

# Modeling spatially explicit population dynamics of *Pterostichus melanarius* I11. (Coleoptera: Carabidae) in response to changes in the composition and configuration of agricultural landscapes

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## Abstract

The intensification of agricultural practices has induced the local, national and regional extinction of many species and also affected ecosystem services provided by biodiversity such as biological control of agricultural pests. We model the population dynamics of *Pterostichus melanarius* (Coleoptera: Carabidae), a carabid beetle often used as indicator species of habitat changes, by a joint model that combined a matrix model of population dynamics including local dispersal with an explicit model of the patchy landscape of the polders of the Bay of Mont St. Michel (Brittany, France). We used this model to evaluate the effects of landscape composition and configuration on the spatial population dynamics of this carabid beetle, and also investigated the consequences that different management strategies of the structure and composition of an agricultural landscape can have on its abundance and spatial distribution. The results of this study highlight that semi-habitats (field edges, dykes, hedgerows) usually considered as shelters for wintering play a key role as well for summer recruitment. We find that there is an optimal cluster size of patches for population viability that is induced by the seasonal movement of *P. melanarius*. However, the effect of increasing the amount of semi-natural habitats patches on the viability of this population critically depend on the spatial arrangement, connectivity and spatial alternation of the network of semi-natural habitats, a feature that should be considered in the conservation and management actions in the landscape context.

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**Keywords:** Spatially explicit models; Landscape; *Pterostichus melanarius*; Dispersal; Leslie matrix model; Management

## 1. Introduction

The intensification of European agriculture has led to local, national and regional extinction of numerous species of the European flora and fauna over the last 40 years, as well as profound changes in the ecosystem functioning of European farmland. The impact of agricultural intensification on biodiversity (as well as on water and soil quality) are no longer debated since many studies have shown the decrease of species number of plants, insects, birds and mammals both at the European (e.g. Krebs et al., 1999; Donald et al., 2001; Robinson and Sutherland, 2002) and national scales (e.g. Benton et al., 2002; Kleijn and Sutherland,

2003; Fox, 2004). In addition, agricultural intensification has also affected ecosystem services provided by biodiversity such as biological control of agricultural pests (Thies and Tschantke, 1999; Östman et al., 2003). This intensification has entailed three main driving processes: the simplification and specialization of agricultural landscapes leading to a decrease of permanent pastures and semi-natural landscape elements, the transformation of less fertile areas into shrubs and early successional forests and an overall loss of landscape diversity, and the increase in the use of chemicals (herbicides, pesticides and fertilizers) per unit area (Robinson and Sutherland, 2002).

Carabid beetles are often used as indicators of habitat change because of their relatively fast response to environmental changes, their well-known biology and ecology and the relative ease of sampling (Thiele, 1977; Wallin, 1985; Burel et al., 1998). Furthermore, carabids beetles are often numerically dominant among the entomofauna of European agricultural landscapes,

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they are key food resources for threatened bird species (e.g. Fuller et al., 1995) and have a great agronomic importance because of their important predation pressure on crop pests, which can help reduce the use of pesticides and their harmful effects on non-targeted species (Thomas and Parkinson, 2001; Collins et al., 2002; MacLeod and Wratten, 2004). The intensification of European agriculture has entailed a significant reduction in landscape complexity and structure through the elimination of hedgerows to enable the expansion and consolidation of small agricultural fields in larger ones that are more amenable to mechanization and higher production (Benton et al., 2002; Robinson and Sutherland, 2002). Because semi-natural habitats such as hedges, dykes and other non-cultivated habitat serve as refuges for carabid beetles in intensive agricultural areas, their progressive decline has decreased their local abundance and their spring colonization from neighboring agricultural fields (Wallin, 1985; Coombes and Sotherton, 1986; Chiverton, 1989). A proposed management option to counter the impact of loss of semi-natural habitats on carabid beetle abundance and distribution has been the establishment of beetle banks within the crops that provide additional wintering sites (Thomas and Wratten, 1991; Collins et al., 2002).

Habitat composition (as characterized by the types of land use) and spatial configuration (as denoted by the spatial distribution, shape, area of patches and their connectivity) are key features for population persistence in fragmented landscapes (e.g. Fahrig and Merriam, 1985; Burel, 1989). This is especially the case for species such as carabid beetles that require habitat continuity for successfully dispersing between suitable patches during the year and throughout their life cycle (Charrier et al., 1997; Martin et al., 2001). Nevertheless, most spatially explicit modeling approaches (see Dunning et al., 1995) issued from the metapopulation paradigm considered the landscape as being simplistically divided into “suitable” and “non-suitable” habitat from the viewpoint of a focal species. Levins’ (1969) seminal work introducing metapopulation dynamics described the persistence of a focal species in a landscape as resulting from local extinction and colonization events. This fundamental model was not a spatially explicit model (i.e. distances between suitable patches did not affect parameter values) and it considered dispersal to be independent of the distances separating patches. Subsequent developments of the metapopulation paradigm (summarized in Hanski, 1998) are largely modifications of Levins’ original model to add realistic features such as distance-dependent dispersal and patch-size dependent extinction rates. Nevertheless, according to the more recent developments of metapopulation theory, dispersal is typically a decreasing function of the distance separating suitable patches and to be independent of any attribute of the interspersing non-suitable habitat (Etienne, 2004; Hanski, 1994; Johnson et al., 1992) that have been shown to affect the dispersal success of many arthropod species such as its quality, permeability to movement, patch shape and the degree of connectivity between habitable patches (e.g. Fahrig and Merriam, 1985; Clarke et al., 1997; Söndgerath and Schröder, 2002). Most models of spatio-temporal population dynamics have considered space either as homogenous or as divided into (a rather small number of)

