields exploited for beef cattle farming. This agro-ecosystem is both a feeding resource for cattle and the habitat of a grassland bird species the lapwing (Vanellus vanellus). The landscape is composed of 64 fields, represented in a lattice grid of 64 square pixels of 4 ha. The model includes discrete time dynamics on a monthly time step with a twoyear timeline. It links the grassland dynamics of a set of fields to the dynamics of a population of lapwings. Both dynamics are adapted from Sabatier et al. (2010). The grassland dynamics sub-model simulates grass growth, controlled by grazing or mowing in each field. The bird sub-model simulates the dynamics of a lapwing population in response to the direct and indirect effects of grazing and mowing on bird demographic parameters. It includes the juveniles' movements between the various fields in the month following hatching. In grazed fields, grazing has a direct negative effect on the lapwing's average brood size through the destruction of nests by cattle trampling. It also has an indirect positive effect on the juvenile's survival which depends on short grass heights. In mowed fields, only grass height impacts the juveniles' survival. We simulated landscapes composed of pairs of complementary land uses and more complex landscapes consisting of three land uses (Table 1). These three land uses corresponded to "productive grazing", "ecological grazing" and "spring mowing". This functional classification of land uses was derived from Sabatier et al. (2010), where land uses were identified based on differences in impacts on the key stages of bird life cycle (Table 1). For each pair (or threesome) of land uses, we used Neyman-Scott processes to simulate a set of landscapes with different proportions of land uses and different levels of clustering. Each simulated landscape was characterized by the proportion of land uses, by an index of landscape structures and by its ecological and productive performance. The ecological performance was the total lapwing population. The productive performance was given by a grazed grassland production index that corresponds to the number of days for which cattle feeding was provided by grasslands. The higher this index, the greater the forage production of the landscape will be. It was expressed in livestock unit days per ha of grazed pastures (LU days/ha). This index is a linear function of the proportion of grazed grasslands.

 Table 1 Different land uses taken into account in the model and their qualitative effects on the demographic parameters of lapwings

Landscapes	Land uses	Impact of land uses	
		Fecundity	Survival
Two complementary land	Mowing	+	-
uses	Productive grazing	-	+
Three land uses	Mowing	+	-
	Productive grazing	-	+
	Ecological grazing	+	+

Results and Discussion

In landscapes with two complementary land uses, simulations showed a non-monotonous effect of the proportion of mowing on bird population sizes (Figure 1). The best population sizes were obtained for intermediate mowing proportions. For a given mowing proportion, variance in the range of population sizes was wide. The residual variance of population sizes was then explained by the landscape structure (Figure 1). High levels of structure indices, and thus high complexity of spatial arrangement of land uses, favoured the bird populations. This result illustrated the importance of interfaces between different land uses when they generated complementary habitats for birds. In landscapes made of three land uses, a strong trade-off existed between productive performance and ecological performance (Figure 2). The fact that, for a constant mowing proportion, the relationship between the grazed land uses proportion and the productive performance was linear, means that there was a strong relationship between ecological performance and the proportion of the two types of grassland. There was nevertheless a large part of variance that was not explained by the proportion of land use. For a constant proportion of ecological pastures (e.g. 10%; +/- 1% in the example in Figure 2), this residual variance was strongly explained by the landscape structure. For a constant proportion of land uses, an increase in the complexity of spatial arrangement of land uses was therefore a way to improve the ecological performance of landscapes without losing on the productive dimension (Figure 2). Our results showed that an increase in the complexity of landscape structure could favour mechanisms of complementation between habitats. Due to limited data availability, the model was partially validated. Therefore, outputs should not be considered as quantitatively exact predictions but rather as criteria for the comparison of simulated landscapes, aimed at testing the complementary hypothesis. Modulating the spatial arrangement of land uses therefore seems to be a promising way to improve trade-offs between production and conservation. Such approach is now being taken into account in European conservation policies. However, working on larger spatial scales means bringing together several actors to

implement wildlife friendly management. The "mosaic management" scheme introduced for wader conservation is a good example of such territorial management. Today, coordination tools are developed under this scheme in order to facilitate synergies among farms (Melman 2010). However, it is still unclear which spatial arrangement can be attained when all farm constraints are taken into account. We conjecture that all levels of landscape structure cannot be envisaged from an agricultural viewpoint. As many obstacles still hinder the efficiency of schemes targeting optimal levels of heterogeneity for biodiversity, considerable efforts are still needed to develop tools for coordinating different actors' efforts.



Figure 1 Effect of the proportion of land uses (left) and structure on the ecological performances of 38,100 grassland landscapes made of two complementary land uses. Landscapes in red were composed of 60% (+/- 1%) of mowing.



Figure 2 Trade-off between ecological and productive performance of 22,356 grassland landscapes with three land uses (left) and effect of the landscape structures on the ecological performance (right). Mowing proportion is set to 39% (+/- 1%). The landscapes in red correspond to landscapes composed of 10% (+/- 1%) of ecological pasture. The grazed grassland production index has the property of being a linear function of the productive grazing/ecological grazing ratio.

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