Forest Ecology and Management 261 (2011) 2029–2037

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Reduced tree health and seedling production in fragmented *Fagus sylvatica* forest patches in the Montseny Mountains (NE Spain)

Adrià Barbeta[a,*], Josep Peñuelas[a], Romà Ogaya[a], Alistair S. Jump[a,b]

[a] *Global Ecology Unit CREAF-CEAB-CSIC, Centre for Ecological Research and Applied Forestry, Edifici C, Autonomous University of Barcelona, 08193 Bellaterra, Spain*
[b] *School of Biological and Environmental Sciences, University of Stirling, FK9 4LA, UK*

ARTICLE INFO

Article history:
Received 23 December 2010
Received in revised form 23 February 2011
Accepted 24 February 2011
Available online 22 March 2011

Keywords:
Defoliation
European beech
Forest fragmentation
Inbreeding
Isolation
Demography
Mortality
Reproduction
Establishment
Range edge

ABSTRACT

Habitat fragmentation results in smaller and more isolated populations that may be at higher risk of extirpation or further decline in comparison with their more continuously distributed progenitors. Risks to fragmented populations have frequently been considered from the perspective of population genetics, however, disruption of normal plant demography may be an equal or greater threat to population persistence. We compared demographic performance and tree health in continuous and fragmented forest plots with similar tree size structure and local climatic and physiographic conditions in order to determine if fragments are characterized by poor health and reproduction. We found that beech forest fragments showed lower seedling density, more tree crown damage and also higher percentage of dead trees. However, mortality of juveniles in the youngest age class was substantially lower in fragments such that long-term population structure remained similar between the two forest types. If reduced mortality compensates for reduced seedling establishment, as our data suggest, then fragmented populations should show greater long-term persistence than would be predicted based on comparison of young age cohorts alone. However, despite such demographic compensation, the decreased health of adult trees may pose an increasing future threat to the fragmented populations. Our results demonstrate the importance of integrating demographic patterns over long time periods and not relying on single year or cohort comparisons and may partly explain population genetic differences previously reported for the same populations.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Habitat fragmentation can have a significant impact on plant populations because the creation of small patches reduces local population sizes which, in combination with their increased isolation, can have negative impacts on plant performance. In many species, individuals in populations declining to low numbers experience diminished viability and reproduction for both non-genetic effects, such as edge effects, and genetic reasons, such as decreased genetic diversity and increased inbreeding (Lande, 1988). Because of enhanced edge effects, fragmented landscapes experience more exposition to wind speed and turbulence leading to forest structural damage, or warmer air and soil temperatures caused by increases of light transmission (Saunders et al., 1991; Ferreria and Laurance, 1997; Harper et al., 2005; Heithecker and Halpern, 2007). Heithecker and Halpern (2007), reported that most microclimatic variables were altered significantly at or near the edge in Douglas-fir dominated forests. This included increase in light ranging from <5 m to >40 m from the forest edge, and also more elevated minimum and maximum air and soil temperatures by the forest edge. Furthermore, tree damage and mortality increase rapidly when the size of the fragment falls below about 500 ha in tropical forests (Ferreria and Laurance, 1997). Plant–animal interactions are also likely to be altered; forest fragmentation can lead to density compensation, where loss or reduced abundance of some species allows increased density of competitors (Cordeiro et al., 2009). Density compensation in seed predator communities, such as rodents (Laurance, 1994) and birds (Wethered and Lawes, 2003) could increase predation rates of undispersed seeds and/or seedlings in fragments. Moreover, reduced seed dispersal may occur if key dispersal agents are absent or too scarce to effectively remove fruits and disperse seeds (Howe, 1977; Schupp, 1993). Cordeiro and Howe (2003) and Cordeiro et al. (2009), reported much lower overall bird visitation in fragments than in continuous forest of the endemic African tree *Leptonychia usambarensis*.

Isolated populations can also be characterized by reduced gene flow from other populations as a consequence of the reduction pollen flow and seed transfer between patches (Ellstrand and Elam, 1993). Such reductions may result from increased distance alone, or disruption to biotic interactions, such as reduced pollinator services

---

[*] Corresponding author. Tel.: +34 93 5811312; fax: +34 93 5814151.
E-mail address: adria_sigfrid@yahoo.es (A. Barbeta).

0378-1127/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2011.02.029

for entomophillous species (Broadhurst and Young, 2006; Rathcke and Jules, 1993; Klein et al., 2003; Aizen and Feinsinger, 1994; Ghazoul and McLeish, 2001; Tomimatsu and Ohara, 2002) although increases in pollen or seed transfer have also been reported in some fragmented forest systems (Bacles et al., 2006; Nazareno and de Carvalho, 2009). In isolated populations, dispersal limitation can negatively impact recruitment rate, which at the landscape scale is largely explained by the distance to the nearest population of mature trees (Turner et al., 2005; Kunstler et al., 2007). Furthermore, reduced seed germination success has also been noted for fragmented populations (Bruna, 1999; Henríquez, 2004).

