1   **EFFECTS OF THE SPATIAL PATTERN OF DISTURBANCE ON THE**

2   **PATCH-OCCUPANCY DYNAMICS OF JUNIPER-PINE OPEN WOODLAND**

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1   **Abstract**

2

3   Typically, studies of the disturbance effect on metapopulation dynamics are limited to

4   understanding the effect of habitat loss although, recently, the spatial pattern of the

5   disturbance has been shown to influence dynamics. In this study, we used a stochastic

6   patch-dynamic model to investigate the effects of spatial disturbance patterns on the

7   persistence of an open woodland community of *Juniperus* spp. and *Pinus* spp. First, we

8   estimated patch occupancy dynamics by using the coefficients that best predicted the

9   occupancy observed in 1998 based on occupancy data from 1957. Next, we evaluated

10   the effects of the rate and pattern of the disturbance on the extinction probability. In

11   modeling the disturbance, we considered (1) the degree of disturbance produced by

12   scenarios of complete destruction or degradation (with the potential for recolonization),

13   (2) the overall rate of disturbance, and (3) the spatial autocorrelation of habitat

14   destruction. Twenty 40-yr simulations predicted a 25% increase in the number of

15   patches, and the impact was more pronounced after complete destruction than it was

16   after degradation of the area. Predictions based on scenarios of complete destruction,

17   including random, contiguous, Brownian, and autoregressive noise, demonstrated that

18   the impact of disturbance depends upon the spatial structure of the disturbance regimen.

19   The autocorrelated structure of the disturbance regimen had the greatest impact on patch

20   persistence. Patch occupancy was higher after 20 40-yr simulations when habitat loss

21   was randomly distributed than when it followed an autocorrelated patch destruction,

22   which was simulated using autoregressive noise to produce 50% habitat destruction. In

23   addition, while habitat loss was negatively linearly correlated with patch persistence

24   when habitat destruction was randomly distributed, a dramatic transition shift occurred

25   when habitat destruction was simulated following an autoregressive spatial distribution

1   after a certain threshold of habitat destruction (40% of the actual open woodland

2   habitat). Our study suggests that the spatial patterns of the disturbance should be

3   considered when predicting the consequences of fragmentation and improving

4   management strategies.

5

6   Key words: fragmentation; metapopulation; metacommunity, spatial autocorrelation;

7   Ebro Valley, Spain

8

9   **Introduction**

10

11   The conservation of species in fragmented landscapes is an important aspect of

12   conservation ecology because ecosystem fragmentation is one of the main factors

13   influencing extinction risk (Thomas et al., 2004). The two main aspects of habitat

14   fragmentation are overall habitat loss and habitat configuration (MacArthur and Wilson,

15   1967). Although the contribution of habitat loss to species extinctions is widely

16   recognized, the effects of spatial configuration warrants more attention (Moloney and

17   Levin, 1996; Fahrig, 2002; He and Legendre, 2002). Evidence suggests that landscape

18   disturbances are seldom randomly distributed; rather, they operate in a self-organized

19   manner (Bak and Chan, 1991) or are subjected to multi-scaled randomness (Halley,

20   1996; Hausdorff and Peng, 1996; Halley and Kunin, 1999). Indeed, spatial and temporal

21   autocorrelations in environmental factors such as weather and habitat degradation can

22   influence the response of populations to changes in the landscape. For example, some

23   correlated spatial conditions can affect significantly the probability of the destruction of

24   nearby patches (e.g., anthropogenic patch destruction or natural as drought or

25   epidemic); consequently, processes acting at very different scales can affect the

1   probability of patch occupancy. Thus, recently, the spatial patterns of disturbance

2   regimes have received considerable attention (Durrett and Levin, 1994; Moilanen and

3   Hanski, 1995; Moloney and Levin, 1996; Bascompte and Solé, 1998; Bevers and

4   Flather, 1999; With et al., 1999; Flather and Bevers, 2002; Johst and Drechsler, 2003;

5   Xu et al., 2006)

6   The importance of the spatial component of disturbance has been recognized for some

7   time (Watt, 1947), although a better understanding of the consequences of habitat

8   fragmentation on the persistence of plants and communities remains an active area of

9   research (Scariot, 1999; Tabarelli et al., 1999; Johst and Drechsler, 2003). The impact of

10   disturbance on population dynamics depends at least partially on the spatial structure of

11   the disturbance regimen and, in highly fragmented landscapes, more habitat is needed

12   for populations to have a high probability of persistence (Hill and Caswell, 1999a; With

13   and King, 1999a). Within a metapopulation (populations separated spatially, but

14   interconnected by dispersal) (Freckleton and Watkinson, 2002), the persistence of

15   populations depends on the colonization of vacant habitats (Hanski and Gilpin, 1997),

16   and species differ in their threshold of habitat availability (Lande, 1993; Gibbs, 1998;

17   Eriksson and Kiviniemi, 1999). In plants, decreased recruitment into patches is believed

18   to be a primary factor in local extinctions (Cardoso Da Silva and Tabarelli, 2000).

19   Small fragments can favor seed predation (Santos and Telleria, 1997; Curran and Webb,

20   2000) and reduce seed dispersal by frugivorous vertebrates (Santos and Tellería, 1994;

21   Santos et al., 1999).

22   In our study, we evaluated the effects of spatial patterns of disturbance on the

23   persistence of a juniper-pine open woodland community dominated by *Juniperus*

24   *thurifera* L. or *Pinus halepensis* L., which is the best preserved natural vegetation in the

25   Middle Ebro Valley, Spain (Braun-Blanquet and Bolòs, 1957; Rivas-Martínez and

Costa, 1970). On the western Mediterranean Basin, *Juniperus thurifera* L is an endemic

dioecious species that forms open woodlands, which traditionally have been managed

for grazing and wood harvesting (Gauquelin et al., 1999). In the Ebro Basin, Spain, *J.*

thurifera was abundant until the 18th Century. (Braun-Blanquet and Bolòs, 1957), but

livestock activity and wood removal was very intense up until the 1950s, when these

activities were greatly reduced (Lasanta et al., 2000). Recovery of this woodland habitat

was expected, but the fragmentation of remnant stands and a decrease in fruit

production constrained the regeneration of open woodlands (Santos and Tellería, 1994;

Pueyo and Alados, 2007). Our study evaluated the importance of colonization and

extinction mechanisms in the recovery of open woodland and how the spatial patterns of

disturbance mediated the recolonization and persistence of open woodland patches.

