

Assessing the effect of habitat fragmentation on population dynamics: An implicit modelling approach

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Abstract

To better understand the impact of habitat fragmentation on population dynamics at the landscape scale, we develop a model combining a spatially implicit landscape model, a multisite Leslie-type model and an implicit model of habitat fragmentation. The studied species (*Abax parallelepipedus*, Coleoptera: Carabidae) is a corridor forest insect sensitive to wood fragmentation. The population of *A. parallelepipedus* was divided into three stages and move in the landscape between four classes of elements: wood, lane bordered by two hedgerows, hedgerow and agricultural matrix. The landscape representation was supposed to be implicit and the four classes of elements were randomly distributed in space. The originality of this approach is that we fit the movement frequency between elements according to woodland forest fragmentation. When wood fragmentation increases, the movement process can be very frequent and the method of aggregation of variables allows us to simplify the analysis of the model. Outputs of the model include the asymptotic population growth rate, stable stage structure and asymptotic spatial distribution that allow comparison of the influence of different spatial scenarios of wood fragmentation on population dynamics. Our results indicate that a single large patch of wood is better than several small patches of wood for population viability, that hedgerows have negative effects on population viability but lanes border by two hedgerows have positive effects even if they are randomly distributed at the landscape scale. When wood fragmentation is important, hedgerows create a population drain in woods and individuals pass and die more frequently in agricultural matrix.

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1. Introduction

Landscapes (“heterogeneous land area composed of cluster of interacting ecosystems” [Forman and Godron, 1986](#)) are heterogeneous and dynamic. The way quality and spatial structure of landscapes evolved since 1950s increases risk of extinction of a large number of species,

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by various human activities (alterations of human land use pattern, industrial activity, and intensive agriculture) or natural disturbances. Habitat fragmentation is one of the major causes of this biodiversity erosion (Soulé, 1987; Burel and Baudry, 2003; Fahrig, 2003). In this context, specialist species, that is, those using only one landcover type, have been abundantly studied because they are sensitive to habitat fragmentation (Farina, 1998).

Metapopulation models are well suited to assess the effect of habitat loss and breaking apart of habitat on the local and regional population dynamics (Lebreton and Gonzalès-Dàvila, 1993; Hanski and Simberloff, 1997; Caswell, 2001; Morris and Doak, 2003; Fahrig, 2003). However, some effects of the spatial landscape structure on the metapopulations cannot explicitly be studied via metapopulation models (Wiens, 1997): they do not explicitly consider effects of neighbouring elements (e.g. element: distinct ecosystems that make up a landscape) on characteristics and dynamics of a particular patch of “suitable element” (i.e. “habitat”), they cannot assess the impact of boundaries on movements of organisms and processes both within and between elements. Finally, they cannot consider effect of spatial and temporal variation of element quality on population dynamics. In this context, spatially explicit population models (SEPMs: see Dunning et al. (1995) for definition and applications) allow considering spatial heterogeneity in its continuity and its complexity. They are designed for specific landscapes, but results are difficult to transfer to other types of landscapes. On the other hand, some spatially implicit population models (SIPMs) allow identifying general patterns linking population and landscape, at the expense of losing accuracy on the description, understanding of processes changing with spatial structure (Levins, 1969; Pulliam, 1988; Pulliam and Danielson, 1991; Doak et al., 1992; McKelvey et al., 1993; Bascompte and Solé, 1996). So in order to assess the response of a population according to habitat fragmentation, we have developed a generic model that combines an implicit landscape model, a multisite Leslie-type model and an implicit model of habitat fragmentation. The model of habitat fragmentation is divided in two sub-processes: habitat loss and breaking apart of habitat (habitat fragmentation per se) (Fahrig, 2003). This distinction allows determining “how much habitat is enough?” (Fahrig, 2001) or for a given proportion of habitat, what kind of

spatial management must be maintained: a single large or several small (SLOSS) patches of habitat? (McCoy, 1983; Simberloff, 1988). The goal of this study is also to assess demographic and spatial consequences of habitat fragmentation. We present an application to a corridor forest species sensitive to woody element fragmentation at the landscape scale (Burel, 1989; Petit and Burel, 1998a) *Abax parallelepipedus* (Coleoptera: Carabidae). We finally discuss the relative applicability of our modelling approach in comparison with other models of population dynamics that consider landscape components for a modelling point of view: we propose to quantitatively assess for a species the spatial conditions for which a particular model is better designed to assess population dynamics (a simple non spatial model, a metapopulation model with or without cost of dispersal, or other more explicit population models as grid cells models).

2. Material and methods

2.1. Biology of *A. parallelepipedus*

A. parallelepipedus (Coleoptera: Carabidae) is a common apterous insect of the temperate forests in Europe (Chaabane et al., 1996) and Eastern Canada (Lindroth, 1961–1969; Spence, 1990). Adult length ranges from 16 to 22 mm. It lives under bracken (Buse, 1988), in moss, on clusters of dead leaves and stones (Du Chatenet, 1986). *A. parallelepipedus* belongs to the group of corridor forest species (Burel, 1989; Charrier et al., 1997) and may be considered as an “indicator” of the evolution and fragmentation of woody habitats in landscapes. Petit and Burel (1998b) showed that *A. parallelepipedus* can be considered to have a metapopulation structure in the agricultural landscape in Brittany. Previous works on *A. parallelepipedus* population dynamics in agricultural landscapes showed that this species prefers woody habitat (Burel, 1989; Petit and Burel, 1993; Petit, 1994; Fournier and Loreau, 2001; Martin et al., 2001). It also uses hedgerows and lanes bordered by two hedgerows as corridors for movement. The individuals may even penetrate into the agricultural matrix (for example cornfields), where their mortality rate is high. *A. parallelepipedus* may live more than 3 years (Loreau, 1990; Chaabane et al., 1996). Adults are active from April