patch types for mathematical tractability because of the inherent difficulty of dealing with complex spatial structures and of localized movement (Murrell and Law, 2000). As a result, traditional spatially explicit modeling approaches cannot consider in detail the influences of changes in the landscape configuration and composition on the spatial dynamics of populations. Nevertheless, the spatial structure and temporal dynamics of realistic landscapes is of central importance to understand the effects of fragmentation of suitable habitat on population persistence (e.g. Fahrig and Merriam, 1994; Tilman et al., 1997; Keymer et al., 2000; DeWoody et al., 2005). The main goal of this paper is to formulate a coupled model of local population dynamics with an explicit model of a patchy landscape in order to assess the effects of landscape structure and configuration on the abundance and distribution of a carabid beetle population living on a realistic agricultural landscape. Our model is intermediate between explicit patchy-population models where individuals disperse only between ephemeral, suitable patches (e.g. Fahrig, 1992; DeWoody et al., 2005) and reaction-diffusion models (e.g. Turchin, 1991; Lewis, 2000; Alder, 1999) where individuals are considered as a single class (i.e. age/stage structure is not considered) and population abundance is redistributed over a continuous space composed of only suitable patches. We aimed to investigate the consequences that different management strategies of composition and configuration features of an agricultural landscape have on the abundance and distribution of a carabid beetle.

## 2. Methods

### 2.1. The species

*Pterostichus melanarius* H11. (Coleoptera: Carabidae; also called *Platysma vulgare*) is a very prolific and widespread European carabid beetle (Lys and Nentwig, 1991; Thomas and Parkinson, 1998) that typically colonizes open habitats such as agricultural areas (Fournier and Loreau, 2001a; Thomas and Parkinson, 2001). This polyphagous species winters as larvae in crops during its first year and thereafter as a non-reproductive adult on hedges and field margins (Thiele, 1977; Wallin, 1985). In Western Europe, adults start breeding from early May to end of October of their second year of life and only few of them will survive to breed thereafter (Thiele, 1977; Wallin, 1989). Despite that *P. melanarius* has wing dimorphism in part of its geographic range (Ribera et al., 2001), it has no functional wing-like appendages (Holland, 2002) and relies on walking for dispersal (Firle et al., 1998). *P. melanarius* is ranked as a “medium dispersal power” among carabids (Fournier and Loreau, 2001b).

### 2.2. Demographic model

The dynamics of *Pterostichus melanarius* at the level of each agricultural field (~0.3 Ha) resulted from the local demography and the net dispersal of adults from neighboring fields. The local demography was modeled with a Leslie matrix of 13 age classes (one for eggs, eight for larvae, three for nymphs and the last one for adults), using a time step of 10 days that roughly corresponds

to the shortest duration observed for any demographic transition of *P. melanarius* (from egg to larvae; Legrand and Gaucherel, in press; Hajnalka and Tréfas, unpublished data). The annual dynamics was divided into the breeding and the wintering (early November–end of April) periods, each of which had a different transition matrix. Unlike the Leslie matrix just described for the breeding period, the matrix for the winter period was a diagonal matrix containing the probabilities that individuals survived and remained at an age class. The annual demography of *P. melanarius* at an agricultural field was then modeled as a sequence of products of these two matrices. Adult dispersal from and to neighboring fields (dispersal rules are described below) was the second component of the dynamics of *P. melanarius* at the level of each agricultural field. Schematically, the local dynamics per time step can then be written as:

$$\begin{bmatrix} \text{eggs} \\ \text{larvae} \\ \text{nymphae} \\ \text{adults} \end{bmatrix}_{t+1}^{in} = (\text{Demographic Matrix}) \times \begin{bmatrix} \text{eggs} \\ \text{larvae} \\ \text{nymphae} \\ \text{adults} \end{bmatrix}_t^{in} + \sum_1^k \begin{bmatrix} 0 \\ 0 \\ 0 \\ \text{Disp}_{\text{out} \rightarrow \text{in}} - \text{Disp}_{\text{in} \rightarrow \text{out}} \end{bmatrix}_t \quad (1)$$

where the vector denote the abundance per age classes in an agricultural field, the Demographic Matrix corresponds to the either breeding or wintering matrix, and  $\text{Disp}_{\text{in} \rightarrow \text{out}}$  is the proportion

of individuals that disperse from the patch in to the patch out. Note that  $\text{Disp}_{\text{in} \rightarrow \text{out}}$  is always smaller than the population size of the field in ( $\text{Pop}_{\text{in}}$  cf. Eq. (2)) before dispersal.

