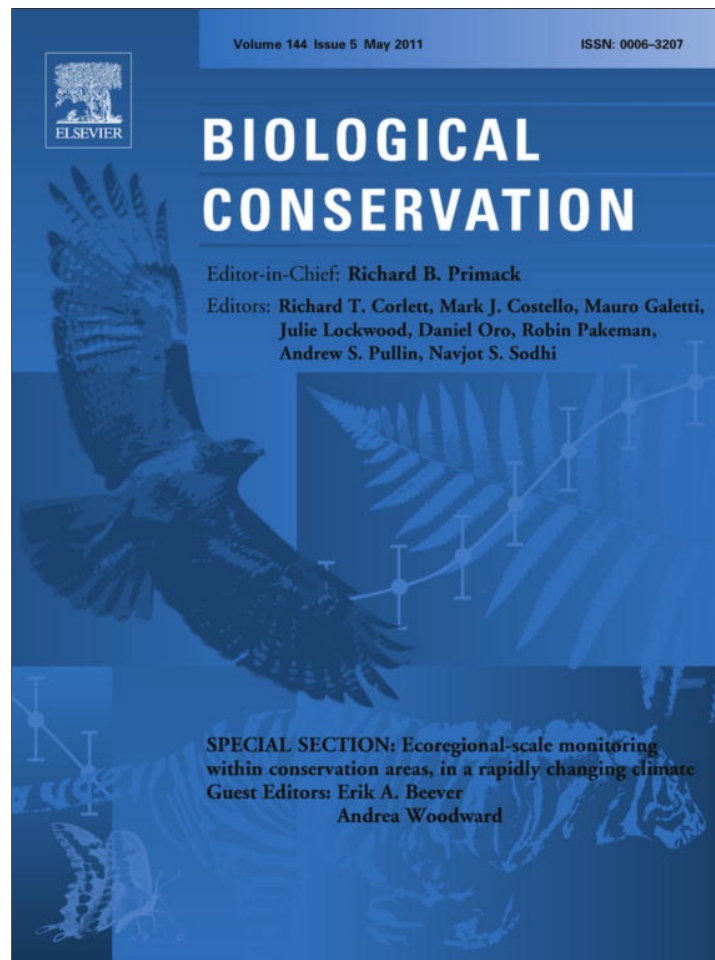


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Biological Conservation

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## Plantation clearcut size and the persistence of early-successional wildlife populations

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### ARTICLE INFO

#### Article history:

Received 30 September 2010

Received in revised form 29 December 2010

Accepted 2 February 2011

Available online 23 February 2011

#### Keywords:

Clearcutting

Patch size

Ephemeral habitat

Metapopulation persistence

Individual Based Model

### ABSTRACT

Plantation clearcuts represent an important habitat for many open-area wildlife species – including conservation-concern species – in landscapes dominated by industrial forests. However, due to the ephemeral nature of clearcuts, species using this type of environment face a “shifting mosaic” in which their ability to successfully relocate to another habitat patch may play a crucial role in the species' persistence in the landscape. Although several studies have shown a positive effect of patch size on the persistence of open-habitat species, forest clearcutting represents a special case in which, on average, larger patches also tend to be more isolated from each other, likely creating a trade-off between area and isolation effects. We developed an individual-based spatially-explicit model to test the effect of clearcut size (a critical management variable in plantation forestry) on the persistence of generic early-successional wildlife species in a landscape dominated by forest plantations. We simulated a landscape covered with a plantation harvested regularly over a 25-year rotation and different versions of a wildlife population whose habitat was constituted only by 1–4 year-old patches. We observed that when the species could perceive the attributes of the neighboring pixels persistence time was higher at intermediate clearcut sizes agreeing with our prediction. Also, species with a high dispersal capacity were less limited by connectivity and reached their maximum persistence at higher clearcut sizes. Results also showed a positive effect of habitat lifetime on persistence. Our results suggest large clearcuts may be incompatible with the conservation of many early-successional vertebrates that have limited dispersal capacity, unless additional conservation measures, such as the use of corridors or special spatial arrangement of clearcuts, are taken to overcome the lack of connectivity.

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### 1. Introduction

One of the most noticeable and ecologically important aspects of most forest (mostly conifer) plantations is the use of clearcutting as a harvesting technique. In general, clearcutting is a method that has been a matter of a strong debate, because there are concerns about its potentially significant ecological impacts (e.g. nutrient cycling; Prescott, 1997; erosion; Knight et al., 1985; Iroumé et al., 2006; wildlife habitat; Mannan and Meslow, 1984; promoting invasive species; Selmants and Knight, 2003, etc.). Besides, public perception of clearcutting is usually negative, because of the added aesthetic effects of large harvested areas (Levine and Langenau, 1979).

Despite the many documented negative effects that clearcutting has on some forest wildlife, plantation clearcuts represent an important habitat for many open-area species in landscapes dominated by industrial forests. For example, in some regions of

Europe, even-aged plantation systems are important reservoirs for some early-successional bird species (Paquet et al., 2006; Wilson et al., 2010) and some conservation-concern arthropods (Brocknerhoff et al., 2008). Also, in the Eastern United States, many prairie or shrubland wildlife species find valuable habitat in forest clearcuts (DeGraaf et al., 1992; DeGraaf and Yamasaki, 2003).

There is also a number of typical forest wildlife species that rely on forest openings, at least, during some stages of their life cycle (e.g. lekking Black grouse, *Tetrao tetrix*, Rolstad et al., 2009; juveniles of several forest passerines, Vitz and Rodewald, 2006, etc.). This group of species is not considered in our definition of early-successional species, which only includes species whose preferred habitat is an open area (prairie, steppe, shrubland, etc.).