Stochastic patch-occupancy models are valuable in linking habitat occupancy and

population ecology when a large proportion of the landscape is unused and the

persistence of the metapopulation depends on the connectivity of occupied habitats

(Caswell and Etter, 1993; Hanski, 1994; 1999; Moilanen, 1999; Etienne et al., 2004;

Moilanen, 2004; Verheyen et al., 2004; Purves et al., 2007). The assumptions that apply

to the metapopulation apply as well to the metacommunity, which is a set of interacting

species that are connected by dispersal (Wilson, 1992; Mouquet and Loreau, 2002;

Guichard et al., 2004; Leibold et al., 2004). The objective was to identify the patterns of

occupancy/extinction in an open woodland community in which patches were occupied

by juniper, pine, or both. In addition, we examined systematically the effects of

different rates and configurations of disturbance on extinction probabilities. To

understand the implications of the spatial structure of fragmented habitats for land

management, a systematic approach to the study of the interactions between the spatial

configuration of the disturbance and the persistence of populations is required. If the

1 extinction probabilities under different conditions can be predicted, the conditions can

2 be manipulated to maximize the persistence probabilities of species. Typically,

3 extinction models rely upon stochastic variability, but extinction models that

4 incorporate correlated environmental noise, e.g., autoregressive models are popular

5 (Ripa and Lundberg, 1996; Petchey et al., 1997; Halley and Kunin, 1999; Morales,

6 1999; Morris and Doak, 2002). In the models, we estimated the implications of

7 contiguous, random, Brownian, and autoregressive spatial configurations of habitat loss

8 on extinction risk. Ultimately, we wanted to identify the conditions under which

9 spatially structured habitats can support habitat persistence.

10 This study addressed the following questions: (1) How are the extinction and

11 colonization probabilities influenced by the size of remnant woodland patches and the

12 distances between them?, (2) How is the extinction threshold affected by scenarios of

13 complete destruction or degradation (with the potential for recolonization)?, and (3)

14 How does the spatial autocorrelation of open woodland destruction affect the extinction

15 threshold?

16

17 **Methods**

18

19 **Study Area**

20 The study was conducted in the Middle Ebro Valley, northeastern Spain, where the

21 elevation ranges between 120 m at the bottom of the valley to 800 m at the highest peak

22 in the Alcubierre Mountain Range. The climate is semi-arid Mediterranean. Typically,

23 annual rainfall varies between 200 and 350 mm year^{-1} and most of the rain occurs in

24 spring and autumn. The substrate is mainly a gypsum substratum that alternates with

25 carbonate layers (marls and limestone) and, to a lesser extent, clays (Quirantes, 1978).

1   The landscape is hills that have moderate slopes and shallow soils, and a flat basin that

2   receives run-off water and where grasslands have developed (Guerrero et al., 1999a;

3   Guerrero et al., 1999b). The vegetation of the Middle Ebro Valley includes a number of

4   endemic gypsophile plants, e.g., *Gypsophila hispanica* Wilk., *Ononis tridentata* L.,

5   *Helianthemum squamatum, Lepidium subulatum* L., and *Herniaria fruticosa* L. (Braun-

6   Blanquet and Bolòs, 1957; Rivas-Martínez and Costa, 1970; Parson, 1976). In the area,

7   the most developed vegetation occurs in the open woodlands of *Juniperus thurifera* L.

8   and *Pinus halepensis* L. (Braun-Blanquet and Bolòs, 1957; Rivas-Martínez and Costa,

9   1970).

10   Centuries of degradation caused by timber harvesting and livestock grazing have lead to

11   successional vegetation regression towards a dwarf-scrubland dominated by

12   *Rosmarinus officinalis* L. In the bottom of the valley, where the soils are more

13   developed because of the downward movement of water, fine particles, and ions

14   (Navas, 1990a; b; Guerrero et al., 1999a; Guerrero et al., 1999b), agriculture is

15   widespread and crops covered 50% of the study area (Pueyo and Alados, 2007).

16

17   **Data Analysis**

18

19   To fit a stochastic patch-dynamic model, we identified all of the suitable areas of patch

20   occupancy in digitized vegetation maps derived from orthorectified aerial photographs

21   taken in 1957 (1:33,000 scale) and 1998 (1:5,000 scale) (Pueyo and Alados, 2007). To

22   correct for a difference in scale, the maps were digitized at the same spatial resolution

23   (1:20,000). In fragmented landscapes, suitable and unsuitable areas can be

24   distinguished; e.g., the identification of suitable habitat for juniper-pine open woodlands

25   assumed rosemary (dwarf-scrubland dominated by *Rosmarinus officinalis* L.) is suitable

1 habitat because transitions to open woodland occur (Pueyo and Alados, 2007), but

2 steppes (dominated by *Lygeum spartum* L., *Salsola vermiculata* L., and *Artemisia*

3 *herba-alba* Asso) and croplands are not suitable habitats because their transformation to

4 open woodland is negligible (Pueyo and Alados, 2007). Categories of plant cover were

5 based on plant associations, which consist of a plant community that has a definitive

6 floristic composition, uniform physiognomy, and grows in uniform habitat conditions.

7 From within the 45,650-ha study area, we identified 326 patches (1142 ha), which

8 included all of the juniper-pine open woodland patches (88 patches) and all of the

9 dwarf-scrub patches in which juniper-pine could colonize (239 patches). Other habitats,

10 such as steppes, croplands, and human settlements were not included in the analysis

11 because colonization by juniper-pine woodland does not occur there. Patch coordinates

12 were derived by averaging the X-Y coordinates of the 20m-pixels within each patch. If

13 >50% of the area of an individual patch in 1957 was present in 1998, the patch was said

14 to have persisted; otherwise, the patch was considered extinct.

15 To estimate patch-occupancy dynamics, we used the coefficients that best predicted the

16 observed occupancy in 1998 based on occupancy data from 1957. To find the maximum

17 likelihood estimates, the logistic regressions for extinction and colonization were fitted

18 separately following Moilanen (1999) and Morris and Doak (2002). The low

19 germination and growth rate of juniper species can hinder the recovery of a juniper-pine

20 open woodland. To compensate for the long lifespan of juniper and pine, which can

21 mask population extinctions, in the analysis, we extended the time grain to four decades

22 (see Verheyen et al., 2004). The state of the metacommunity at any time *t* is given by

23 the population vector $O_i(t)$. At any time *t*, each site is either occupied (i.e., $O_i(t) = 1$) or

24 unoccupied (i.e., $O_i(t) = 0$). The observed pattern of occupancy in open woodland in

25 1957 is denoted by $O_i(1)$ and in 1998 by $O_i(2)$. The metacommunity dynamic is driven

1   by local extinction and colonization probabilities. The transition probabilities between

2   1957 and 1998 for each site is denoted by $P[O_2|O_1]$, which is determined by the

3   separate probabilities of observed patterns of extinction $E_i(t)$ and colonization $C_i(t)$

4   between year 1957 and year 1998 (Moilanen, 1999; Morris and Doak, 2002):

5    $P[O_2|O_1]$

6    $$= \prod_{i=1}^{N} \begin{cases} C_i(1) & \text{if } O_i(1) = 0 \text{ and } O_i(2) = 1 \\ 1 - C_i(t) & \text{if } O_i(1) = 0 \text{ and } O_i(2) = 0 \\ E_i(t) & \text{if } O_i(1) = 1 \text{ and } O_i(2) = 0 \\ 1 - E_i(t) & \text{if } O_i(1) = 1 \text{ and } O_i(2) = 1 \end{cases}$$

7   (1)

8   where N is the number of patches.