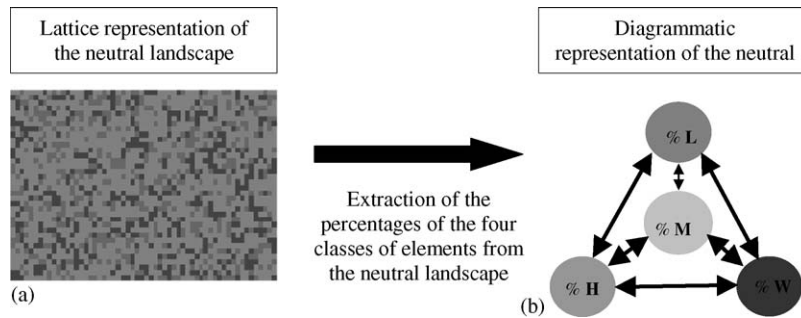


Fig. 1. Lattice (a) and diagrammatic (b) representation of a neutral landscape by using four classes of habitats: M for the agricultural matrix, H for the hedgerows, L for the lanes and W for wood. The four classes of habitats are supposed to be randomly distributed. Arrows between compartments represent the movement process between the four types of elements.

to October (Greenslade, 1965; Loreau, 1985), and during this period disperse in the landscape. After that, they hibernate from November to March. Egg laying was observed in the second year of adults only after hibernation. Females lay on average 12 eggs from April to October in woods (Chaabane et al., 1996, 1997). Because emergence of new adults was observed in lanes (Petit, 1994) and because variance of fecundity is not important in woody environment (Chaabane et al., 1996, 1997), we assume fecundity identical in lanes and in woods. No eggs, larvae or emergence of new adults were observed in hedgerows or in cornfields (Petit, 1994). Although, few field data exist on its survival, we assume that survival also depends on the type of elements and is the same in woods, lanes, hedgerows and lower in cornfields (Petit, 1994; Chaabane et al., 1996, 1997; Charrier et al., 1997; Tischendorf et al., 1998).

2.2. The mathematical model

We combine an implicit landscape sub-model with a multisite Leslie-type model and an implicit sub-model of habitat fragmentation. The three sub-models and their connections are described below:

2.2.1. The landscape model

In agricultural landscapes, agricultural matrix (e.g. further denoted as M), hedgerows (H), lanes bordered by two hedgerows (L) and woodlands (W) are distinguished for description of *A. parallelepipedus* movement and demography. We use an implicit representation of a landscape having an infinite surface, where the

four landcover types (i.e. “elements”: W, L, H and M) are randomly distributed in space (Fig. 1). We assume that the relative proportion of the four types of elements can describe this type of landscape.

2.2.2. The model of population dynamics

2.2.2.1. The demographic sub-model. We construct a “partial life cycle” for *A. parallelepipedus* that summarizes the population demography in each element (see Fig. 2a and b). Caswell (2001) and Oli (2003) recall the

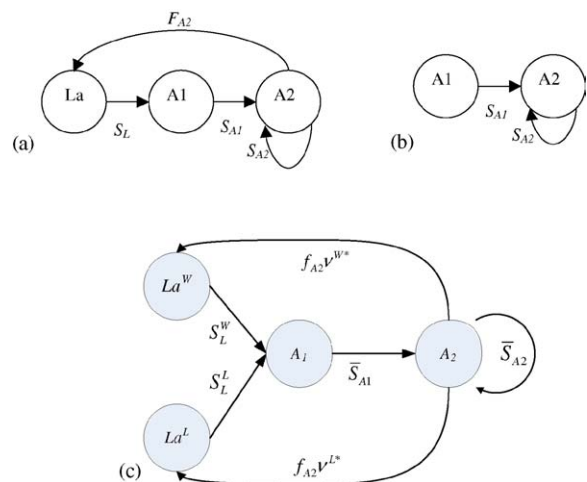


Fig. 2. Life cycle of *A. parallelepipedus* in element W and L (a), or in M and H (b): parameters describe survival and fecundity of the complete model; movement parameters are not described in this figure. Figure (c) represents the new aggregated life cycle for the fast dispersing stages: the new parameters describes the spatial aggregation of the demographic parameters (demographic parameters are pondered by the movement parameters when movement between elements are sufficiently frequent to aggregate the model).

good approximation and the usefulness of the partial demographic approach. *A. parallelepipedus* life span is divided into three stages: larval instars (La) and two adult stages (A₁: non-breeders, and A₂: breeders). Each stage lasts 1 year on average, and this time is used as the time unit for the Leslie-type model.

Transition probabilities between these three different stages are the life-history rates of the species (fertility and survival rates). They are defined for the time step of the model (1 year). Survival rates are relatively identical between females and males (Loreau, 1990). We assumed all vital rates to be density-independent.

- *f-fecundity*. Because reproduction occurs from April to October, fecundity is defined as a function of “maternity function”, A₂-survival and survival rate from egg-stage to larval-stage (see Caswell, 2001). Females lay on average 12 eggs from April to October, and 3 weeks after emerging of hibernation. Sex ratio is on average 1:1 (Chaabane et al., 1996). *Fecundity parameter* is defined as follows:

$$f_{A_2} = \sqrt{s_{A_2}} \times m \times \sqrt{s_0} = \sqrt{0.45} \times \frac{12}{2} \times \sqrt{0.6} = 2.81$$

with s_{A_2} the survival rate of breeders A₂ ($s_{A_2} = 0.45$ defined in Loreau (1990)), s_0 the survival rate from egg to first instars and m is the maternity function: e.g. number of female offspring per female ($s_0 = 0.6$ defined in Chaabane et al. (1997)). Chaabane et al. (1997) showed a relatively good stability of the maternity function in different experimental conditions.

- *s_jⁱ-survival rate*. It is defined as the proportion of individuals belonging to stage j which survive from stage j to stage $j+1$ in element i , where $j \in \{\text{La}, A_1, A_2\}$ and $i \in \{\text{W}, \text{L}, \text{H}, \text{M}\}$. Survival rates are summarized in Table 1. Those from W were taken from Loreau (1990) and Chaabane et al. (1996), those for L from Petit (1994). High survival of larvae in W and L can be justified by their great resistance and their low density that reduce predation risks (personal communication with Loreau). For H, no quantified survival data were available, so we assume that adult survival rates in H are the same as in W and L. For M, we used survival rates in cornfield (Charrier et al., 1997; Tischendorf et al., 1998): they are extremely low in comparison with those in other elements.