Due to the ephemeral nature of clearcuts, species using this type of environment face a “shifting mosaic”, particularly in the case of fast growing species (e.g. pines), where the open habitat may only last for a few years. For example, in most pine plantations in South-Central Chile, first canopy-closure occurs at 4–5 years after planting, drastically reducing the herbaceous layer (Estades, Personal observation).

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The problem of the persistence of metapopulations using ephemeral habitats has been studied by several researchers (e.g. Keymer et al., 2000; Amarasekare and Possingham, 2001; Wimberly, 2006), mostly focusing on a comparison between dynamical vs static systems. In general, these theoretical studies have shown that metapopulation occupancy of ephemeral habitats is lower than that of permanent habitats (Amarasekare and Possingham, 2001) and that habitat turnover rate is negatively correlated with patch occupancy (Keymer et al., 2000).

An intuitive implication of these shifting mosaics is that, at some point, as habitat conditions worsen, individuals using a patch will need to relocate into other patches of suitable habitat. Therefore, dispersal ability may play a crucial role in the species' persistence in the landscape (Travis and Dytham, 1999).

However, modeling studies that have explored the spatial implications of shifting mosaics on metapopulations have obtained mixed results. For example, Fahrig (1998) concluded that spatial structure of ephemeral habitat had a negligible effect on population persistence. In a similar system, Hodgson et al. (2009) found that the relationship between connectivity and patch occupancy was rather weak.

On the other hand, Loehle (2007) suggested that ephemeral habitats might act as stepping stones, hence, enhancing dispersal. Along the same line, Wimberly (2006) showed that a dynamic landscape might increase patch occupancy for species that cannot cross gaps.

A critical management variable in forest clearcutting is the size of individual patches. First, larger clearcut sizes are more economical because more timber is removed at one time and fewer roads need to be built. Thus, normally the Net Present Value of plantations increases with maximum clearcut size (Boston and Bettinger, 2001). On the other hand, large clearcut sizes produce undesirable effects such as an increase in erosion and runoff levels (Iroumé et al., 2006). For that reason, many countries and companies limit the maximum size of harvest areas (Carnus et al., 2003; American Forest and Paper Association, 2005; Pawson et al., 2006).

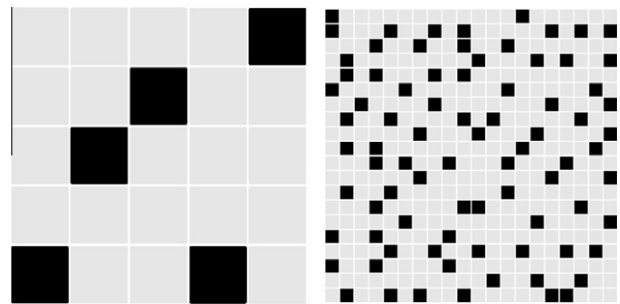
However, the effect of individual clearcut size on the performance of early-successional species is yet unclear (Pawson et al., 2006). For example, in a regulated plantation where each year an area of size *A* is harvested, will it make a difference for early-successional species whether this area is harvested in just one patch of size *A* or in many small patches that sum up to *A*?

Although several studies have shown a positive effect of patch size on the persistence and performance of prairie and shrubland species, particularly birds (Johnson and Temple, 1990; Helzer and Jelinski, 1994; Johnson and Igl, 2001; Herkert et al., 2003; Davis, 2004), forest clearcutting represents a special case in which, on average, larger patches also tend to be more isolated from each other, because when the latter develop they, in turn, become larger gaps of forest between clearcut areas (Fig. 1). Although there might be exceptions to the latter (see comments in the methods and discussion sections), clearcut harvesting likely creates a trade-off between area and isolation effects for early-successional species.

Using a simulation model we explored the effect of clearcut size on the persistence of generic early-successional wildlife species in a landscape dominated by even-aged forest plantations. With this model we tested the hypothesis that, in the described case, there might be a non-monotonic relationship between the size of habitat patches and the performance of early-successional species, undetected by previous, more general, studies.

## 2. Methods

We developed a simple individual-based spatially-explicit population model (IBSEPM), built on VisualBasic. IBSEPMs have been



**Fig. 1.** The effect of clearcut size on the isolation between clearcuts. The two landscapes are covered with even-aged plantations 1/5 of which have been cut (black squares). In the left landscape the harvested area is comprised of only five large patches, whereas in the right landscape, the same area is distributed in 80 smaller patches. All cut patches were assigned randomly. It is clear that the average distance between patches is larger in the left (large clearcuts) landscape than in the right (small clearcuts) landscape.

increasingly used in understanding how landscape structure influences individual dispersal and interactions between habitat configuration and population demography (Wiegand et al., 1999; Melbourne et al., 2004).

### 2.1. Model

The model consisted of a dynamic landscape of  $80 \times 80$  pixels containing plantations of different ages and individuals of a generic wildlife species. One pixel represented the minimum harvest unit.

The landscape dynamics were governed by plantation growth and harvesting, which occurred at a temporal scale of years. Harvesting set the age of a patch to 0 and that patch subsequently increased in age as years elapsed. We defined a rotation time of 25 years (seasons) and, therefore, each season  $80 \times 80 / 25 = 256$  pixels were “harvested”.

As a first approach to studying the problem, our model did not include any optimality considerations into the spatial arrangement of forest harvests (e.g. see Baskent and Keles, 2005). Therefore, in every experiment and replicate, “stand” age was randomly assigned, with the only restriction being that each age class should add up to 256 pixels.