Lacking estimates of the demographic rates for the species at our study site, we collated available estimates obtained for intensively managed agricultural areas in Western Europe, and expressed them at the time step of the model (10 days; Table 1). While eggs remain scattered on the ground (Lövei and Sunderland, 1996), larvae, nymphs and adults of *P. melanarius* remain nearly motionless in the soil during winter, and we used a probability of surviving and remaining at an age class of 0.3 for eggs and of 0.95 for all other age groups during winter (Briggs, 1965). During the breeding season, motionless eggs of *P. melanarius* are particularly sensitive to local changes in temperature and humidity and only 40% of eggs laid in fields reach the first larval stage (Brandmayr and Zetto-Brandmayr, 1979). Although better protected by a chitinous exoskeleton, the nymphs' prolonged immobility give them a lower transition rate than that of mobile larvae, and thus, we set transition probabilities to  $0.6^3 = 0.216$  for nymphs, to  $0.93^6 = 0.646$  for larvae (Brunsting et al., 1986) and to 0.985 for mobile adults (Larochelle, 1975a,b). Fecundity, expressed as the number of eggs laid per female, was set to 98 eggs per female per year (Hanse, 1990) assuming a balanced sex ratio (Tomlin, 1975; Desender et al., 1985). Following Lévesque and Pilon (1980) and Basedow (1994), fecundity rates were assumed to be similar for all crops in the study area (Table 1). We introduced two generic parameters (Pa and Pf) that would represent the differential demographic response of *P. melanarius* according to landscape composition: the parameter Pa decreases the value of

Table 1  
Values of the demographic and dispersal parameters and results of the sensitivity analyses of the demographic (A) and coupled (B) models expressed as elasticities (i.e. proportional changes in the population growth rate due to a proportional change in the values of a parameter)

Model parameters	Parameter value	Source	Elasticity												
<b>(A) Demographic</b>															
Breeding period (adult survival)	0.985	Lövei and Sunderland (1996)	0.135												
Winter period (eggs, larvae, nymphs survival)	0.95	Briggs (1965)	0.245												
Pa	0.997	–	0.376												
Pf (no fecundity in semi-natural habitats)	0	–	3.96E–05												
Pf (no differential fecundity between semi-natural habitats and crops)	1	–	1.52E–06												
	<table border="1" style="width:100%; border-collapse: collapse;"> <thead> <tr> <th colspan="2">Winter period</th> <th colspan="2">Breeding Period</th> </tr> <tr> <th>Parameter value</th> <th>Source</th> <th>Parameter value</th> <th>Source</th> </tr> </thead> <tbody> <tr> <td></td> <td>Elasticity</td> <td></td> <td>Elasticity</td> </tr> </tbody> </table>		Winter period		Breeding Period		Parameter value	Source	Parameter value	Source		Elasticity		Elasticity	
Winter period		Breeding Period													
Parameter value	Source	Parameter value	Source												
	Elasticity		Elasticity												
<b>(B) Coupled</b>															
Pf = 1															
Disp Field to Field	0.01		0.00E+00												
Disp Field to Semi-natural habitats	0.7	Estimated values	3.00E–04												
Disp Semi-natural habitats to Field	0.01		0.00E+00												
Disp Semi-natural habitats to Semi-natural habitats	0.01		0.00E+00												
			0.4												
Pf = 0															
Disp Field to Field	0.01		–2.63E–06												
Disp Field to Semi-natural habitats	0.7	Estimated values	2.17E–04												
Disp Semi-natural habitats to Field	0.01		4.67E–06												
Disp Semi-natural habitats to Semi-natural habitats	0.01		5.62E–03												
			0.4												

all age-dependent survival rates by a constant fraction in crops. We chose  $P_a = 0.997$  to obtain a population growth rate roughly equal to one that would qualitatively match the observed annual dynamics of *P. melanarius* in the study area. Using a constant  $P_f$  value would allow us focus exclusively on the relative effects of changes of landscape composition and configuration on population abundance and distribution (Fig. 4). In turn,  $P_f$  decreases the value of the fecundity in the semi-natural habitats. This value can vary between 0 (no fecundity in semi-natural habitats during the breeding period) and 1 (unchanged fecundity rates). In this study, changes in  $P_f$  value would allow us evaluate the importance of reproduction in semi-natural habitats on population dynamics for different densities of this type of habitat (Fig. 3).