Table 1

Survival rates and fecundity for each stage in each element of the landscape

Elements	Stages		
	L	A ₁	A ₂
Fecundity			
M	0	0	0
H	0	0	0
L	0	0	2.81
W	0	0	2.81
Survival			
M	0	0	0
H	0	0	0
L	0.5	0.45	0.45
W	0.5	0.45	0.45

Let \mathbf{L} be the Leslie block matrix of the demographic model. Because \mathbf{L} integrates all demographic parameters for each stage in each element, the dimension of the model is (10×10) , and \mathbf{L} is defined as follows:

$$\mathbf{L} = \begin{pmatrix} 0 & 0 & F_{A_2} \\ S_{La} & 0 & 0 \\ 0 & S_{A_1} & S_{A_2} \end{pmatrix} \quad (1)$$

with $F_{A_2} = \text{diag}[f_{A_2}, f_{A_2}]$ the block matrix of fecundity, $S_j = \text{diag}[s_j^W, s_j^L]$ is the block matrix of survival from larval to adult and $S_j = \text{diag}[s_j^W, s_j^L, s_j^H, s_j^M]$ are the bloc matrices of survival for adults, $j \in \{A_1, A_2\}$.

2.2.2.2. The movement sub-model. We call d_{ik} the movement coefficient representing the proportion of individuals present in element of type k and moving toward the element of type i , where $0 \leq d_{ik} \leq 1$. The diagrammatic landscape model (Fig. 1) allows us to simplify the movement process, and is represented here as a combination of two processes:

- *Movement within an element right up to its boundary*: we assume that between two time steps t and $t+1$, an individual being in element k at time t and moving randomly within this element meets a boundary between k and i at a rate proportional to p_i . If the proportion of one type of landscape element i is abundant, an individual moving randomly in the landscape will often encounter it.
- *Boundary behavior*: we denote q_{ik} as the probability of an individual leaving the element of type k at the boundary and going towards element of type

Table 2
Transition coefficients q_{ij} from the element (cell) of type j (line) towards the element (cell) of type i (column)

	W	L	H	M
W	1	0.5	0.5	0.05
L	0.5	1	0.5	0.1
H	0.5	0.5	1	0.2
M	1	1	1	1

i : q_{ik} is assumed to be independent of the stage j and $0 \leq q_{ik} \leq 1$. The parameters q_{ik} were measured experimentally (Petit, 1994; Martin et al., 2001; and personal unpublished data). These values are given in Table 2. These parameters show that beetles stay preferentially in suitable elements (W, L and H), that they leave M to go towards W, L and H and that they have the same probability to be in W, L and H because they are not sensitive to boundaries between woody elements (Petit, 1994).

The proportion of dispersers, d_{ik} , from the element k towards element i is supposed to be proportional to the parameters q and p , and for the implicit landscape representation (see Section 2.2.1) d_{ik} can be defined as follows:

$$d_{ik} = q_{ik} p_i \quad (2)$$

Let I be the identity matrix of dimension (2×2) for larval stage in W and L. We assume that stage 1 and 2 adults disperse in a similar way. Let P_A the block matrix for the dispersing stage $\{A_1, A_2\}$. We give the formulae:

$$P_A = \begin{pmatrix} 1 - d_{LW} - d_{HW} - d_{MW} & d_{WL} & d_{WH} & d_{WM} \\ d_{LW} & 1 - d_{WL} - d_{HL} - d_{ML} & d_{LH} & d_{LM} \\ d_{HW} & d_{HL} & 1 - d_{WH} - d_{LH} - d_{MH} & d_{HM} \\ d_{MW} & d_{ML} & d_{MH} & 1 - d_{WM} - d_{LM} - d_{HM} \end{pmatrix} \quad (3)$$

Therefore, we define $P = \text{diag}[I, P_A, P_A]$ as the (10×10) movement matrix of the movement model. P represents the complete process of movement.

2.2.2.3. The multiregional Leslie-type model. We use a classical multisite Leslie model (Rogers, 1966; Lebreton and Gonzalès-Dàvila, 1993; Caswell, 2001) describing the *A. parallelepipedus* population dynamics. This type of model is represented such that:

$$\vec{n}_{t+1} = L P \vec{n}_t \quad (4)$$

where $\vec{n}_{j,t}^i = (\vec{n}_{L,t}, \dots, \vec{n}_{A_2,t})^T$ is a 10-dimensional vector giving the number of individuals of stage j in element i at time t (if $j \in \{L\}$ then $i \in \{W, L, H, M\}$, or if $j \in \{A_1, A_2\}$ then $i \in \{W, L, H, M\}$).

2.2.3. The model of habitat fragmentation

2.2.3.1. The complete model of population dynamics with different time scales. We model habitat fragmentation as a landscape-scale process involving both habitat loss and the breaking apart of habitat (i.e. habitat fragmentation per se) (Fahrig, 2003). First, W loss is measured with p_i -parameter in (Eq. (2)). In addition, we consider not only breaking apart of W but also breaking apart of all types of elements in the landscape. This process increases the probability that an individual encounters a boundary between two elements, so it increases the movement frequency between adjacent elements. For an individual, let k define the number of transition from one element to another for one demographic time unit (1 year). To distinguish between these two time scales, a modification of Eq. (4) has been proposed (Sanchez et al., 1995):

$$\vec{n}_{t+1} = L P^k \vec{n}_t \quad (5)$$

The model allows adjusting movement frequency between adjacent patches of elements: k is applied to all elements, but because habitat fragmentation per se is a landscape scale process (Fahrig, 2003), k can also

represent a measure of “W-fragmentation per se”: so when k increases, the more important is W-fragmentation per se. The combination of these two sub-processes governed by the k - and p_i -parameters leads to a good approximation of the relationship between the degree of W-fragmentation and the movement response at the landscape scale.

This implicit modelling approach suggests a particular case of the spatial structure, where the different elements are randomly distributed on the lattice (see

Fig. 1). This representation assumes that each type of patch of element interacts equally with any other type of patch of element, that the explicit arrangement of patches has no effect on the results, and that such models tell us nothing about how explicit spatial arrangement of habitat destruction effects a population. However, being the result of economic exploitation and social and environmental constraints, agroecosystems are clearly not randomly structured, and H are linear elements. However, considering H and the agricultural landscape as random structures can be very useful as a first approximation to focus on the role of the element quality and boundaries. Our model can be thus defined as a “ H_0 -hypothesis” that can be compared to other models where the spatial structure is explicitly integrated (see Hill and Caswell (1999) for a similar example).