9

10   The logit models for extinction and colonization are

11   $E_i = \dfrac{e^{u_e}}{1 + e^{u_e}}$ and $C_i = \dfrac{e^{u_c}}{1 + e^{u_c}}$ (2)

12   where

13   $u_e = a_e + s_e A_i + \beta_e \sum\limits_{j \neq 1}^{N} \exp(-\alpha D_{ij}) p_j A_j^{\ b}$ (3)

14

15   $u_c = a_c + s_c A_i + \beta_c \sum\limits_{j \neq 1}^{N} \exp(-\alpha D_{ij}) p_j A_j^{\ b}$ (4)

16

17   A is area of patch i or j, D_{ij} is the distance from patch i to patch j, p_j is 0 if site j is empty

18   and 1 if it is occupied, and a_e, s_e, β_e, β_c, a_c, s_c, b, and α are model parameters. Patch-edge

19   to patch-edge distances were calculated by subtracting patch radiuses (assuming patches

20   are circles) from the Euclidean center-to-center distances (Moilanen, 2004). In

21   equations (3) and (4), the last term corresponds to the migration probability equation

1 $(M_i = \beta \sum_{j \neq 1}^{N} A_j^{\ b} \exp(-\alpha D_{ij}) p_j)$ (Hanski, 1994). M_i is the sum of all of the individuals

2 originating from the surrounding populations apart from the focal patch (N), which

3 takes into account the distances to all of the nearby populations weighted by the size of

4 the patches.

5 To estimate the equation parameters, we used the Maximum Likelihood Parameter

6 Estimation Method (Moilanen, 1999). To calculate the log-likelihood, $LogL$, of seeing

7 the entire data set, we estimated the log-likelihoods for each year of colonization and

8 extinction data, as follows:

9

10 $$log L(data \mid_{E,C}) = log L(O_1 \mid_{E,C}) + log L_E + log L_C \qquad (5)$$

11 where

12 $$log L_E = \sum_{i=1}^{N} [O_i \ ln(E_i) + (1 - O_i) ln(1 - E_i)] \qquad (6)$$

13 $$log L_C = \sum_{i=1}^{N} [O_i \ ln(C_i) + (1 - O_i) ln(1 - C_i)] \qquad (7)$$

14 In using equation (5), occupancy patterns were assumed to be near equilibrium, which

15 will mask any evidence of a decrease in the metacommunity. If stability cannot be

16 assumed because changes in metacommunity size indicate a long-term increase or

17 decrease, it is better to use extinction and colonization functions, only, and to set

18 $log L(O_1 \mid_{E,C}) = 0$ (Morris and Doak, 2002). Although the extent of open woodland

19 cover in the study area changed little between 1957 and 1998 (Pueyo and Alados,

20 2007), increased demand for land for agriculture, industry, and the expansion of urban

21 areas was significant and, therefore, we could not assume stability. The probabilities of

22 extinction and colonization were fitted to a 40-yr interval, which reflected the interval

23 encompassed by the data.

1   To simulate the expected dynamics of patch occupancy over time, we calculated the

2   probabilities of extinction and colonization of individual patches using parameter

3   estimations, their sizes, and nearest-neighbor distances. To determine the fate of a patch,

4   we drew a uniform random number between 0 and 1, and compared it to the

5   probabilities of extinction and colonization. Beginning with the initial occupancy data

6   from 1998, we projected the metacommunity into 20 40-yr time intervals.

7   Systematically, at intervals of 10%, we evaluated the effect of removing 10-90% of the

8   open woodland cover area. The simulation removed patches from the model until the

9   desired proportion (%) was reached, then the analysis proceeded.

10   Patches were ordered in an ascending sequence of their distance to their nearest

11   neighbor and we assigned a number to the order. Patches were removed using the

12   following procedures:

13   (i) Select a contiguous sequence of closest patches to an initial randomly selected

14   position.

15   (ii) Generate a sequence of independent random numbers and select the patch based on

16   its position. To that end, we placed the patches in order, assigned a number to the order,

17   and selected one of the numbers randomly. The corresponding patch was then removed.

18   (iii) Generate a Brownian process by adding an independent normal random variable, z_t,

19   (with mean $= 0$ and variance $= 1$) to the previous value (Saupe, 1988).

20   $\varepsilon_{t+1} = \varepsilon_t + z_t$ (8)

21   The procedure was similar, but, after we placed the patches in order and assigned a

22   number to the order, we added a normal random term to the previous random term and

23   selected the corresponding patch.

1 (iv) Generate autoregressive random noise by a relaxation process on a characteristic

2 spatial scale (Schroeder, 1991). We used a first-order autocorrelation, ρ, where the

3 space scale, τ, was 1 spatial unit. The following equation generated noise:

4 $\quad \varepsilon_{t+1} = \varepsilon_t + X_{t+1}$ $\hspace{8cm}$ (9)

5 where $X_{t+1} = \rho X_t + \sqrt{1-\rho^2}\, z_t$, and where ρ is the desired correlation coefficient between

6 adjacent samples. It is related to the space scale τ by the equation $\rho = \exp(-1/\tau)$ (Halley

7 and Kunin, 1999), (e.g., for $\tau = 1$, $\rho = 0.37$).

8 The procedure was similar but, in each successive selection, we added the

9 autoregressive distribution, X_t, term and selected the corresponding patch.

10 The Cumulative Distribution Function (CDF) of extinction time, which estimates the

11 probability that a metacommunity starting at the current patch occupancy will be extinct

12 before each set of future time steps (Morris and Doak, 2002), was estimated using 500

13 computer iterations.