### 2.3. Landscape models

The population dynamics of *P. melanarius* was studied in a series of realistic landscapes formulated for the polders of the Bay of Mont St. Michel (48°36'N, 1°32'W; NW France). This area currently consists of 283 ha of mainly intensive agriculture, with vegetables, cereals and corn being the dominant crops (35.6, 32.6 and 22.9% of the surface area) and other habitat types such as built areas, roads and hydrographical network (18%) and semi-natural habitats distributed along a dyke network (2%) cover the remaining surface. The average surface area of agricultural fields was  $\cong 0.3$  ha. Our study site is broadly representative of intensively managed areas elsewhere in France and Western Europe.

We used the L1 program (Gaucherel and Giboire, 2006) to generate a series of identically sized, patchy landscapes that differed in their composition (patterns of land use) or in the geometry (size or shape of fields and of other habitat types). For every landscape thus generated, we used three indices (review in Fortin et al., 2003) to characterize their structural composition and spatial configuration: (1) the relative composition (measured by the proportion of the total surface occupied by each crop and other habitat types), (2) the connectivity of each habitat type as measured by  $H_c = -\sum_{i=1}^n \sum_{j=1}^n p_{ij} \times (\ln(p_{ij})/2\ln(n))$  where  $p_{ij}$  is the probability that a field  $i$  is adjacent to another field of composition  $j$  and  $n$  the number of fields in the landscape, and (3) the cluster number denoting the number of contiguous fields in the landscape having identical type of land use.

We first assessed the effects of variation in landscape composition on population viability by generating a set of landscapes with an increasing semi-natural habitat density. Starting from the current (2005) landscape without semi-natural habitats, we considered landscapes having 0.015, 0.03 and 0.075 of their surface area as linear, semi-natural habitat. Four landscapes of different spatial configurations were generated for each of the three proportions of semi-natural habitats. Our second objective was to assess the effects of landscape configuration on population viability. In order to generate many landscapes with a high diversity of landscape configuration features, we worked on a cut-out of the real landscape and with a semi-natural habitats density fixed at  $\cong 5.25 \pm 0.25\%$ . This final dyke density, while higher than the real landscape, is still realistic and thus relevant in a conservation and management view. We generated 140 landscapes,

each of which was created following four types of realistic construction rules that yielded different spatial configurations of crops and semi-natural habitats. The first rule (circular) generated landscapes whose fields of annual crops were surrounded by semi-natural habitat. The second rule (linear) yielded landscapes in which semi-natural habitats were disposed along only one edge of each field of annual crop. According to the third rule (diagonal), semi-natural habitats were allocated as continuous patches along all fields of annual crops. In the last rule (localized), all patches of semi-natural habitats were localized in a specific zone of the landscape.

### 2.4. Coupling demographic and landscape models

The coupling between these models required establishing a set of explicit rules and rates of directional movement of individuals between patches according to the composition and spatial configuration of the local landscape. We assumed that adult dispersal and all demographic events take place at the same time scale and can be described for each habitat type at each time step. Dispersal of between contiguous plots was assumed to depend on the accessibility and shape of neighboring patches (e.g. Wiens and Schooley, 1997; Westerberg and Wennergren, 2003). In this study, we did not consider intra-field (or patch) dispersal as we focused on the movement of individuals between contiguous elements of the landscape. The proportion of individuals,  $\text{Disp}_{\text{in} \rightarrow \text{out}}$ , moving from a departure patch 'in' to an arrival patch 'out' per time step was determined by:

$$\text{Disp}_{\text{in} \rightarrow \text{out}} = \text{NbInd}_{\text{in}} \times \text{Disp} \times \text{LinCom}_{(\text{in}-\text{out})} \times \left( \frac{\text{Surf}_{\text{in}}}{\text{Surf}_{\text{out}}} \right) \quad (2)$$

where  $\text{NbInd}_{\text{in}}$  is the number of individuals of the patch in,  $\text{LinCom}_{\text{in}-\text{out}}$  is the proportion of the perimeter shared between fields (be they crops or semi-natural habitats),  $\text{Surf}_{\text{in}}$  and  $\text{Surf}_{\text{out}}$  are their surface areas, and  $\text{Disp}$  is the basal probability that an individual would leave a field; the values of the latter would reflect the influence of the landscape composition on dispersal between contiguous patches of different composition during the wintering and breeding periods (Thomas and Wratten, 1991; Thomas and Green, 1997). Working on *P. melanarius* in an agricultural landscape (Beauce, France) Fournier and Loreau (2002) found that individuals left a field and arrived to the adjacent one with probability of 0.7 over 2 days, and rebounded from the edge and remained in a patch with a probability of 0.3. We assumed that transition probability between adjacent fields during the breeding period was equal to 0.3, and the transfer rate between patches of semi-natural habitats during the breeding period equal to 0.4 in order to take into account the connectivity (Petit and Burel, 1998). Because carabids have a minimal activity rate during winter,  $\text{Disp}$  for all habitat types were set to 0.01, except for that of crop  $\rightarrow$  semi-natural habitats that was set to 0.7 to denote the reversal movement of individuals during winter (Table 1). The remaining parameters of Eq. (2) modulate the intrinsic movement rate  $\text{Disp}$ . The discontinuous way of walking of carabid beetles (Wallin and Ekblom,