2.2.3.2. The aggregated model. The aggregation of variables method (Simon and Ando, 1961; Iwasa et al., 1987; Auger and Poggiale, 1998) is designed to approximate a fast dynamical system involving many variables into a reduced system described by a few number of global variables. Bravo De La Parra et al. (1995) mathematically proved the feasibility of this method for multisite population dynamics, provided that the LP^k -matrix (Eq. (5)) is primitive, e.g. the Perron–Frobenius theorem applied. Some non-exhaustive examples describe potentialities and usefulness of this method in an analytical point of view for ecological studies: for metapopulation dynamics (Charles et al., 2000), for prey–predator dynamics (Auger et al., 2000), for Game-theory (Pontier et al., 2000), for food chains dynamics (Kooi et al., 2002), for bioeconomical control (Mchich et al., 2002). Here we also show the feasibility of this methods for multisite studies at the landscape scale when one stage (Larvae) did not move through space. We apply this method to simplify the analysis of the complete system described by (Eq. (5)). The gist of the aggregation of variables method is:

- Let $N_{j,t}$ be the aggregated variable defining the total number of individuals of each dispersing stage:

$$N_{j,t} = \sum_{i \in \{W,L,H,M\}}^4 n_{j,t}^i \quad \text{with } j \in \{A_1, A_2\} \quad (6)$$

- Let I be the dimension 2 identity matrix and $\mathbf{1}$ be a row-vector of dimension 4 with all the entries equal to 1, and let $U = \text{diag}\{I, \mathbf{1}, \mathbf{1}\}$ be the “aggregation matrix” of dimension (4×10) . The aggregated vector is

$$\vec{N}_t = [\vec{n}_{L,t}^W, \vec{n}_{L,t}^L, \vec{n}_{A_1,t}, \vec{n}_{A_2,t}]^T \quad (7)$$

where \vec{N}_t is a vector of dimension 4 whose components are either the total number of individuals in each dispersing stage, or the number of individuals in each type of elements of each non-dispersing stage. When W -fragmentation increases, the movement process can be very frequent between different elements, and when k tends to infinity the movement dynamics at the landscape scale tends to a stable equilibrium characterized by constant proportions of individuals on element i , noted, v^{i*} with:

$$n^{i*} = v^{i*} n \quad \text{and} \quad \sum_i v^{i*} = 1 \quad (8)$$

where $\vec{v}^{i*} = (v^{W*}, v^{L*}, v^{H*}, v^{M*})^T$ is the vector describing the proportion of individuals of a stage in the population. At this stable equilibrium, the complete model (Eq. (5)) can be replaced by an aggregated one (Eq. (9)) which governs the aggregated variables for each stage:

$$\vec{N}_{t+1} = \bar{L} \vec{N}_t \quad \text{with } \bar{L} = UL\bar{P}_c \quad (9)$$

where $\bar{P}_c = \text{diag}\{I, v_{A_1}^*, v_{A_2}^*\}$ is a matrix of dimension (10×4) . \bar{P}_c integrates the movement frequencies on the fast equilibrium where $\lim_{x \rightarrow \infty} P^k = \bar{P}_c U$.

The matrix \bar{L} is a (4×4) primitive Leslie-type matrix with constant transition coefficients:

$$\bar{L} = \begin{pmatrix} 0 & 0 & 0 & f_{A_2} v^{W*} \\ 0 & 0 & 0 & f_{A_2} v^{L*} \\ S_L^W & S_L^L & 0 & 0 \\ 0 & 0 & \bar{S}_{A_1} & \bar{S}_{A_2} \end{pmatrix} \quad (10)$$

with the blocks of survival defined as $\bar{S}_{A_1} = \sum_i S_{A_1}^i v_{A_1}^{i*}$ and $\bar{S}_{A_2} = \sum_i S_{A_2}^i v_{A_2}^{i*}$.

Therefore, the method consists of a “spatial aggregation” of the fast dispersing stages. The new aggregated life cycle is represented by Fig. 2c.

2.2.4. Model analysis

Construction and analysis of the model was performed using Maple 7[®]. The model can be analytically processed through population-level endpoints of the matrix LP^k or \bar{L} : the dominant eigenvalue of the matrix, λ is an estimate of the overall asymptotic population growth rate. We also performed the asymptotic demographic structure and the asymptotic spatial structure of the population from the right eigenvector, \vec{w} , associated with λ (Caswell, 2001). We denote as $\bar{\lambda}$ the new eigenvalue and as $\vec{\bar{w}}$ the new eigenvector of the aggregated model. Bravo De La Parra et al. (1995) showed that the complete and aggregated models have the same dominant eigenvalue and the same eigenvectors when k tends to infinity. The use of the aggregated model allows us in certain conditions to simplify the analysis of the study for different landscape managements corresponding to an increase of W-fragmentation. We first build a pilot study that just includes W and C. We then compare this study with three others where landscapes have 5% of H, or 5% of L or 5% L and 5% H. Comparison of these four studies must give some information on the importance of H and L on the population viability according to W-fragmentation.

3. Results and discussion

3.1. Study of the convergence of the complete model toward the aggregated model

We choose to define an acceptable threshold of convergence of the complete model to the aggregated one at 5% (see Fig. 3). Results show that this ratio evolves according to degree of W-fragmentation. To aggregate the model, k must be higher when the percentage of W decreases. The four studies show that the more significant diversity of elements is in a landscape and the higher is fragmentation per se and percentage of W, the more possibilities of aggregation of the model are significant according to the degree of W-fragmentation (Fig. 3). When there are only W and M in the landscape, the model cannot always be aggregated either when the percentage of W or k -value is weak (Fig. 3a). For landscapes where there are 5% of H, the possibility of aggregating the model does not really change in comparison with landscapes without H (Fig. 3b). For landscapes where there are 5% of L the possibilities of aggregation are superior according to W-fragmentation and the model can always be aggregated when $k = 24$