We simulated the population of an early successional animal species for which only young stands were considered habitat. The following paragraphs describe the characteristics and behavior of a “base” species (BASE) whose parameter values were arbitrarily defined so that the population would persist under continuous habitat. Later on we describe the changes to the latter parameters that defined the different species types used in the experiments.

Habitat for BASE was restricted to stands aged from 1 to 4, whereas stands 5 to 16 years old were considered marginal habitat and older stands were not habitat.

#### 2.1.1. Movement

Individuals moved across the landscape in daily time steps. There were 100 days in a “season”.

Movement pattern for BASE was a modified “random walk”. First, individuals assessed a probability of leaving the current cell and compared that value to a random number. The daily probabilities of leaving a non-habitat cell, a marginal habitat cell or a habitat cell were, 100%, 50% and 0.1%, respectively. This Habitat-related Movement Probability (HMP) produced a tendency of individuals to stay in their habitat and to abandon the less suitable cells.

Additionally, we incorporated a Density-dependent Movement Probability (DMP) that was proportional to the number of other

individuals present in the cell. For BASE this probability was equal to the number of additional conspecifics present in the cell divided by 3. The latter produced a tendency of individuals to leave “crowded” cells.

Finally, the probability of leaving the cell was the addition of HMP and DMP. Because this value could add to more than 1 the number was truncated at 1.

We simulated two “versions” of the species:

A “blind” version could not discriminate between habitat types when defining a movement step. That means that once the algorithm determined that the individual would leave a cell it would do it in a completely random direction without assessing the quality of the target cell. This simple movement pattern likely represents species with limited perceptual capabilities such as insects (Fahrig, 1998).

On the contrary, a “perceptive” version discriminated between habitat types in neighboring cells and tended to avoid moving to marginal habitat and non-habitats when in good quality cells. Additionally, it tried to move towards good habitat when present in low quality cells. This means that, when in a habitat cell, and the algorithm had determined that the individual would leave that cell, the probability of moving to a marginal or non-habitat cell was only 10% (otherwise the individual would chose another cell and run a new random number). In the alternative case (present in a low quality cell), the probability of moving into a new habitat cell was 100%. On the other hand, the probability of moving from a low quality cell to another low quality cell was 50% of that of moving to a good habitat cell (if present in the immediate neighborhood).

In order to avoid edge effects we simulated a toroidal landscape (i.e. individuals leaving the right “edge” of the landscape appeared at the left side).

### 2.1.2. Reproduction

Individuals reproduced at the beginning of the season. The process was very simple as BASE was assumed asexual. First, the individual assessed the habitat-specific annual probability of reproduction (50%, 5% and 0%, for habitat, marginal habitat and non-habitat, respectively) and, if successful, it produced two offspring. The new individuals were all located in the same cell as the parent individual.

### 2.1.3. Mortality

Individuals faced three different sources of mortality, whose probabilities were assessed sequentially in the following order:

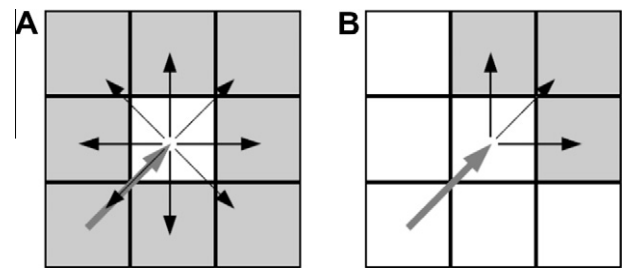
**2.1.3.1. Constant Death Rate (CDR).** All individuals had a daily probability of dying of 0.2%.

**2.1.3.2. Landscape-induced Death Rate (LDR).** Individuals experienced different mortality rates depending on the habitat type in which they were present. For BASE there was a 0.4% and a 4% daily probability of death in the marginal habitat and the non-habitat, respectively. LDR in habitat cells was 0.

**2.1.3.3. Density-dependent Death Rate (DDR).** Individuals experienced different daily mortality rates depending on the number of conspecifics present in the same pixel. The value used for BASE was equal the number of conspecifics in the cell divided by 5000.

## 2.2. Experiments

The experiments considered two factors: clearcut size and species type. We simulated five different clearcut/stand sizes ( $1 \times 1$ ,  $2 \times 2$ ,  $4 \times 4$ ,  $8 \times 8$  and  $16 \times 16$  pixels). One pixel was considered enough to hold, at least, one individual (i.e. the individual could live the entire season without the need to leave the pixel). Even



**Fig. 2.** The difference between the movement pattern for (A) BASE species and (B) HIGHDISP species. In (A) all possible future movement directions (small black arrows) have the same probability of occurring regardless of the previous movement (large gray arrow). In (B) future movements are restricted by previous movement.

for simple models such as ours exploring all potential combinations for parameter values is unfeasible (Fahrig, 1998; Wimberly, 2006). For that reason we simulated different species types as syndromes, trying to reflect qualitatively distinct behaviors. The following paragraphs describe the different species tried.

### 2.2.1. Slow movement (SLOW)

The only difference between this species and BASE is that the landscape-related probabilities of leaving a given cell were substantially reduced to only a 10% of the original values. Additionally, the denominator in the formula for DMP was raised from 3 to 5, making individuals less sensitive to crowding.

### 2.2.2. High dispersal (HIGHDISP)

This species moved two cells per time step (as opposed to just one in BASE). Second, they had smaller turning angles resulting in more straight trajectories. For this purpose, each individual “remembered” the direction of the previous movement and used that information to restrict the following movement. Fig. 2 shows the difference between the movement pattern for BASE (A) and HIGHDISP (B).