1994) makes a change of direction after each stop very likely (Baars, 1979), and the probability of reversing the direction and remaining in the starting field (Firle et al., 1998) was an increasing function of the mean distance between the departure and arrival patches. The ratio of surfaces ( $Surf_{in}/Surf_{out}$ ) weights the dispersal rates whenever the surface area of the arrival field was smaller than that of the starting one. In order to have  $Disp_{in \rightarrow out}$  at time step  $(t + 1) > NbInd_{in}$  at time step  $(t)$ , we fixed  $(Surf_{in}/Surf_{out})$  equal to one if  $Surf_{in} > Surf_{out}$ , so that the product  $Disp \times LinCom_{in-out} \times (Surf_{in}/Surf_{out})$  could never be greater than one.

2.5. Model output

We simulated the coupled demographic and landscape models for 20 years (=720 time steps) using reflective borders for the overall landscape. The main model output was the population abundance in each patch over time and for each specific landscape considered. We also estimated the realized population growth rate as the ratio between consecutive population abundances, this variable being a relevant indicator of the population response to the landscape properties. Whenever a stable age structure was reached, the asymptotic population growth rate  $\lambda$  is calculated to assess the viability of the carabid beetle population. We evaluated the sensitivity of the asymptotic growth rate to changes of  $\pm 5, 10$  and  $15\%$  of the initial values of each of the demographic and dispersal parameters. Results of these analyses were expressed in terms of elasticity  $((d\lambda/\lambda)/(dpar/par))$  of the asymptotic growth rate to changes in each model parameter (par). While analytical methods of sensitivity analysis are well defined for non-spatial matrix models (e.g. Caswell, 2001), we had to numerically calculate the elasticities of our coupled demographic-landscape model involving dispersal. Unlike the elasticities of non-spatial matrix model (Caswell, 2001), it should be noted that those of the coupled demographic and landscape model need not add to unity.

Carabid beetles typically have an uneven spatial distribution between crops and adjacent semi-natural habitats that can harbor 95 and 5% of the total population at the middle of the breeding season (Wallin, 1985). Assuming an average density of 0.26 females/m<sup>2</sup> (Thomas and Green, 1997; Thomas and Parkinson, 1998), we set the starting densities to

0.285 females/m<sup>2</sup> in crops and 0.015 females/m<sup>2</sup> in semi-natural habitats for each of the landscapes.

3. Results

As expected, the modeled population initially increased over time and, after the spatial redistribution of individuals leading to a more homogeneous spatial distribution, it tended to level off by the 7th year of the simulation (Fig. 1a and b). The seasonal dynamics of all stages of *P. melanarius* showed a clear pulse of reproduction between May and October (Fig. 1a), with most individuals being concentrated in crop fields (Fig. 1b). During winter, there was an increase in the number of individuals in semi-natural habitats, which functioned as a sink from individual dispersal from neighboring crops.

The intrinsically asymmetric dispersal of individuals between crops and semi-natural habitats was substantially modified by the different compositions and spatial configurations of the landscapes considered. The main effect of changes in landscape configuration was a tendency of stronger dispersal from small crop fields whenever they were surrounded by several large-sized patches than when the former was surrounded by a large number of small patches. Population density maps (Fig. 2) showed a spatially heterogeneous distribution of individuals across the landscape and the concentration of carabids in semi-natural habitats during the winter period.

The elasticity analysis of the demographic model showed that the asymptotic growth rates were most sensitive to changes in adult survival during the breeding period, and of larvae, nymphs and adults survival during the wintering period (Table 1). To explore further whether the coupling between the demographic and the landscape models modified the sensitivity of the demographic model, we repeated the analyses for the coupled version for those parameters having the highest sensitivity in our previous analysis while keeping  $Pa = Pf = 1$ . The results showed that the coupling of the demographic and the landscape models had a rather minor effect on the elasticity of the growth rate: 0.0109 (uncoupled model) vs. 0.0135 (coupled model) for adults in activity; 0.0264 versus 0.0245 for larvae nymph adults in wintering (Table 1). Testing the sensitivity of the model to differential demography parameters ( $Pa$  and  $Pf$ ) showed that the