14

15 **Results**

16

17 *Effects of patch size and distance on the probabilities of extinction and colonization*

18

19 In 1957, 349 (27%) of the 1298 ha of suitable habitat in the study area (45,650 ha) were

20 covered by 88 patches of open woodland (mean = 3.96 ha ± 1.14 SE) (Figure 1). In

21 1998, the area included 83 patches of open woodland that covered 348 ha (mean = 4.20

22 ± 1.43 ha).

23

24 $\hspace{3cm}$ #Fig1 approximately here#

25

1   Patch size and the probability of extinction (s_e=-0.139) were negatively correlated; i.e.,

2   the smaller the size of the patch, the higher the probability of extinction. Patch size and

3   the probability of colonization were positively correlated (s_c = 1.315). The intercept

4   parameter values of a_e and a_c were 0.043 and -2.391, respectively. The parameter β,

5   which is the intercept value of the migration function (migration rate independent of the

6   distance; i.e., all patches can be colonized regardless of inter-patch distance), was

7   negatively correlated with the extinction probability (β_e = -0.010) and positively

8   correlated (β_c= 0.042) with the probability of colonization. The parameter α is the

9   inverse of the average dispersal distance. A high value (9.04) indicates the strong effect

10 of neighboring populations on extinction and colonization probabilities; i.e., the

11 probability of colonization decreased dramatically with an increase in the distance

12 between populations, whereas the probability of extinction increased with increasing

13 distance). The parameter b scaled the patch area to -0.804, which indicates that patch

14 area counterbalanced the negative effect of distance between fragments. The maximum

15 likelihood estimate for the logistic regression model was -132.05 (Table 1). The number

16 of occupied patches in the second partition was 6 in 1957 and 14 in 1998, which

17 paralleled the recovery observed in the simulations; nevertheless, the number of patches

18 in the second partition was less than the number recommended by Hanski (1999) for the

19 model parametrization. We then calculated averaged parameter values from 100

20 nonparametric bootstrap simulations (repeatedly sampling from the original data with

21 replacement). The estimated parameters are included into the confidence limits of the

22 bootstrap parameters (Table 1).

23

24 *Probability of metacommunity extinction under current conditions and under simulated*

25 *stochastic scenarios of habitat destruction*

1

2   Starting with the conditions in 1998, after 20 40-yr intervals and 500 iterations the

3   probability of metacommunity extinction was approximately 0. At the end of the 40-yr

4   period, the average number of occupied patches was 118.55 ± 0.39 (mean ± se) and the

5   negative log-likelihood was 69.93. The simulation predicted an increase of almost 25%

6   in the number of patches (Fig. 2). If 50% of the open woodland patch cover is removed

7

8   # Fig. 2   approximately here #

9

10   (complete destruction of the area), the predicted number of patches at the end of the

11   simulation period was 39.35 ± 0.87 (negative log-likelihood, NLL, = 21.25). Simulation

12   of the probability of patch occupancy after the stochastic transformation of 50% of the

13   open woodland community into a dwarf-scrubland community predicted 117.92 ± 0.43

14   (NLL = 85.78) patches at the end of the 40-yr period.

15

16   *Probability of metacommunity extinction based on simulations of the spatial*

17   *distributions of habitat destruction*

18

19   In the study area, the forces driving changes in habitat are the expansion of urban and

20   peri-urban areas, rather than the traditional factors such as overgrazing and wood

21   harvesting, which were responsible for the degradation toward dwarf-scrubland. We

22   evaluated the effects of patch destruction on the simulation by generating different

23   spatial distribution sequences for the removal of 50% of the patches, including

24   contiguous, random, Brownian, and autoregressive patch destruction. When patch

25   destruction followed a stationary random distribution, the number of patches at the end

14

1 of the simulation was significantly ($F_{3, 1996} = 321.06$, $P < 0.001$) higher than the number

2 of patches when destruction followed a contiguous spatial pattern (Fig. 3). When

3

4 # Fig. 3 approximately here#

5

6 patch destruction was generated by simulating spatial environmental variability

7 following Brownian noise and autoregressive noise, the average number of patches at

8 the end of the simulation was even lower (Fig. 3).

9 In addition, patch destruction was simulated by reducing patch area by 10% to 90 %

10 after the addition of random and autoregressive noises (Fig. 4). Contiguous and

11 Brownian noises were excluded because they did not add more information beyond

12 what was provided by the addition of the two extreme cases (white noise and

13 autoregressive noise).

14

15 # Fig. 4 approximately here #

16

17 At the end of simulation, the number of patches had decreased linearly when patches

18 were removed randomly, but when land was destroyed following an autoregressive

19 spatial distribution, patch removal had a pronounced effect when destruction occurred

20 on >40% of the suitable land. Beyond that critical threshold, the average number of

21 patches at the end of the simulation period (20 40-yr intervals) rapidly approached

22 extinction values. Autoregressive removal simulates the contagious destruction of

23 neighboring habitats, which results in an increase in the difficulty of connecting isolated

24 patches when the distance to neighboring populations reaches a connectivity threshold,

1   but under a low level of habitat destruction, the impact is lower than it is for random

2   destruction.

3

4   **Discussion**

5

6   In this study, the impact of disturbance depended on the overall rate of disturbance and

7   the spatial autocorrelation of habitat destruction. The number of patches that remained

8   at the end of the simulation decreased in direct proportion to the amount of habitat loss

9   when habitat loss was randomly distributed, but when habitat loss followed an

10   autoregressive distribution, the number of patches that remained dropped dramatically.

11   Where patches suitable for colonization are widely spaced (52% of the habitat is

12   unsuitable croplands and only 7% of the area is covered by open woodland),

13   colonization is limited by the ability of the diaspora to reach suitable habitat. Initially,

14   the effect of habitat destruction is limited to the amount of habitat loss but, as the

15   number of occupied sites destroyed increases, some patches become isolated and it

16   becomes more difficult to colonize distant patches. In addition to habitat destruction,

17   after some critical amount of habitat loss, further destruction results from the isolation

18   effect, which reduces the probability of colonization. The effect is equivalent to the

19   phase transition near the critical point, and the critical fraction of destroyed habitat is

20   the percolation threshold (Solé and Bascompte, 2006). Thus, if the juniper-pine open

21   woodland community is to be preserved, it appears that there is a specific threshold of

22   habitat loss (in our study, 40%) that should not be exceeded. Overall community

23   persistence was sensitive to habitat fragmentation, which is consistent with the low

24   germination and growth rates of juniper (*Juniperus thurifera* L.), which produces fleshy

25   seeds that are dispersed by passerine birds that are very sensitive to habitat

1   fragmentation (Santos and Tellería, 1994; Santos et al., 1999). Others studies have

2   shown that an extinction threshold can depend on the spatial pattern of habitat

3   destruction, e.g., random or fractal habitat destruction (Hill and Caswell, 1999b; With

4   and King, 1999a; Ovaskainen et al., 2002; Kallimanis et al., 2004), and the spatial

5   correlation of disturbance can reduce the persistence of metapopulations (Johst and

6   Drechsler, 2003).

7   To estimate extinction and colonization parameters, and to simulate open woodland

8   patch dynamics under various scenarios of habitat destruction, we used a stochastic

9   patch-occupancy model, which was parameterized using patch-occupancy data (Hanski,

10   1994; Moilanen, 1999; Morris and Doak, 2002; Moilanen, 2004). We used data from

11   326 patches in the Middle Ebro Valley, Spain, where the amount and distribution of

12   open woodland cover changed little between 1957 (3406 ha) and 1998 (3471 ha),

13   although 389 ha were transformed into cropland and 454 ha reverted to open woodland.