### 2.2.3. Sexual reproduction (SEXUAL)

This species differed from BASE only in that, additionally, it required the presence of at least one conspecific in the neighboring cells to be able to reproduce. Because DDR was maintained (same value as BASE) there was still a decline in individuals’ fitness at higher densities reflecting an Allee effect. Because our definition of SEXUAL is a proxy for a real two-sex model, we consider it a conservative expression of the constraints imposed by the need of organisms to find a mate for breeding.

Because previous research (e.g. Wilcox et al., 2006) suggests that habitat turnover rate is likely a crucial parameter in our model, we changed the duration of the habitat patches by reducing it in 50% (2 years) and increasing it in 100% (8 years). Additionally we considered a static case in which patches did not change in attributes during the entire simulation (based on the 4-year habitat duration case). We conducted this experiment only for BASE with all its variants.

We also conducted a sensitivity analysis on the LDR for all species, running additional simulations with 50% and 200% of the base value.

All simulations were initiated with 1000 individuals randomly distributed in the landscape. Simulations for all scenarios were replicated 100 times. A complete simulation covered a total of five 25-year rotations of the plantation. Therefore there was a maximum of 125 years of persistence for a given metapopulation. For each scenario we recorded the number of years before extinction.

### 3. Results

#### 3.1. BASE species

Fig. 3 shows the relationship between clearcut size and population persistence for BASE. All points are represented by the average persistence and the 95% confidence interval (in many cases the error bars are not visible because of their small size due to low variability and the large sample size,  $n = 100$ ). There was a clear effect of LDR on persistence time, with cases with higher mortality experiencing a lower persistence time.

On average, survival time was substantially higher for the “perceptive” versions than for their “blind” counterparts (Fig 3). However, the most striking difference between these two types of species was that the persistence time for the “blind” species increased monotonically with clearcut size, whereas for the “perceptive” species values were higher at intermediate clearcut sizes. The latter trend was not detected with a LDR of 50% of the base value because the population persisted for at least 125 years in all scenarios.

##### 3.1.1. Effect of habitat duration

Fig. 4 compares the behavior of BASE for scenarios where habitat lasted for: (A) 2 years and (B) 8 years. Note that Fig. 3 represents an intermediate case (4 years) between Fig. 4A and B.

Persistence time consistently increased with habitat duration. In the case of the “blind” species, the latter effect was more significant when larger clearcut sizes were used. For the “perceptive” species, this pattern was obscured in most cases by the fact that both scenarios reached the maximum simulation period (125 years).

##### 3.1.2. Dynamic vs static system

Fig. 5 shows the persistence time for the static version of BASE. For the “blind” species the static scenario produced significantly higher persistence times than its dynamic counterpart (Fig. 3), particularly with larger clearcut sizes and LDR. Again, a clear comparison for the “perceptive” species was impeded by the fact that most cases persisted until the maximum simulation time.

#### 3.2. Other species

Fig. 6 shows the relationship between clearcut size and persistence time for: (A) SLOW, (B) HIGHDISP and (C) SEXUAL. The SLOW

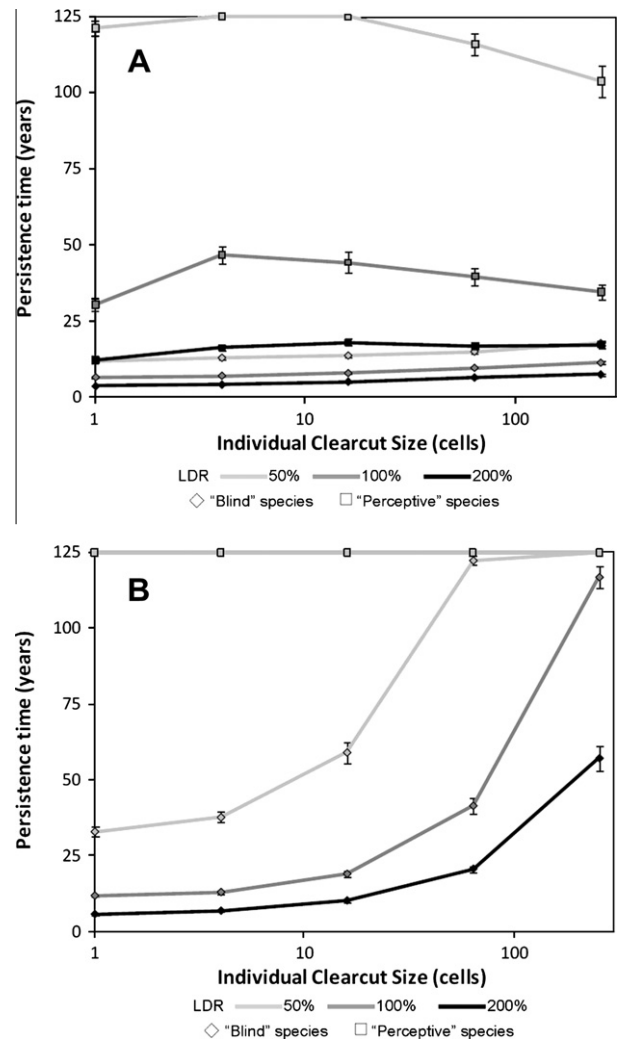


Fig. 4. Effect of habitat duration and individual clearcut size on persistence time for the BASE species (in six versions). (A) Habitat duration = 2 years. (B) Habitat duration = 8 years.