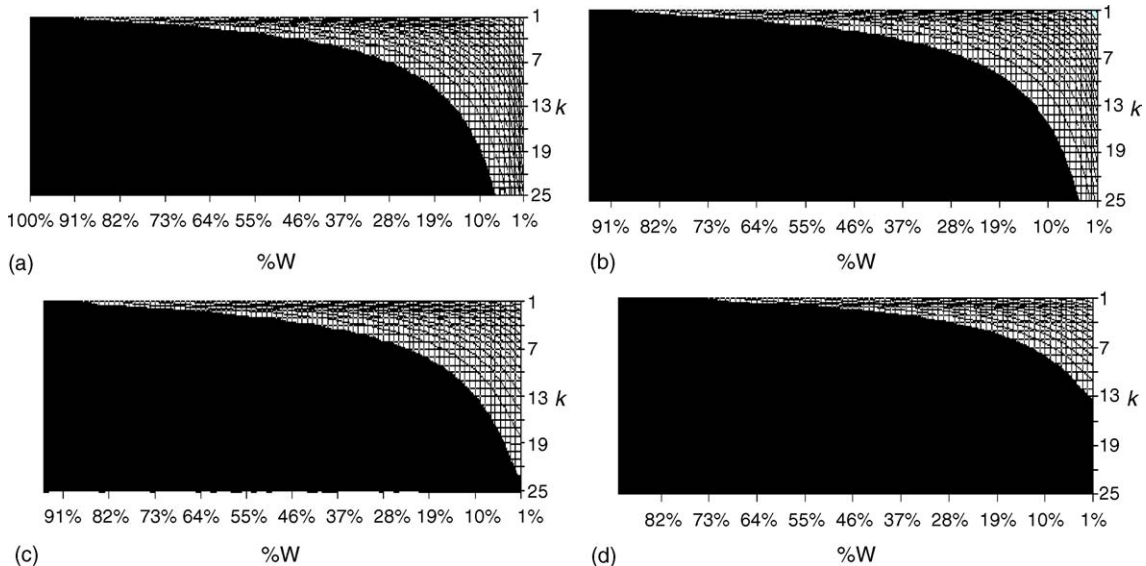


Fig. 3. Evolution of the ratio $\bar{\lambda}/\lambda$ according to W-fragmentation, for landscapes where there are only W and M (a), W and M with 5% of H (b), W and M with 5% of L (c), and W and M with 5% of H and 5% of L (■, $\bar{\lambda}/\lambda \geq 95\%$: population increases; □, $\bar{\lambda}/\lambda < 95\%$: population extinction).

(Fig. 3c). More complex landscapes where there are all the four elements (5% of L and 5% of H) always allow us simplifying the model when $k \geq 13$. $k = 13$ means that there are on average 1.5 transitions by month (between March and November: the period of activity) from one element to another adjacent element in the landscape. 1.5 transitions by month on average can be a realistic movement pattern in a landscape for *A. parallelepipedus*.

3.2. Effects of the landscape fragmentation on population level endpoints

At a patch scale, λ would be equal to 1.06 in W and L. In H or M, it would be equal to 0. These two λ -values are used as extreme-values compared to those obtained at

the landscape scale for scenarios of W-fragmentation. At the landscape scale, our results show that *A. parallelepipedus* population viability is sensitive to W-fragmentation, that this sensitivity is nonlinear and that there are critical thresholds of W-fragmentation depending on W-loss and W-fragmentation per se (Fig. 4). The pilot study (see Section 2.2.4) shows that W-fragmentation has a negative impact on λ (Fig. 3a). Distinction between W-loss and W-fragmentation per se shows that if woodlots cover more than 33% of a landscape, W-fragmentation per se has not significant effect: the population is viable and sensitivity of λ to W-fragmentation (first derivative of eigenvalue, e.g. tangent of the eigenvalue curve) is quasi-null, so the spatial context (M and fragmentation) around W-patches is not important for the population demography. For a