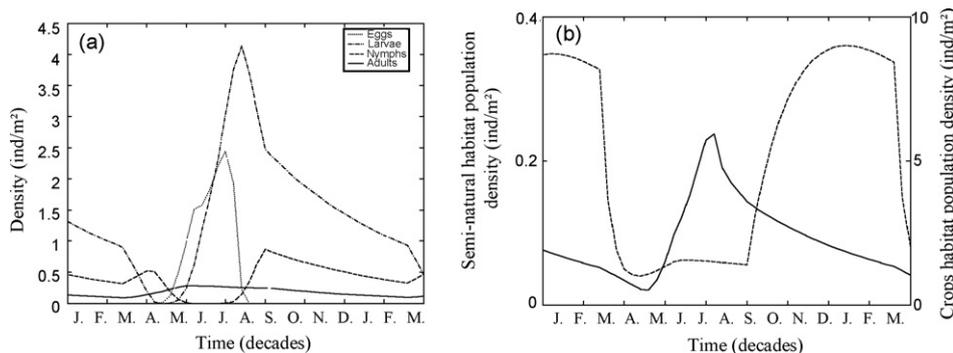


Fig. 1. Annual dynamics per months (shown as population density) of *Pterostichus melanarius* (simulation with  $Pa = 0.997$  and  $Pf = 0$ ). (a) By stage (eggs, larvae, nymphs, adults). (b) For adults in annual crop (continuous line) and semi-natural habitats (dotted lines).

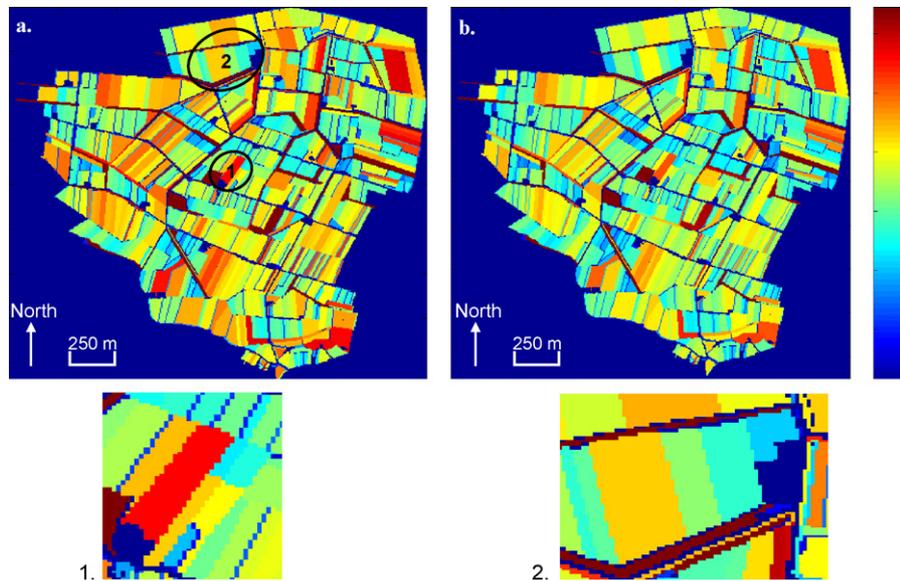


Fig. 2. Map of population density in landscapes of polders with a proportion of semi-natural habitats of 0.07 (simulation with  $P_a = 0.997$  and  $P_f = 1$ ). (a) 433rd time step (first 10 days of August). (b) 409th time step (first 10 days of February); red color for high population densities and blue color otherwise. Zoom 1 and 2: The main effect of landscape configuration was a tendency of stronger dispersal from small crop fields whenever they were surrounded by several large-sized patches than when the former was surrounded by a large number of small patches. Maximum density in bright red = 6 individuals/pixel  $\times 25\text{ m}^2$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

model was most sensitive when  $P_a$  was close to one and least sensitive whenever  $P_f$  was close to one and zero (Table 1). Sensitivity analyses were also made for the dispersal parameters using  $P_a$  and  $P_f$  values equal to one to avoid interference of differential demography, and with  $P_f$  value equal to zero. The results showed that the demographic model was rather insensitive to variation in the dispersal parameter  $Disp$  when there was no differential demography ( $P_f = 1$ ). However, model sensitivity to variation in the dispersal parameter  $Disp$  increased when there was no reproduction in semi-natural habitats. Dispersal between crops and semi-natural habitats were the most sensitive parameter among all dispersal parameters (Table 1).

Concerning the influence of landscape composition, the population asymptotic growth rates had a linear relation with the proportion of semi-natural habitats, but the slope was negative when there was differential fecundity (Fig. 3;  $P_f = 0$ ,  $r^2 = 0.94$ ,  $p < 0.01$ ), and positive in its absence ( $P_f = 1$ ,  $r^2 = 0.99$ ,  $p < 0.01$ ). A five-fold increase (0.015–0.075) in the proportion of the landscape occupied by semi-natural habitats led to a decrease in the population growth rate of 1.48% when there is a differential fecundity, and a small increase (0.67%) in the absence of differential fecundity. We observed that, for a group of landscapes roughly having the same semi-natural habitats density, the scatter of population asymptotic growth rate was higher with differential fecundity (Fig. 3).