14   Indeed, habitat isolation reduced the likelihood of the recovery of the open woodland

15   community (Pueyo and Alados, 2007). By incorporating patch connectivity into the

16   model, open woodland habitat increased almost 25% after 20 40-yr simulations;

17   specifically, the number of patches increased from 88 to 118. The long-term persistence

18   of isolated fragments of open woodland in the Middle Ebro Valley might be the result

19   of long generation times, which reflect the historical landscape configuration (including

20   the historical distribution of the forest and land use), rather than recent changes in the

21   landscape, which can lead to an extinction debt (Tilman et al., 1994; Honnay et al.,

22   2005).

23   By comparing the results from models that used a fixed disturbance rate, we can better

24   understand the effects of disturbance on the persistence of an open woodland

25   community. In our study, the greatest effect of a fixed disturbance rate of 50% occurred

1   when habitat was destroyed, rather than merely degraded (and able to be colonized). In

2   the Middle Ebro Valley, historically, habitat degradation was the result of overgrazing

3   and timber harvesting, which led to a transformation into dwarf-scrubland and steppe

4   (Braun-Blanquet and Bolòs, 1957). Currently, recovery is hampered by livestock

5   shelters (Pueyo and Alados, 2007), but grazing and timber harvesting (habitat

6   degradation) are no longer significant threats in the area (Olano et al., 2008). Instead,

7   increased demand for land for agriculture and the expansion of industry and urban areas

8   (habitat destruction) are the main threats to the natural open woodland habitat (Pueyo

9   and Alados, 2007).

10   Spatially autocorrelated environmental degradation caused by, for example, direct

11   human activities or global climate change is important because correlations in local

12   extinctions greatly elevate the overall extinction probability of metapopulations (Lahaye

13   et al., 1994; Moilanen and Cabeza, 2002; Johst and Drechsler, 2003). The outcome of

14   sequential patch destruction changes dramatically when autocorrelation structure is

15   included in the simulation (Hill and Caswell, 1999a; Kallimanis et al., 2004). By

16   comparing the effects of the spatial patterns of disturbance on the patch dynamics of the

17   open woodland community, we found that the effect on model outcomes varied

18   depending on the autocorrelation structure of the disturbance regime. The number of

19   patches that remained after 20 simulations of the model was less than half of the number

20   of patches that remained when patch removals were random, rather than autocorrelated.

21   In this study, the model included patch occupancy stochasticity, but it did not consider

22   the temporal variability caused by environmental change. Several years of additional

23   data are required before temporal stochasticity can be included in the analyses.

24   The effect of spatial habitat structure on the likelihood of ecosystem preservation might

25   be very important. Recent ecological models have shown that, when spatial

1   environmental heterogeneity is included, the response of the system (gradual or

2   catastrophic) depends on the spatial patterns of environmental heterogeneity (van Nes

3   and Scheffer, 2005). In fragmented ecosystems, spatial connectivity is greater in fractal

4   landscapes (i.e., those that have an autoregressive pattern of habitat loss) than it is in

5   random landscapes, and the percolation threshold occurs at a smaller proportion of

6   habitat abundance (With and King, 1999b). Consequently, successful dispersal is more

7   strongly enhanced in fractal landscapes than it is in random landscapes, although

8   dispersal success decreases dramatically when habitat is scarce.

9

10   In summary, our study indicates that, in addition to the intensity of disturbance,

11   predictions of the impact of disturbance on patch persistence need to consider the spatial

12   distribution of the disturbance pattern. When spatial structure is present and the

13   extinction probability is a function of the area of the specific patch, patch-based models

14   are appropriate. Those models improve our ability to estimate patch persistence in

15   fragmented landscapes and provides a better understanding of population and

16   community responses to environmental change. We have demonstrated how large-scale

17   patterns and processes (environmental autocorrelation destruction) influence habitat

18   persistence. Patch-occupancy simulation models that incorporate autocorrelated

19   environmental stochasticity of real-world landscapes can be used to estimate habitat

20   persistence probabilities in the face of regional or global change.

21

22

23   **Acknowledgements**

24

4

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1

2 Legends:

3 Fig 1. The distribution of patches of an open woodland community in the Middle Ebro

4   Valley, Spain, where juniper-pine existed (black) and patches of dwarf-scrub

5   where juniper-pine open woodland could colonize (grey) based on 1957

6   orthorectified aerial photographs.

7

8 Fig. 2. Predicted mean number of patches following 500 iterations of twenty 40-yr

9   intervals for three scenarios of juniper-pine open woodland abundance (actual

10   conditions, 50% of habitat degraded, 50% of habitat destroyed) based on data

11   from the Middle Ebro Valley, Spain.

12

13 Fig. 3. Predicted mean number of patches present at the end of twenty 40-yr intervals

14   following 500 iterations for juniper-pine open woodland patches in the Middle

15   Ebro Valley, Spain, after 50% complete destruction that followed one of four

16   spatial sequences (random, Brownian, autoregressive and contiguous).

17

18 Fig. 4. Predicted mean number of patches present at the end of 500 iterations for a

19   juniper-pine open woodland community in the Middle Ebro Valley, Spain, by

20   reducing patch area by 10% to 90% after the addition of random and

21   autoregressive noises.