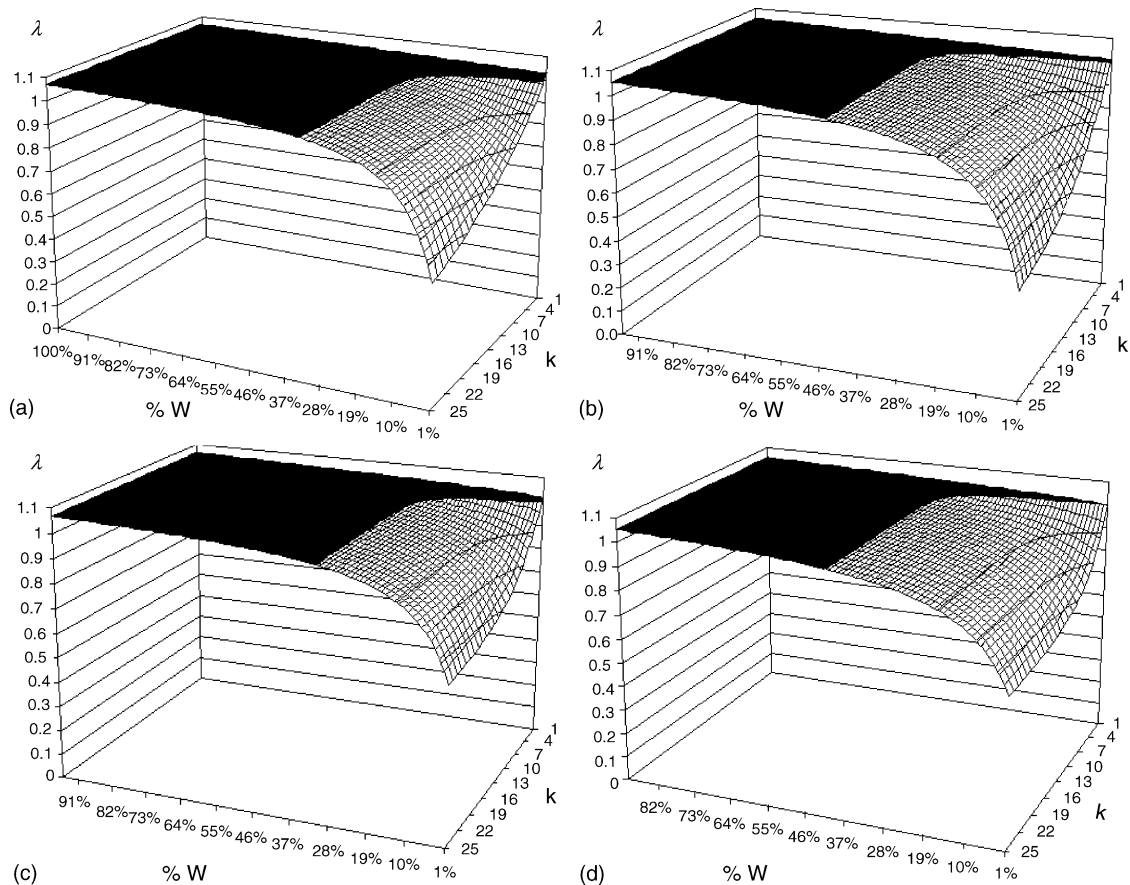


Fig. 4. Effect of W-fragmentation on asymptotic population growth rate (λ), for landscapes where there are only W and M (a), W and M with 5% of H (b), W and M with 5% of L (c), and W and M with 5% of H and 5% of L (d). (■, $\lambda > 1$: population increases; □, $\lambda < 1$: population extinction).

very low degree of W-fragmentation, individuals do not leave W, therefore the overall population growth rate is almost the same as in W: $\lambda = 1.06$. Below 33% of W, effect of W-fragmentation on population viability depends on degree of W-fragmentation per se. When there are only one single large patch of W ($k = 1$) population is viable but sensitivity of λ to W-fragmentation per se is important (first derivative of eigenvalue is not null). When there are several small patches (k tends to 25: e.g. W-fragmentation per se is important) population is not viable and sensitivity of λ to W-loss increases exponentially (i.e. population viability decreases exponentially). Fig. 4b shows that when W-fragmentation increases, H has a negative, while L a positive effect on *A. parallelepipedus* population viability and sensitivity

of λ . For landscapes with 5% of H the critical threshold of W-loss increases to 44% when W-fragmentation per se is a little bit important. Above 44% of W, sensitivity of λ to W-fragmentation is not important, so the spatial context (M, H and fragmentation) around W-patches is not important for population demography. Instead of H, 5% of L decreases the critical threshold of W-loss to 30% (Fig. 4c). When there are 5% of L and 5% of H, the critical threshold of W-loss is 41% (Fig. 4d).

We also show that W-fragmentation affects the asymptotic demographic structure at the landscape scale (Fig. 5). Pilot study (Fig. 5a) shows that W-fragmentation does not destabilize significantly demographic structure at the landscape scale and that this “landscape demographic structure” tend to the

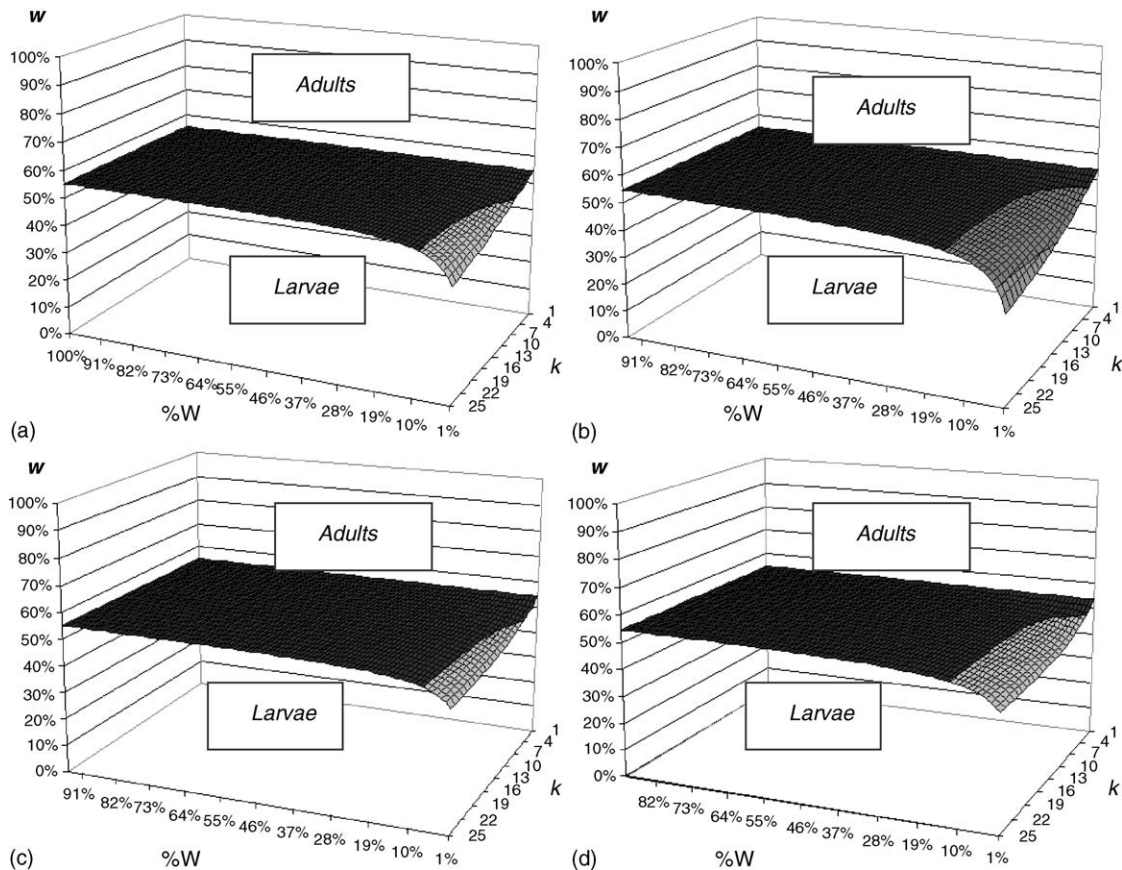


Fig. 5. Effect of W-fragmentation on asymptotic demographic structure growth rate (w) (presented: proportion of larvae (La) and adults (A)), for landscapes where there are only W and M (a), W and M with 5% of H (b), W and M with 5% of L (c), and W and M with 5% of H and 5% of L. the surface area distinguish the proportion of larvae (below) and adults (above). The grey intensity (from black to light grey) corresponds to decreasing levels of adult percentage.

demographic structure in W when W-fragmentation decreases (55% of larvae and 45% of adults). This destabilization corresponds to a decrease of larvae proportion in comparison with adults. For landscapes where there are 5% of H, the demographic structure is even more destabilized when W-fragmentation increases (Fig. 5b), while 5% of L in landscapes (with or without 5% of H) allows a stabilization of the demographic structure (Fig. 5c and d).