We examined the influence of changes in landscape configuration on the population growth for a percentage of semi-natural habitats of  $5.25 \pm 0.25\%$ . We found that the asymptotic population growth rate generally increased with landscape connectivity (Fig. 4a). Of all rules of construction of semi-natural habitats, the circular and localized rules had the lowest values of the asymptotic population growth rate and their connectivity indices had larger scatter compared to those of the two other construction

rules. In contrast, the linear and the diagonal rules led to landscapes having similar connectivity values (equal to about 0.305). However, the diagonal rule leading to higher connectivity within the landscape was associated with the highest values of population growth rate, and to the largest number of crop fields being in contact with semi-natural habitats. We found a non-linear relation between the cluster number and the population growth

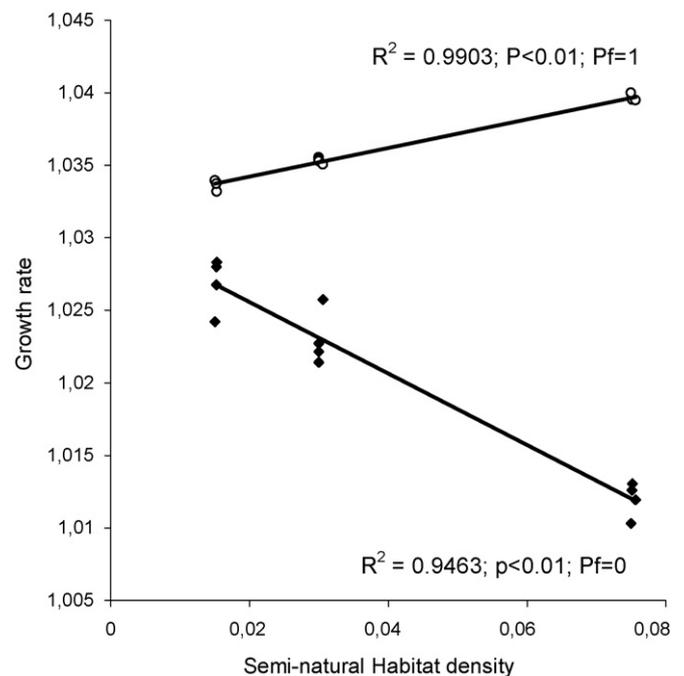


Fig. 3. Asymptotic population growth rates in relation to the proportion of semi-natural habitat in the landscape without differential fecundity ( $P_f = 1$ ; open dots) and with no fecundity ( $P_f = 0$ ; filled dots) in semi-natural habitats.

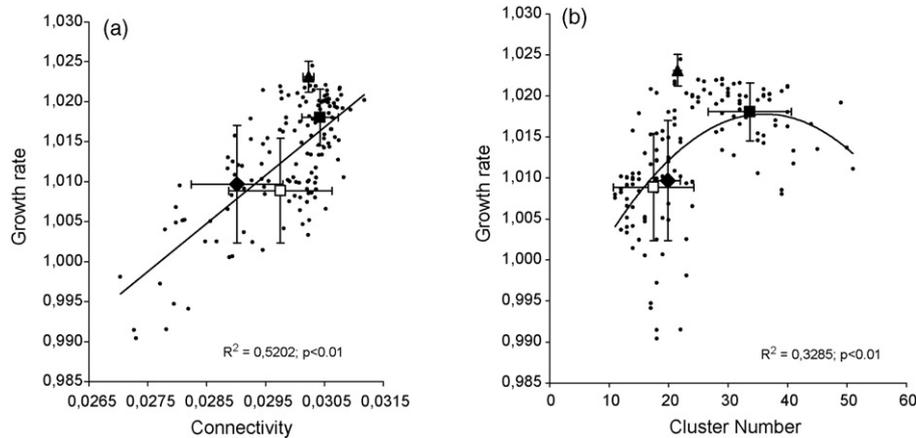


Fig. 4. Asymptotic population growth rates in relation with (a) landscape connectivity and (b) number of clusters. Circular rule (◆); linear (■); diagonal (▲); localized (○). All simulations were done with  $P_a = 0.997$  and  $P_f = 0$ . Error bars correspond to mean standard deviations of each landscape type.

rate, with the latter being higher for an intermediate value of cluster number ( $r^2 = 0.33$ ,  $p < 0.01$ ; Fig. 4b). The circular and localized rules led to landscapes that had a lower cluster number (i.e. shorter dispersal paths of like habitat) than the linear rule. Semi-natural patches generated according to the linear rule were more isolated patches those obtained with the diagonal rule. Landscapes constructed with the diagonal rule had intermediate cluster number and the highest asymptotic population growth rate values.