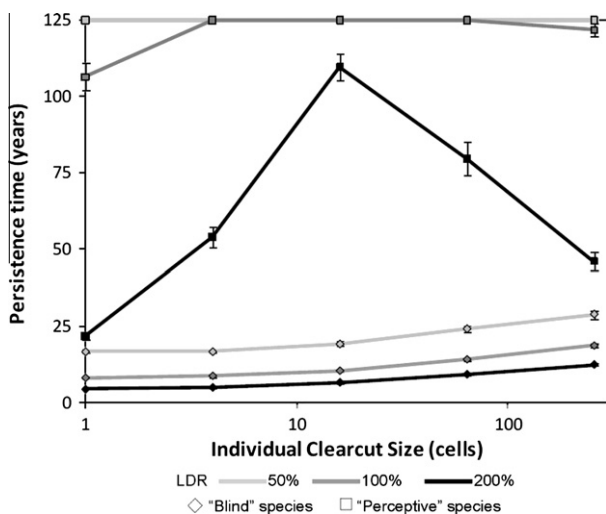


Fig. 3. The effect of individual clearcut size on the persistence time of the BASE species, in six versions (“Perceptive” vs “Blind”, and three levels of Landscape-induced Death Rate, LDR). There was a maximum simulation time of 125 seasons.

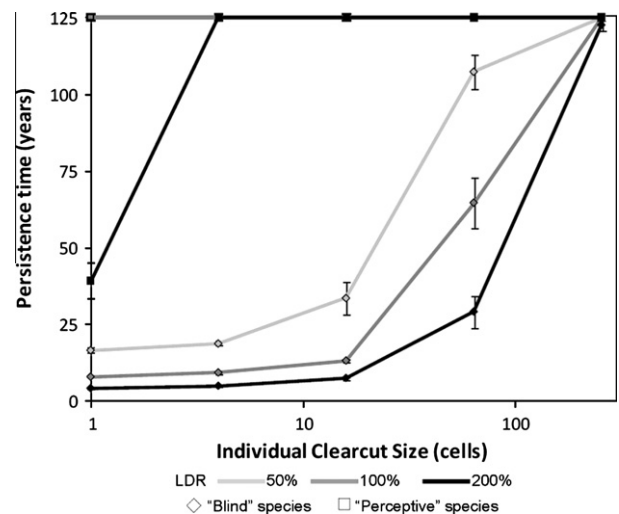


Fig. 5. The effect of individual clearcut size on the persistence time of the BASE species in a static scenario (i.e. stand ages are fixated at the beginning of the simulation period).

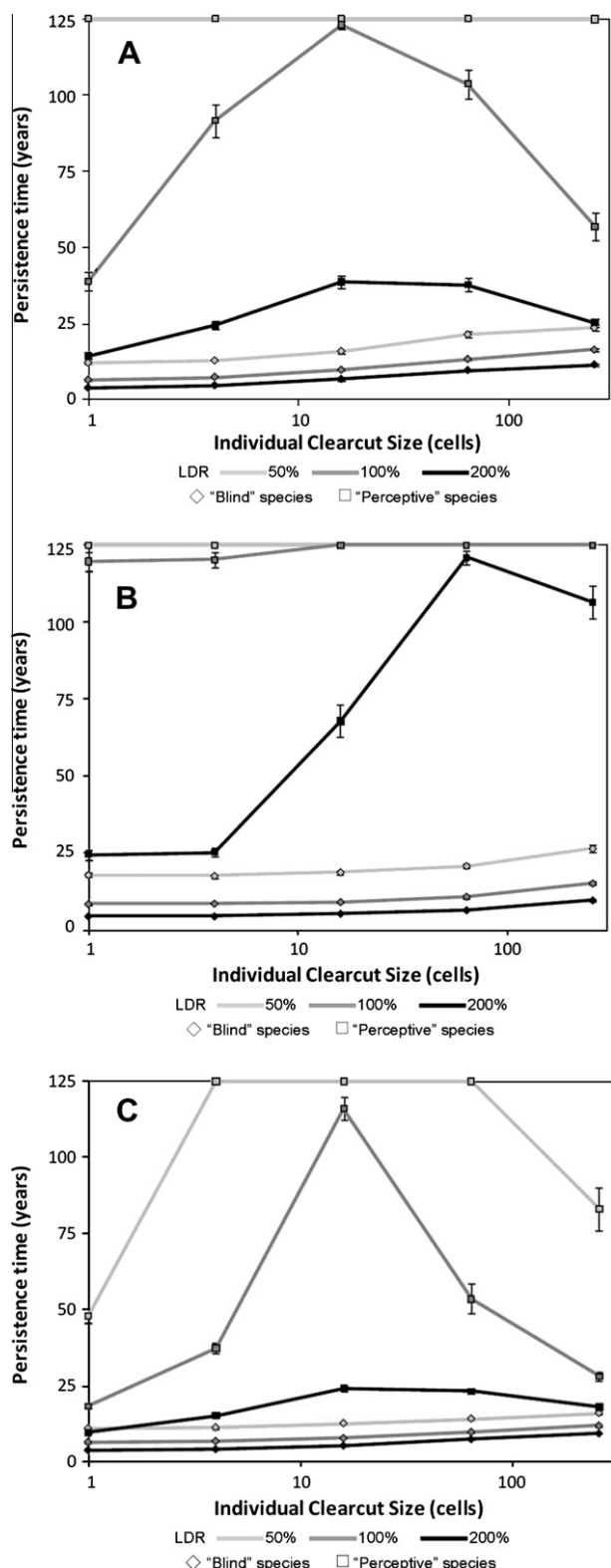


Fig. 6. Effect of clearcut size on persistence time for: (A) SLOW, (B) HIGHDISP, and (C) SEXUAL species (in six versions each).

species had a qualitatively similar behavior as BASE (Fig. 3) but with a lower level of persistence for all cases, with the only exception being the “perceptive” version with the lowest LDR, in which both SLOW and BASE reached the maximum of 125 years.