22

Figure
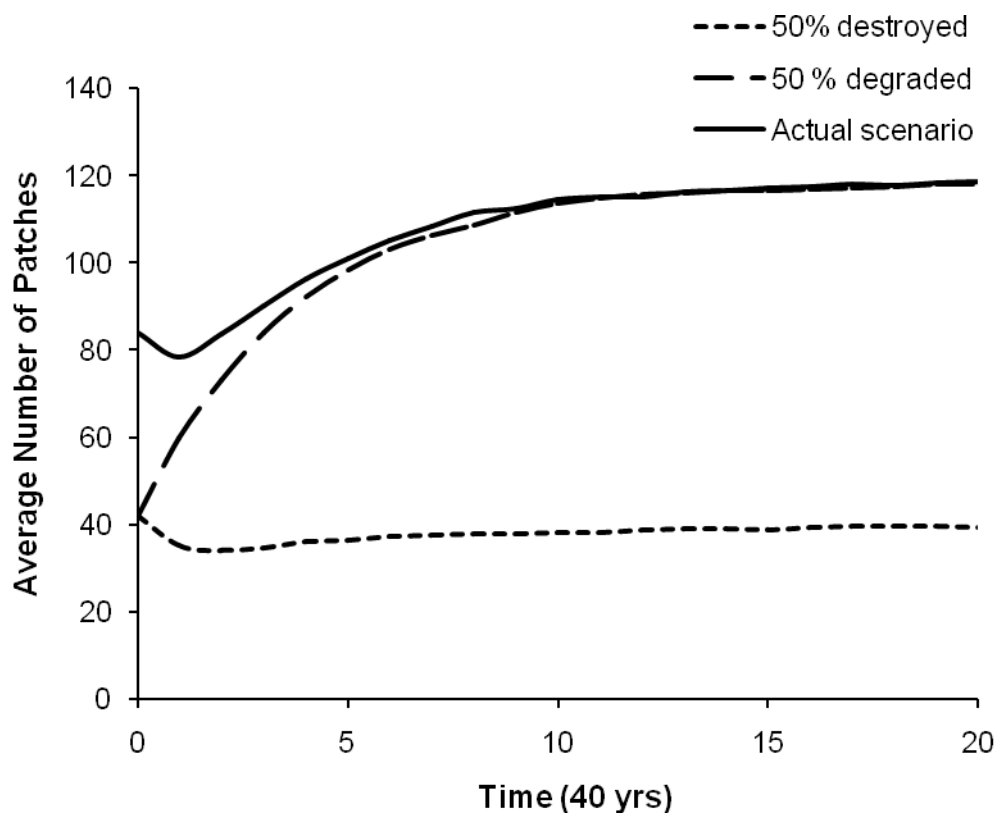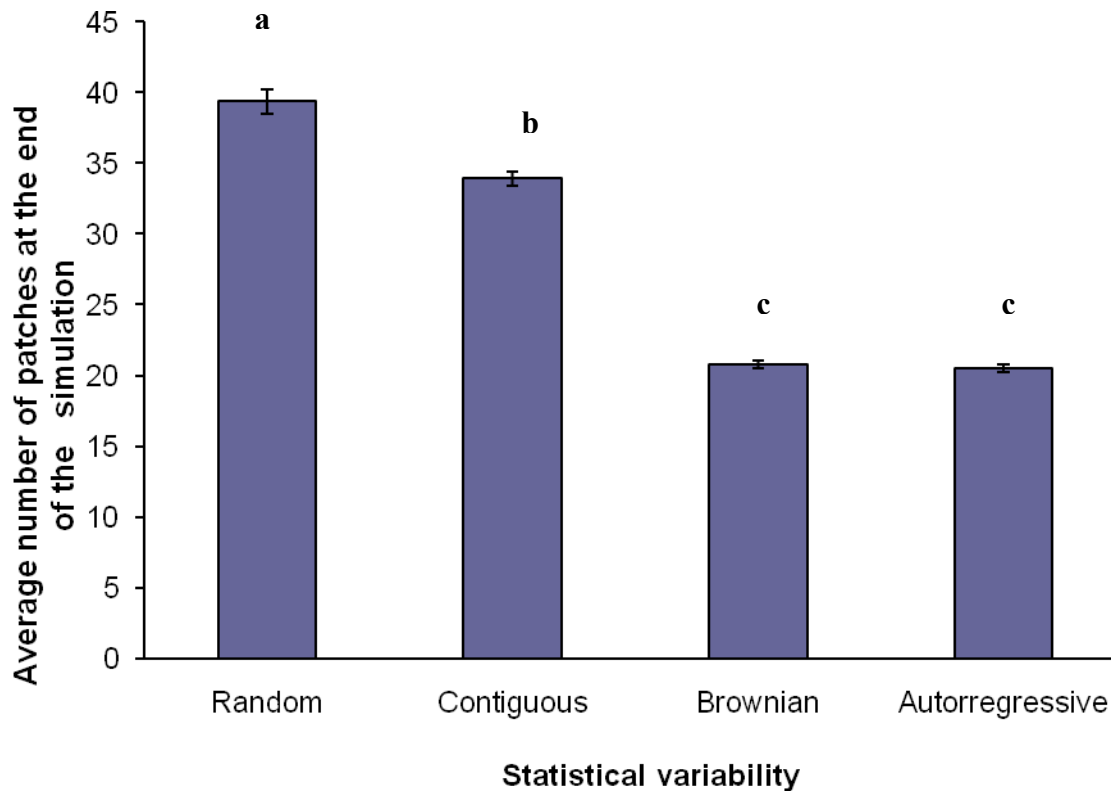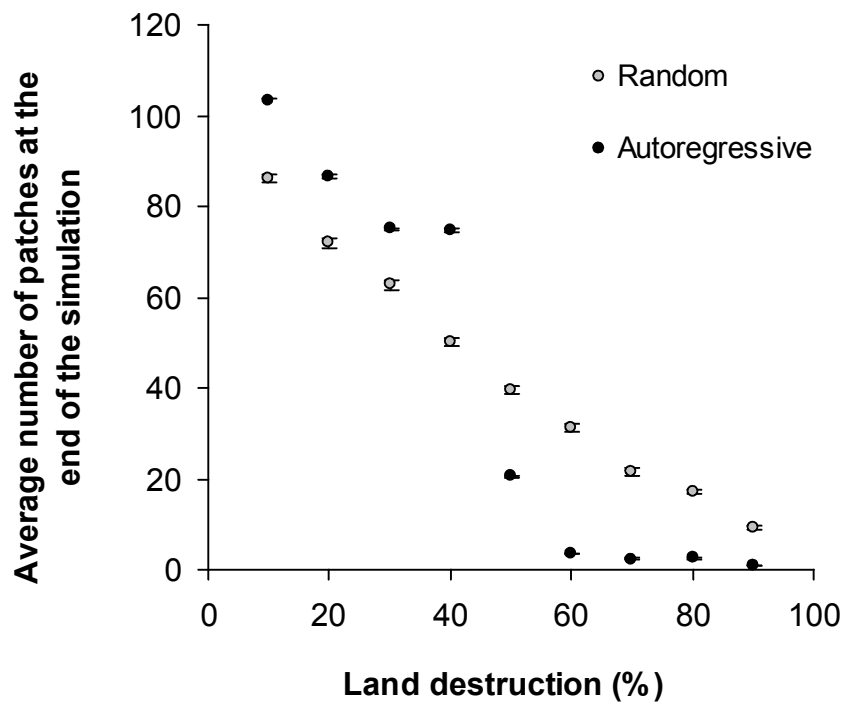
Tables

Table 1. Extinction and colonization estimated parameters and averaged parameter values with their 95% confidence intervals obtained from 100 bootstrap simulations.