For a spatial point of view, we also show that W-fragmentation combined with H and L modifies the asymptotic spatial pattern at the landscape scale (Fig. 6). The pilot study shows that W-Fragmentation alone does not affect the ratio between individuals in W and M: 100% of individuals on average are located

in W (Fig. 6a). The presence of H or/and L in the landscape modify the asymptotic spatial structure and it becomes sensitive to W-fragmentation: proportion of individuals decreases in W at the benefit of H or/and L (Fig. 6b–d). L has an important proportion of individuals when W-fragmentation increases because L produces new individuals and are suitable for larvae contrary to H. We can thus explain this pattern as the fact that W-fragmentation forces adults (non-breeders and breeders) to leave suitable elements as W through H toward M where they cannot reproduce and where mortality is important, and therefore, decreases mean population fecundity and survival. However, L compensates this “drain” with a production of new individuals contrary to H.

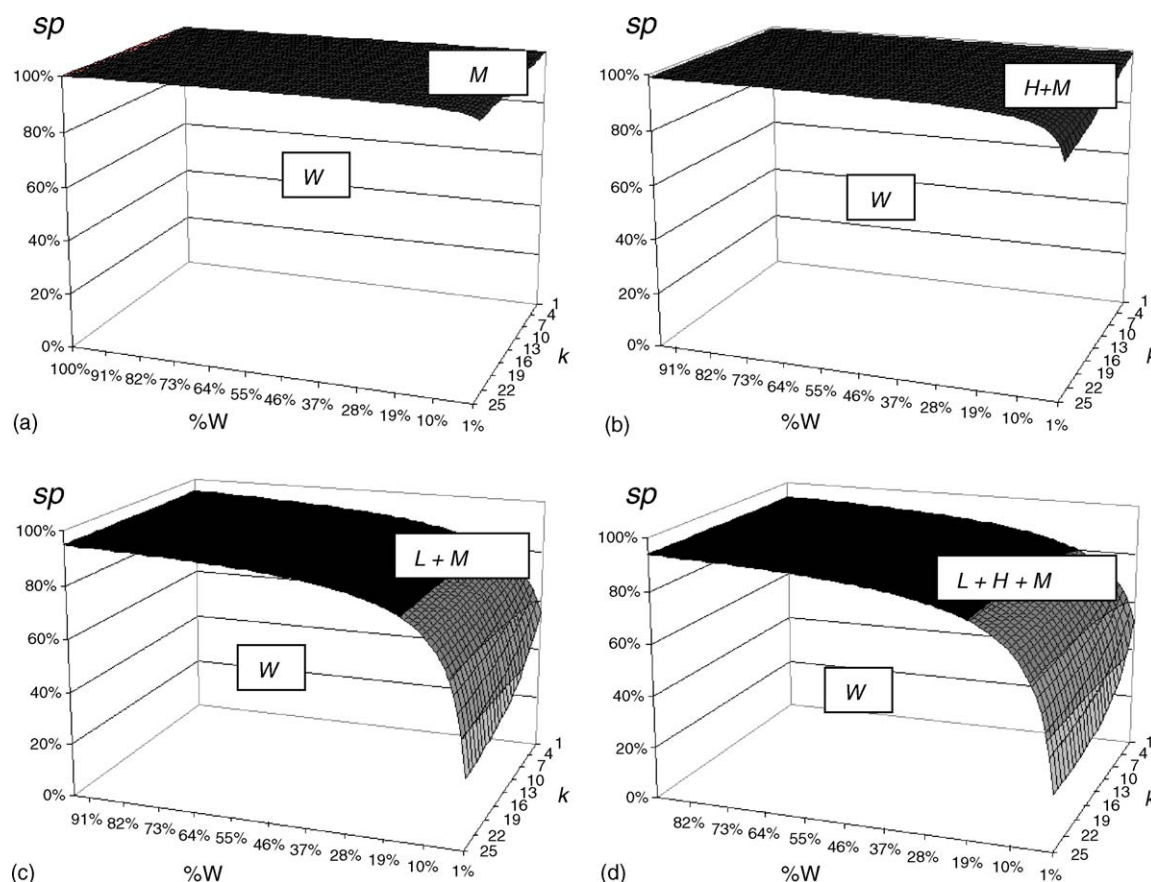


Fig. 6. Effect of W-fragmentation on asymptotic spatial structure (denoted here sp, for landscapes where there are only W and M (a), W and M with 5% of H (b), W and M with 5% of L (c), and W and M with 5% of H and 5% of L (d)). The surface area distinguishes the proportion of individuals in W (below) and in M, H and/or L (above). We present the proportion in W, L or H. Proportion of individuals in M are not presented because they are close to zero. The grey intensity (from black to light grey) corresponds to decreasing levels of percentage of insects in W.