The “blind” versions of HIGHDISP (Fig. 6B) had a slightly lower persistence time in relation to BASE (Fig. 3). The “perceptive”

versions of this species also showed a lower persistence time, but at intermediate clearcut sizes (4 and 16 cells). In the rest of the cases this species increased its persistence time in relation to BASE, but this time, the maximum value (only detectable for the case with the highest LDR) occurred at higher clearcut sizes.

Finally, SEXUAL (Fig. 6C) showed a similar trend as SLOW, basically reducing persistence time in all versions compared to BASE.

#### 4. Discussion

Based on a simulation model similar to the one used by us, Fahrig (1998) concluded that the spatial structure of habitat had a negligible effect on population persistence of species using an ephemeral habitat. This conclusion is in clear disagreement with our results. In the present study not only many of the simulated cases showed the classical positive effect of patch size on persistence (e.g. Hanski, 1994, 1998; Connor et al., 2000), but some showed a clear non-monotonic pattern where patches of intermediate size produced a higher metapopulation persistence time.

We believe that part of the explanation for this discrepancy has to do with what assumptions are made regarding the fate of the local population inhabiting a patch that disappears. Many of the studies that have addressed the persistence of metapopulations in ephemeral habitats have, implicitly, been based on late-successional species (i.e. habitat is maintained until a disturbance destroys it). Moreover, in some of these models (e.g. Fahrig, 1992; Wimberly, 2006) the individuals present in a patch are directly killed during patch disturbance, which is probably the case for most sessile organisms and species not resistant to the specific mechanisms causing the disturbance. This disturbance-induced mortality likely reduces the overall metapopulation size, probably making it more difficult to detect the eventual effects of the spatial arrangement of habitat.

On the contrary, the habitat of an early-successional species is gradually replaced by a different vegetation type, likely giving the individuals enough time to abandon the area. Even though in our model the change from habitat to marginal habitat status was abrupt, there was not mortality directly caused by this change, thus allowing individuals to “escape” from the areas that had lost their prime-habitat quality.

Moreover, the ability of individuals to abandon a recently-turned unsuitable habitat might cause disappearing patches to temporarily have a disproportionately higher effect as colonizer source because all individuals are forced to leave the area (e.g. fleas leaving dead rats, Keeling and Gilligan, 2000), as opposed to stable patches where only a proportion of the individuals (usually juveniles) engage in dispersal.

Another issue in which basic modeling assumptions had a strong influence on the observed patterns was the movement algorithm. The only difference between the “blind” and the “perceptive” versions of the simulated species was that the latter had some control over which step to take once a movement “decision” had been made. However, that apparently small difference in the algorithm produced a quantitatively and qualitatively different response to habitat spatial patterns.

Persistence of “blind” species was substantially lower than that of “perceptive” species likely because many individuals were randomly “emitted” to the hostile matrix through the patch edges, thus increasing mortality. This blind movement pattern also can explain the observed positive effect of clearcut size on persistence, because, due to the higher edge-to-area ratio, more individuals were “accidentally” lost to the matrix in smaller patches. This mechanism is clearly exacerbated in the case of species moving

with big steps, which would explain the lower persistence time of “blind” HIGHDISP in relation to “blind” BASE.

On the other hand, the “perceptive” species were more likely to maintain populations in small patches because of their tendency to avoid moving into unsuitable habitat and to return to prime habitat once present in the matrix.

The latter differences highlight the importance that basic behavioral assumptions, such as individuals’ perceptual range, may have on the observed patterns in IBSEPMs (Heinz et al., 2007; Pe’er and Kramer-Schadt, 2008).

In many scenarios the populations of the “perceptive” species persisted for the entire simulation period (125 years). In the rest of the cases, persistence time was higher at intermediate clearcut sizes, agreeing with our prediction based on the existence of a trade-off between area and isolation effects. This trade-off may also explain the differences observed between species with different dispersal capabilities (Fig. 3 vs. Fig. 6A vs Fig. 6B), as we show in Figs. 7 and 8.

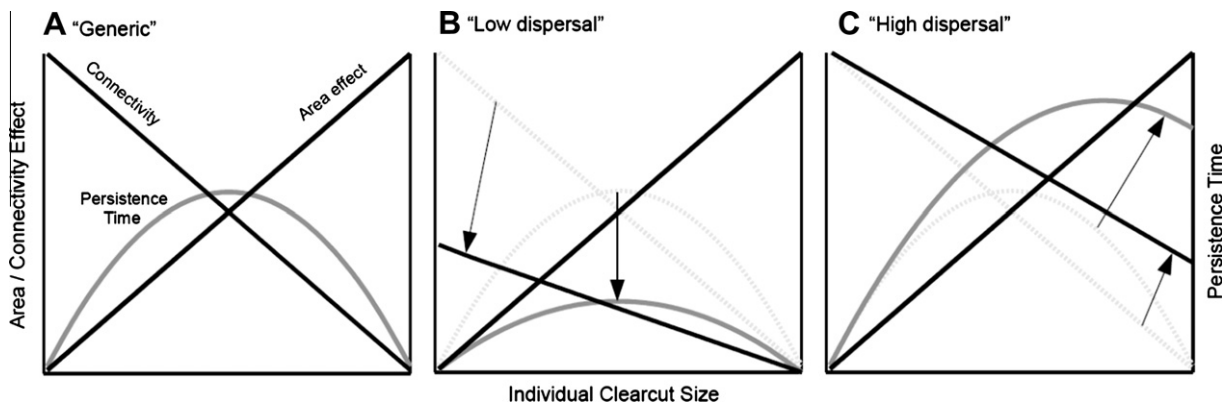
Let us consider a “generic” wildlife species inhabiting clearcut patches present in a regulated forest plantation in which, each year, the same area of forest is harvested. The larger the size of individual clearcuts, the more benefited the population will be from “area” effects (Hanski, 1998). In Fig. 7A the latter effect is represented by a simple linear effect.