	Estimated parameters	Bootstrap Parameters
Extinction		
a_e	0.043	0.045 (-0.014, 0.105)
s_e	-0.139	0.092 (-0.144, 0.328)
β_e	-0.010	-0.006 (-0.010, 0.003)
α	9.045	8.240 (6.260, 10.220)
b	-0.804	-0.775 (-0.827, -0.723)
Colonization		
a_c	-2.391	-2.450 (-2.520, -2.390)
s_c	1.315	1.032 (0.356, 1.709)
β_c	0.042	0.070 (0.040, 0.097)
α	9.045	8.240 (6.260, 10.220)
b	-0.804	-0.775 (-0.827, -0.723)
NLL	-132.05	130.58 ± 13.76

Ecological Modelling Editor

March 24, 2009

Dear Editor

We are pleased to resubmit our <u>manuscript</u> " **EFFECTS OF THE SPATIAL PATTERN OF DISTURBANCE ON THE PATCH-OCCUPANCY DYNAMICS OF JUNIPER-PINE OPEN WOODLAND** " for consideration of publication in Ecological Modelling.

We have reviewed the manuscript accordingly reviewer suggestions as follow:

Reviewer 1:

The english is good, but some sentences are difficult to understand for multinational readers, such as
"page 2 line 3: studies of the affects disturbance on metapopulation dynamics"
I feel "affets disturbance" is not easy to understand.

Page 2 line 3: ""affects disturbance" corrected for "disturbance effect". In addition the manuscript has been again revised by English translator.

Page 8
[19--24] This paragraph is the description of equation (1). However, the mathematical meaning of "P(data|E,C), P[C1]." are not apparent. You'd better write out their mathematical meanings.

We have modified the paragraph of Page 8 [19--24] and 9 [1---7] and followed reviewer indications

Are P(data|E,C), P[O1] probability vectors and P[C1], P[E1] (Markovian) transition matrices?

Yes they are so

Page 10
[6--7] What does p_i and superscript 0 mean in equation (6) and (7)?
In my opinion, for the log-likelihood of extinction data, i.e. in equation (6), p_i should be the observed probability of extinction for patch i. In your case, for an initially occupied patch i, p_i equals 1 if patch i

goes extinct and 0 if patch i survives. And in equation (7), p_i should be the observed probability of colonization for patch I, for an initially empty patch i, p_i equals 1 if patch i is colonized and 0 if patch i keeps empty.

O is number of patches. But we agreed in it is confusing to change notation, and we have modified O by N, already indicated that refer to number of patches. We modified the page 10 line [12-15] accordingly suggestion: *pi* is the observed pattern of occupancy. We have substituted by Oi to be consistent with the way we are presenting the equations in this new version

See also modification in page 9 lines [1—7].

Page 11
[5--19] You'd better add some backgrounds about these 4 kinds of patch-removal procedures, such as in what conditions Brownian-removal is suitable.

We have implemented the explanation in those paragraphs and we have explanation in the discussion section

Page 12
[12--13] What does negatively correlated mean? Since \beta_e=-15.85, by equation (3) we know the larger D_{ij}, the larger u_e. Hence E_i is positively correlated with D_{ij} and C_i is negatively correlated with D_{ij}. And intuitively, colonization probability should be negatively correlated with distance to the nearest population.

The reviewer is right. We corrected in the manuscript in page 13, line [2-6]

Page 13
[4--5] The probability of metapopulation extinction over 20 40- year intervals and 500 iterations was 0.

Since each local population has a positive extinction probability, the probability of metapopulation extinction at any time in the future should be positive and approaches 1 as time increases. Here the "0" is really zero or just approximates 0 (the extinction probability is so small that can be neglectable)?

We have corrected by "approximate to 0"

[6--7] The simulation predicted an exponential decrease in the number of patches (Fig. 2).

Note that in the past 40 years, the number of occupied patches decreases from 88 (in the year 1957) to 84 (1998), however, by the model prediction, in the next 40 years, the number of occupied patches will decrease from 84 (1998) to about 50 (2038), which is 9 times larger than the loss of the past 40 years. Is this prediction reasonable? Why?

We did a mistake when simulated the population with the parameters obtained assuming stability. We have run again the simulation with the parameters obtained not assuming stability. Now the population is maintained with a increasing of 25% along the 800 year of simulation. The manuscript has been corrected accordingly.

 [12--13] What does 'best NLL..' Mean?

NLL is the negative log-likelihood. To obtain the parameter value we maximize the log-likelihood, or what it is the same, minimize the negative-log-likelihood.

We introduced in the text the meaning of NLL.

[8--12] Please give some more detail about how to decide the patch-removal sequence by Brownian noise, random noise and autoregressive noise, i.e. from the generated noise data, how to decide which patch should be removed next.

This is a computational procedure.
While Area < limitArea

      If selection is contiguous
            Select the nearest neighbor patch (after a random selection of the first removal) until the limitArea is reached

      If selection is random
            Select a patch randomly until the limitArea is reached

      If selection is Brown noise
            After ordering the patches in increasing distances to the nearest neighbor, we selected successively patches randomly adding a new normal random term (z_t) such that

$$\varepsilon_{t+1} = \varepsilon_t + z_t$$

      If selection is autoregressive random noise
            After ordering the patches in increasing distances to the nearest neighbor, we selected successively patches accordingly

$$\varepsilon_{t+1} = \varepsilon_t + X_{t+1}; \quad X_{t+1} = \rho X_t + \sqrt{1-\rho^2}\, z_t$$

End

This procedure is now explained in manuscript pages Page 11 line [10—25], page 12 lines [1—9]

[13--14] We found that by incorporating patch connectivity into the model .

Since throughout this paper, patch connectivity are included. What does 'by incorporating patch connectivity' mean here?