#### 4. Discussion

The demographic model and the coupled demographic-landscape model had similar sensitivities to changes in the values of demographic parameters, thus suggesting that these components of the overall model can be analyzed as largely independent modules. The minor sensitivity of the dispersal parameter (Disp) suggests that the uncertainty about the magnitude of the dispersal probability is unlikely to affect the asymptotic growth rate of the coupled model. Induced by our dispersal function (Eq. (2)), the trend of stronger dispersal from small to large patches is in accordance with Turchin's (1986) observations and models that predict that beetle emigration rate should decrease with patch size. On the other hand, local demography had the main role in governing the dynamics and population viability of *P. melanarius* in all landscape configurations considered. The high sensitivity of the population growth rate to changes in  $P_a$  (the differential survival between crop fields and semi-natural habitats) highlights the key role of semi-natural habitats in the annual population dynamics of this species. Although  $P_a$  affected all age classes with a same intensity, this parameter could be useful to predict the consequences of management actions in the agricultural fields and of other environmental perturbations (i.e. polder floods, drought) having differential effects on agricultural fields and semi-natural habitats. A detailed work is in progress to decompose the  $P_a$  role into the effects of other external factors such as the agricultural activities in fields.

A high proportion of semi-natural habitat can be harmful for the population viability of *P. melanarius* whenever fecundity

in this type of habitat is very low: an increase over a value of about 1.6% (the current proportion of the study site covered by dykes) leads to a decrease of the asymptotic growth rate. The influence of the landscape composition on the population growth rate was shown by the progressive addition of patches of semi-natural habitats that had a positive impact on population growth provided that fecundity did not differ between crops and semi-natural habitats. Adding patches of semi-natural habitat leads therefore to a predictable increase in population growth rate (Fig. 3). Non-perturbed habitats such as the hedgerows in agroecosystems are in fact considered as refuge for *P. melanarius* and other predators and the advantages of their preservation in the open landscapes is widely recognized (Fournier and Loreau, 2001a; Lys and Nentwig, 1992). Whenever fecundity in semi-natural habitats is low, the latter habitat functions as a population sink wherein higher local survival cannot compensate for the lower recruitment from individuals dispersing from these habitats to the remaining landscape. The change in sign of the relationship between the population growth rate and the proportion of semi-natural habitat highlights the key role of the differential fecundity between crops and semi-natural habitats (Fig. 3). Because the fecundity rate in the semi-natural habitats plays an important role on the viability of the population, a more accurate estimation of this parameter in field conditions would be needed in order to control the potentially harmful effect for populations of adding semi-natural habitats to an agricultural landscape.

Based on our results, we think that there is an optimal cluster size of patches for population viability certainly that is induced by the seasonal movement of *P. melanarius* in intensively managed agricultural landscapes. The influence of landscape configuration was demonstrated by comparing a set of landscapes having an equal proportion of semi-natural habitats and different spatial configurations. The main consequence of changing landscape configuration on population growth was a significant increase of the latter with increasing landscape connectivity, which is in agreement with previous results (e.g. Burel, 1989; Fahrig and Merriam, 1985; Söndgerath and Schröder, 2002). The presence of diagonal semi-natural habitats allows

increasing connectivity in landscapes having identical compositions because it enhances dispersal in the landscape during the breeding period through a continuous network of patches of the same type. A decrease in the connectivity of semi-natural habitats may explain the differences in population growth rate between linear and diagonal landscapes because the continuous patches of semi-natural habitat in the landscape (characterized by an intermediate cluster number) allow individuals to remain inside sheltered habitats during the wintering period. Population viability, being particularly dependent of the seasonal movement of individuals between fields of annual crops and semi-natural habitats, was strongly affected by changes in the spatial configuration of semi-natural habitat and especially by its degree of clustering. The latter two features need to be taken into account in the management actions destined to preserve populations of carabid beetles in intensively managed agricultural habitats.

We proposed a spatial population dynamic model that explicitly considers the composition and spatial configuration of a landscape. Relatively little work including as many components of landscape structure at this spatial level has been published up to now (see Murrell and Law, 2000). We used this model to assess the influence that alternative changes in landscape structure and composition resulting from different habitat management options could have on population viability. A main output of our model is population density maps over time (Fig. 2) that constitutes an efficient and often used tool for the population distribution analysis. An adjustment and a calibration of the dispersal function with an experimental field study should allow highlighting sensible zones of the landscape where changes in structure and/or configuration would induce important changes in population dynamics. A drawback of the proposed model is the computing time needed for coupling the demographic and landscape models, with the limiting factor being the number of fields and patches of semi-natural habitats in the landscape that determine the dimension of the coupling matrices. Another extension of our model is to couple the dynamics of landscape composition and configuration with that of the target population in order to test one of Fahrig's (1992) conclusion (see also Keymer et al., 2000; DeWoody et al., 2005), namely that resident populations are more affected by the rate of change in landscape composition than by the composition itself. While our coupled model may not account for the full complexity of the landscape structure and dynamics, it provides a theoretical basis that will help understand the effects of changes in landscape attributes (composition and configuration) on population dynamics that is necessary to predict trends in abundance and spatial distribution of populations in response to landscape modifications resulting from changes in agricultural practices.

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