Large clearcuts also imply large stands of mature forest and, because no particular spatial arrangement of clearcuts is considered in this study, on average, larger clearcuts will reduce connectivity between patches. Therefore the latter relationship is also represented as a linear effect, but with a negative slope (Fig. 7A, “connectivity”).

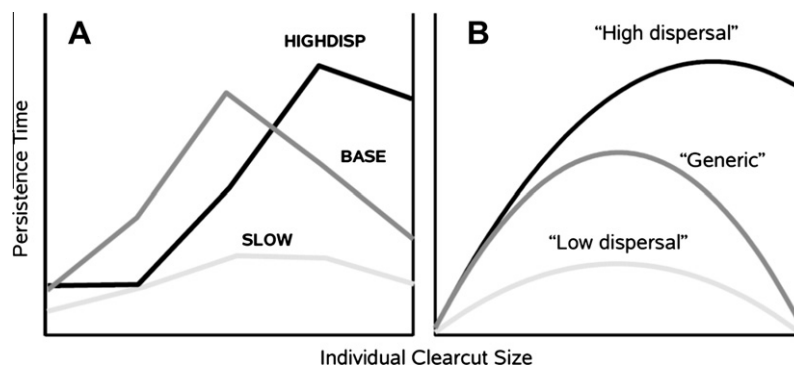
Finally, a simple function of persistence time, calculated as the product of the area and connectivity effects, shows a pattern similar to that recorded by us, with a maximum persistence time at intermediate values of clearcut size (gray line, Fig. 7A). The latter formulation of the relationship between area and connectivity effects implies that no population is viable in complete isolation (even for very large patches) because the studied system is, by definition, ephemeral.

Fig. 7B depicts a species with low dispersal capabilities, meaning that connectivity is additionally reduced due to the nature of the species. For simplicity purposes, the latter reduction is represented as a proportional decrease in the connectivity throughout the range of clearcut values. As a result of the latter, the persistence curve maintains its shape but with a lower maximum (gray line, Fig. 7B).

On the other hand, Fig. 7C shows a species with high dispersal, represented as an increase in the minimum connectivity and a reduction of the slope of the relationship (i.e. connectivity is less



**Fig. 7.** Theoretical model for the response of the persistence of a metapopulation in a system where patch size is positively correlated with patch isolation. (A) For a generic species, connectivity between patches is maximum when the patches are of the smallest possible size (because they are the closest to each other) and declines as patch size increases until reaching a minimum (e.g. no movement is possible). On the contrary, beneficial “area effects” increase with patch size. A persistence function (gray line) is represented as the product of the latter two variables, showing a maximum at intermediate clearcut sizes. (B) A species with low dispersal capabilities is represented by a reduction in the maximum connectivity attained a low patch sizes (e.g. due to sedentariness) and a reduction in the slope of the connectivity-clearcut size relationship. The resulting persistence function shows a similar shape but lower values than the previous case (represented by light gray lines). (C) A species with high dispersal capabilities is represented by an increase in the minimum connectivity at high clearcut sizes (e.g. a higher capacity to cross large gaps) and, consequently, by persistence function with a higher maximum which is also shifted towards the right.



**Fig. 8.** Comparison between the persistence curves obtained for (A) the simulation of SLOW, BASE and HIGHDISP (“perceptive” version and LDR = 200%, Figs. 3, 6A–B) and (B) the curves obtained for the “low dispersal”, “generic” and “high dispersal” species (Fig. 7). The axes of graph (B) do not have an absolute scale and were adjusted to visually match those of graph (A).

affected by isolation). The effect of this change is an increase in the maximum persistence time, which is also shifted towards the right (gray line, Fig. 7C).

In order to compare the predictions of the analytical model described in Fig. 7, in Fig. 8A we show the persistence curves obtained for the simulation of SLOW, BASE and HIGHDISP (“perceptive” version and LDR = 200%, Figs. 3, 6A–B) and in Fig. 8B, the curves obtained for the “low dispersal”, “generic” and “high dispersal” species.

The high resemblance between these two groups of curves suggests that the proposed trade-off model provides a parsimonious explanation for the studied system. However, it is important to highlight the fact that our predictions are only valid in landscapes where the negative association between patch size and inter-patch distance (Fig. 7) exists, which is likely not the case of most naturally and many artificially-created patchy open habitat, where there is a tendency for smaller patches to be more isolated (e.g. Eichel and Fartmann, 2008; Bauerfeind et al., 2009; Wilson et al., 2009).

Our results showed that there was a positive overall effect of lifetime of habitat patches on population persistence, agreeing with previous studies (Boughton and Malvadkar, 2002; Wilcox et al., 2006). Given a fixed rotation time, species being able to use a larger range of plantation ages, actually have access to more habitat, thus increasing population size and persistence, and making spatial pattern of preferred habitat less important for the latter variables (Fahrig, 1992).

Population persistence time increased in the static scenario (Fig. 5, compared to Fig. 3). This result is in accordance with previous work showing that persistence of metapopulations is inversely related to habitat turnover rate (e.g. Keymer et al., 2000). An exception to the latter was observed by Wimberly (2006), who concluded that, when disturbance patches were small, dynamic landscapes might be more favorable than static systems by providing temporary connections for species that cannot cross gaps, thus enhancing persistence.