In the paper of Pueyo & Alados 2007 we did not incorporate connectivity in the simulation (patch distances were not introduced as a variable in that model) as it has been done here. That is why we indicated here "by incorporating patch connectivity into the model"

Figure 2
Since there are 20 simulation periods, you'd better use [0, 20] as the x-axis range instead of [0, 25].

We have corrected the figure accordingly the suggestion

Reviewer #2:

We have changed the keywords introducing new ones one and removing those already present in the title

We have included a table with the parameters and we have modified the following text following the reviewer indications.

Page 11 line [10—25], page 12 lines [1—9]

We have revised it and transferred some paragraph from introduction to methods as later indicated.

We have revised it and shorted it

The SPOM models have a solid theoretical framework and they allow a rapid evaluation of metapopulation processes without requiring extensive data on the demography of focal specie.

In our record, the transition from steppe to open woodland is negligible (0.004) as reported in the table 2 of Pueyo & Alados 2007 paper after 40 years. Indeed, the recent destruction of the habitat due to Zaragoza city expansion is the largest threat for this area. The natural recovery requires hundreds of years and at the same time that the city expansion be stopped, which is far from real.

We have modified the word "unrealistic" from page 8, line 8 by "negligible (Pueyo & Alados 2007)"

Because the recent threat to the area is the result of completely destruction of soil by industry (solar power central, eolic power central, intensive farming and industry) we simulated complete destruction (not able to be recolonized by forest)

Histograma

Media =0,04
Desviación típica =0,114
N =326
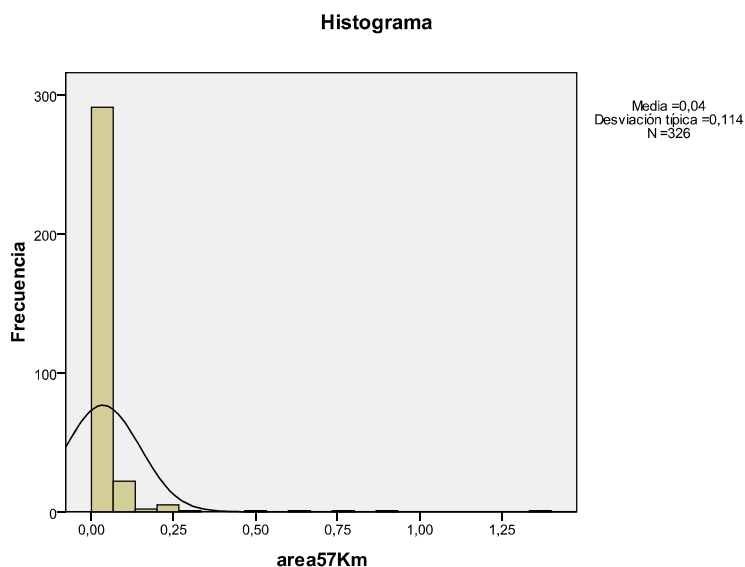
Above is shown the size distribution of patches

Suitable habitat is highly fragmented and separated by barriers of cultivated areas. This provides a mosaic of suitable and not suitable areas. We took in consideration the Moilanen critical conditions to perform the study.

The third critical point is model cross-validation using at least two parts of the dataset: why this validation has not been performed in this study?

We have introduced the validation in the manuscript, although the significance of the validation is mediated by the scarcity of woodland patches in the second partition. We have also performed a non parametric bootstrapping to estimate the confidence limits of parameters. That results are now in the manuscript in table 1.

Model equations: a table with symbols, names, description and values of all parameters would be very helpful, or at least a brief explanation of the parameters in the text. How was the model implemented? Did the authors use SPOMSIM (Moilanen 2004) or other software?

The table has been included
The model has been built in MATLAB 7.0 by the authors based on Moilanen 1999 and on Morris & Doak 2002. We implemented the Morris & Doak 2002 script with the simulation of the stochastic spatial habitat destruction. We did not used SPOMSIM software for this work.

The four procedures applied to generate disturbance patterns are briefly presented p. 11. Explanations are not clear enough for me. What is "the previous value" mentioned in the Brownian process?

We have implemented explanations in the text.

What is tau, the "space scale" (line 14) or the "relaxation time" (line 18)? What is the (socio-)ecological meaning of each pattern, which should justify the comparison?

We replaced relaxation time by space scale, because we are simulation spatial correlation

Which procedure was applied to get the results presented in Fig. 2?
I suppose this was the second one (white noise or random distribution of disturbance) but it should be stated clearly.

We have added in the text a paragraph to explain that the simulation of Fig 2 was based on normal random distribution

I suppose also that disturbance occurred only once, at the beginning of the simulation? In the "actual" scenario starting from the 1957 vegetation (?),

Actual scenario refers to 1998 situation. We have now indicated that in the text. Disturbance occurs at the beginning of the simulation.

We did a mistake when simulated the population with the parameters obtained assuming stability. We have run again the simulation with the parameters obtained not assuming stability. Now the population is maintained with a increasing of 25% along the 800 year of simulation

Natural forest in the region included Pinus and Juniperus, and it is true that Pinus can disperse large distance by wind, but although it is not limited by dispersal, the natural recovery of pines run parallel to juniperus recover

We have corrected With and King literature

corrected

corrected

corrected

we agreed, and the paragraph was moved to page 8, lines [13—20]

corrected

corrected

corrected

corrected

p. 7, l. 18: widespread and crops

corrected

p. 8, l. 3: distinguished;

corrected

p. 9, equations (3) and (4): what is N? number of patches?

Included: N is number of patches

p. 10, equations (5), (6) and (7): logL should be in italic

corrected

p. 10, l. 23; p. 11, l. 21; p. 13, l. 1, 4, 18; etc.: which metapopulation? rather metacommunity?

We agreed, and replaced metapopulation by metacommunity

p. 13, l. 1: rephrase this sub-title (metapopulation? actual?...)

corrected

p. 14, l. 4: contiguous

corrected

p. 18, l. 5: in the model, e.g., Moloney

corrected

p. 20, l. 1: Da Silva, J.M.C.

corrected

p. 21, l. 16: model for

corrected

p. 21, l. 23: He, F.L.

corrected

p. 24, l. 5: intraspecific

corrected

Fig. 3: Random

corrected

We hope that this manuscript now satisfies the Ecological Modelling standards and answer the question raised by the reviewers. We look forward to hearing from you at your earliest convenience with regards to the status of our manuscript. Thanking you in advance for your kind attention.

The enclosed manuscript has not been published or accepted for publication, and is not under consideration for publication in another journal or book. The present submission for publication has been approved by all authors.

Most respectfully yours,

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