3.3. Discussion

All our results show that *A. parallelepipedus* population demography and spatial pattern are sensitive to W-fragmentation (Fig. 4). This sensitivity is not linear and predicts extinction thresholds. This pattern reflects general patterns explained by many researchers on population viability (Andr  n, 1994, 1997; Kareiva and Wennergren, 1995; Bascompte and Sol  , 1996; Hanski et al., 1996; Hill and Caswell, 1999; With and King, 1999; Fahrig, 2001; reviewed in Fahrig (2002)). But we are going further, detailing overall demographic and space processes induced by a change of spatial structure. As it has been presented in this paper, this model can be defined as a H_0 -hypothesis for spatial structure, and we assume via these population end-points, that it is a very useful tool for modelling and management applications:

- For a management point of view, we show that when habitat fragmentation increases (in two dimensions: loss of habitat and habitat fragmentation per se), H and L modify population dynamics at the landscape scale and in W, and population level end-points at the landscape scale diverge compared to those in W patches ($\lambda = 1.06$, $L_a = 55\%$ /adults = 45% in W) (Figs. 4–6). This result indicates that first when fragmentation increases, the spatial context around patches of W affects population level end-points in these patches (overall sensitivity of λ to W-fragmentation increases exponentially below a critical threshold of fragmentation: Fig. 4), as it been suggested by Wiens (1997). Second, that minimizing negative effects of the spatial context to maintain a population at the landscape scale when there are few W (for example 8% on average in Brittany), impose to build a single large instead of several small patches of W (i.e. k -value must be low in the model). In this study, we also show, in the H_0 -hypothesis, that L has positive impact while H has negative impact on population dynamics. Therefore, we suggest that even if L are randomly structured and distributed in space (see Section 2.2.3), they can easily play a positive role to connect different sub-populations of W. If H can play the role of corridors for dispersal, due to spatial simplifications, our model cannot highlight it. With different kind of multi-agent models applied on *A. paral-*

lelepipedus in explicit landscapes, Martin (2000), Tischendorf et al. (1998) and Jopp and Reuter (2005) studied connectivity between two elements via H or forest stepping stones. They also show that H could have negative or positive impact according to their length and width. Our model cannot highlight contributions of some parameters as width, length, surface area or perimeter on population viability, but can help us studying general contributions of boundaries or quality of elements on population viability at the landscape scale, according to habitat-fragmentation. Studying these relative contributions could be assessed more precisely with an elasticity analysis of λ to life history rates summed by elements or boundaries (see Pascarella and Horvitz, 1998 for the methodology, Pichancourt et al., submitted for publication).

- For a modelling point of view, we know that there are a lot of models of population dynamics which reliability has been discussed particularly concerning paucity of data (Wennergren et al., 1995; Ruckelshaus et al., 1997; South, 1999), need of stage structure (Wennergren et al., 1995) or importance to adapt modelling to species movement (South et al., 2001). Jepsen et al. (2005) stressed on “the need to critically compare these models in order to pinpoint the consequences of using one or the other”. With our model, we tend to replace the reliability of the different models of spatial population dynamics according to space for *A. parallelepipedus*: space is not always and everywhere required for this species. For example when there are four classes of elements (W, L, H and C: Fig. 4d) and when $W > 41\%$, λ -value is not very different than λ -value in W ($\lambda = 1.06$) and sensitivity of λ to W-fragmentation is quasi-null. Population dynamics at the landscape scale can thus be summarized only by local population dynamics in a single large patch of W ($k = 1$), and a simple Leslie matrix could assess well the overall population dynamics. Second, spatial data do not need always to be explicit. For example, above the critical threshold of W-loss ($W > 41\%$), when fragmentation per se increases the model supposes that there are several small patches of W organized in a metapopulation way, and that this metapopulation is not sensitive to the spatial context (sensitivity λ to W-fragmentation and H or CC is quasi-null). A mathematical metapopulation model

without cost of dispersal, where the sub-populations are those from woodlots in the landscape, implicitly makes the same assumption. In this case, a simple metapopulation approach between woodlots without real cost of dispersal can be used to focus on extinction–recolonisation processes (Levins, 1969; Hanski and Gilpin, 1991; Hanski and Simberloff, 1997; Moilanen, 2004), or on the demographic consequences of a metapopulation organization of suitable habitats (Akçakaya et al., 1995). Third, if overall sensitivity of λ to W-fragmentation and other elements as H and L have important effects on population viability, elements and boundaries in the landscape matrix between patches of W must be implicitly or explicitly incorporated in a spatial population model (as explicit metapopulation models with real cost of dispersal (Khaladi et al., 2000) or grid-cells models if sensitivity is very important (South et al. (2001) for a clear review, Walters (2001) and Jopp and Reuter (2005) (online) for an example on carabid beetles)). We also affirm that these different models must be tested and replaced quantitatively ones compared to the others for other species.

Finally, our modelling approach suggest another type of spatially explicit population approach. In spatially explicit approaches, landscapes can be represented as a lattice and a cell of the lattice is a compartment defined by demographic parameters and movement parameters from this cell to the four or eight adjacent ones. By this way, a spatially explicit matrix population approach (see Lebreton and Gonzalès-Dàvila (1993) for particularly clear explanations, Wennergren et al. (1995) and Westerberg and Wennergren (2003) for first approaches) combines a stochastic movement matrix with a Leslie-type matrix for particular landscapes. However, Contrary to Westerberg and Wennergren (2003) approach, where movement coefficient are directly adjusted in the movement matrix according to the demographic time step, we propose to distinguish the movement and demographic time steps like in this paper. Because this model has a great number of variables, distinction between movement and demographic time step could be useful to aggregate the model for k processes of local movements between one cell to the four or eight adjacent one (for one demographic time step). This is particularly important for analyzing the population system when it includes density dependent

(Bravo De La Parra et al., 1997) or stochastic (Sanz and Bravo De La Parra, 2000) life history traits.

4. Conclusions

Our model has important implications for biological conservation in heterogeneous landscape. It allows assessing the relationship between degree of habitat fragmentation and population response at the landscape scale. Because it also distinguishes habitat loss and breaking apart of habitat, we can address to important issues in conservation biology, like “how much habitat is enough?” or for a given proportion of habitat, should a single large or several small habitat patches be maintained in the landscape? With the stable demographic and stable spatial structure, we can help on experimental design and managers to know in which element or in which stage individuals are affected by habitat fragmentation. Even if we ought to use stochastic life history traits and that we ought to build a more detailed sensitivity analysis, it can open prospect in comprehension and simplification of analysis of complex population dynamics at the landscape scale. However, because our population model does not take into account actual spatial arrangement of habitat destruction, we suggest that this approach ought to be used only as a first approach to assess the impact of habitat fragmentation on population dynamics. As a further step, spatially explicit models should be used, if and only if data are available. However, we stress on the importance of using them before using complex spatially explicit models, because simple models with few variables can capture and analyze in a reliable way general landscape patterns, and because they allow assessing empirically (if they are well constructed) the type of explicit model that we must choose according to the spatial detail. Implicit population models and aggregation of variables are tools that can help on this way.

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