Although in our study we did not find cases in which the dynamic landscape improved persistence in relation to the static scenario, it is interesting to note that the opposite trend was less significant when clearcut sizes were small which is when temporary connections are more likely to have a positive effect (Wimberly, 2006).

The different species tried in our experiments varied in their response to shifting landscape mosaics (Wimberly, 2006). Traits that increased mortality (SLOW: slow movement through hostile environments) or limited recruitment (SEXUAL: reduced probability of reproduction), decreased the overall persistence time of the metapopulation.

Particularly when using large clearcuts, high mobility (HIGHDISP) allowed “perceptive” individuals to move faster through the landscape, thus reducing landscape-induced mortality and partially overcoming isolation effects. The latter agrees with Wimberly’s (2006) observation that highly mobile species are less sensitive to landscape dynamics at moderate to high amounts of habitat. On the contrary, slow moving species had difficulties relocating after the disappearance of their habitat, if they occurred in large (more isolated) patches. The reason why “perceptive” HIGHDISP showed a lower persistence time at intermediate clearcut sizes (4 and 16 cells)? is probably a result of the small turning angle imposed by us to the species’ movement algorithm. This constraint meant that if an individual accidentally left a habitat cell (event having a 0.1% daily probability), it was impeded from returning to it in the following time step. The latter likely affected more those individuals present in small patches, because they were more easily expelled to the hostile matrix. The reason why this effect was not seen in the case of the smallest clearcut size

(1 cell) seems rather intriguing, but may be due to the fact that, given the high density of small patches of suitable habitat, a high proportion of involuntary movements to the matrix ended up with individuals in the vicinity of other habitat patches, towards which the individuals might move in the following time step.

In our model, a major driving force of the dynamics of the population were landscape-induced deaths (LDR), which are directly related to the time spent by individuals in non-habitat cells (i.e. dispersal mortality). Because we recorded the cause of death of every single individual in our simulations we know that, for example, 52–65% of the deaths among “perceptive” BASE were caused by LDR (compared to just 32–42% caused by CDR), and, in the case of “perceptive” SLOW, LDR-caused deaths raised to 55–73% (with 24–39% caused by CDR). This reflects the importance of dispersal abilities in the persistence populations in dynamic landscapes (Travis and Dytham, 1999).

Among the simplifications of our model, we directly did not consider any variation for the patch size in a given scenario. The implications of patch-size variability on our model are not evident. Theodorou et al. (2009) suggested that size heterogeneity between patches probably reduces metapopulation persistence due to the sink effect of small patches. On the other hand, Schippers et al. (2009) found that a mixture of large and small patches produced a synergistic effect, enhancing metapopulation persistence. Because of the random assignment of initial ages to patches in the landscape in our model, sometimes two or more adjacent patches were assigned the same age class, therefore creating larger stands and some patch-size variability (Fig. 1). Thus, the nominal patch size reported by us in all figures is a slight underestimation of the actual size “experienced” by the virtual metapopulation. Nevertheless, due to the nature of our analyses, we consider the latter situation to have a negligible effect on our conclusions.

Although the main goal of forest plantations is the production of timber and fiber, their role as habitat for biodiversity is increasingly being recognized (Brockhoff et al., 2008). Due to the great expanses covered with forest plantations throughout the world, the implications that different management techniques may have on the conservation of biodiversity are significant. Among the latter, clearcutting is one of the most controversial (Pawson et al., 2006). Therefore, an important goal of modern plantation forestry should be minimizing the negative effects and enhancing the potential benefits of clearcutting, including its role in the conservation of endangered early-successional wildlife species (Paquet et al., 2006).

Defining the size of individual clearcuts is usually the result of a trade-off between economic and environmental constraints (Boston and Bettinger, 2001). Our model makes predictions that can be integrated in such analysis. First, larger clearcut sizes should be relatively more beneficial for early-successional species with limited capacity to actively direct their movement (i.e. those adequately represented by a “random-walk” movement, Fahrig, 1998). Second, for most species that can actively search for a suitable habitat, the highest survival time is achieved at intermediate clearcut sizes, with high-dispersal species reaching a maximum at higher clearcut sizes.

Therefore, very large clearcuts may be incompatible with the conservation of many early-successional vertebrates that have limited dispersal capacity unless additional conservation measures are taken to overcome the lack of connectivity. First, the use of corridors has been shown to be effective in increasing the movement of different wildlife species between clearcut patches in a forested landscape (Haddad et al., 2003). Existing structures such as fire-breaks and low-traffic logging roads may also be redesigned in order to serve the latter purpose. Second, unlike our random stand allocation protocol, managers can resort to different spatial



optimization techniques in order to increase the overall connectivity in the landscape (Hof and Bevers, 1998). Through modified adjacency constraints or clustering of stands (Baskent and Keles, 2005), clearcuts could be arranged in a way that maximizes the temporary connections among these ephemeral habitat patches.

Meeting the requirements of species of various life histories and behavioral traits with those of efficient timber production is a complicated task. In this scenario, IBSEPMs are a cost-effective technique to conduct an initial screening of the response of populations and communities to proposed conservation actions, narrowing the range of treatment choices for the unavoidable (though more complicated) field experiments.

## Acknowledgments

Funds for this study were provided by a Fondecyt Grant (1080463) to C.F. Estades. We thank H.J. Hernández for lending us some fast computers that saved us days of simulation time. Two anonymous reviewers provided very useful criticism on an earlier version of this work.

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