The disruption of plant breeding systems that can occur as a consequence of habitat fragmentation can lead to increased inbreeding and population differentiation and the erosion of genetic variability within populations (Ellstrand and Elam, 1993; Petit et al., 2002; Young et al., 1996; Hamrick, 2004; Lowe et al., 2005). Such reduction in diversity below typical population levels might reduce the capacity of populations to adapt to changing environmental conditions, thereby hastening their decline (Lande, 1988; Frankham, 1996; Jump et al., 2009). Decreasing diversity and performance within fragmented populations is, therefore, indicative of the combined impact of altered population distribution and a decline in habitat quality. Whereas the former is typically investigated from a population genetic perspective, the latter can be evaluated by measuring changes in vegetative and reproductive capacity, population structure or long-term demography (Adriaens et al., 2009). These two aspects of habitat fragmentation are not, however, independent in their effects, since inbreeding can reduce flowering and seed production (Lienert et al., 2002; Paschke et al., 2002; Lienert, 2004; Robledo-Arnuncio et al., 2004; Wang et al., 2010) in addition to the impacts of reduced habitat quality outlined above.

In long-lived woody species, rare or infrequent reproductive events can be sufficient to maintain population size, or at least substantially reduce population decline, even where mean climatic conditions are unfavorable for plant regeneration (Mejías et al., 2007; Pulido et al., 2008). Furthermore, given limited microsite availability and the particularly high mortality in very young trees, age/size distributions can be maintained through the survival of only a very small number of establishing seedlings in a given area (Peñuelas et al., 2007; Wang et al., 2004). Consequently, the longevity of tree species, combined with effective seed or pollen dispersal, can enhance their resistance to the negative effects of fragmentation on populations (Hamrick, 2004). This potential resistance to habitat fragmentation impacts is reflected in the forest fragmentation genetics literature, where case studies reporting both the presence and absence of negative impacts abound (Kramer et al., 2008; Bacles and Jump, 2011). Nonetheless, in the widespread and wind-pollinated European Beech (*Fagus sylvatica*) (Jump and Peñuelas, 2006), an abundant tree species that forms the matrix of the community offering shelter and food to many other species, having an overriding importance for the ecosystem (Lienert, 2004), it has been reported that forest fragmentation has a negative genetic impact. This negative impact can be linked to low effective dispersal distances in this species, recently estimated in closed stands as 100 m or less for pollen and approximately 20 m for seeds (Wagner et al., 2010).

In order to begin to tease apart the impacts of changes in population distribution and reduced habitat quality, both genetic and demographic studies must be conducted in the same forest populations and in a system where fragmented and continuous forest populations co-occur in the local landscape (Bacles and Jump, 2011). Consequently, we chose to investigate impacts of forest fragmentation on tree condition and demography in the *F. sylvatica* forests of the Montseny Mountains in Catalonia, northeast Spain, where significant negative genetic impacts of forest fragmentation were previously reported linked to deforestation dating back some 600 years (Jump and Peñuelas, 2006). In this region, small *F. sylvatica* forest fragments of up to 52 ha occur alongside a continuous forest covering some 2830 ha. Previously reported negative genetic impacts of forest fragmentation include a reduction in genetic diversity, increased inbreeding and increased genetic divergence indicative of disruption of the normal breeding system of the species in this region (Jump and Peñuelas, 2006). In the present study, we aimed to identify if health and demographic impacts of forest fragmentation were detectable alongside these negative genetic impacts. To assess potential changes in tree condition and demography, we compared seedling density, defoliation index, the percentage of dead trees, and demographic structure of fragment and continuous forest plots whilst controlling climatic and physiographic conditions as far as possible. Considering the consequences of habitat fragmentation described above, we hypothesized that we should find reduced reproductive capacity, poorer tree health status and reduced recruitment into young age classes of fragment forests.

2. Methods

2.1. Study area

The study was conducted in the northeast of the Iberian Peninsula, at the southern edge of the distribution of *F. sylvatica* in Europe. The studied beech forests are located within the Montseny Natural Park, 50 km northeast of Barcelona (Catalonia) (longitude 2°16′-2°33′E and latitude 41°42′-41°52′). Beech colonized the Montseny Mountains more than 4000 years ago (Comps et al., 2001). The northeast ridge of Montseny Mountains rises to 1712 m above sea level and includes 2380 ha of near-continuous beech forest (Jump et al., 2006). The southwest ridge rises 1344 m above sea level and is mainly dominated by pastures that occupy the top of a high plain, and beech forest fragments are restricted to the steeper surrounding areas. Individual fragments cover an area of up to 52 ha (Jump and Peñuelas, 2006) (Fig. 1). Both ridges are separated by a valley such that fragment and continuous forests are separated by 1.5–5.5 km. Beech forests occur above 1000 m above sea level and form the tree line on the highest peaks of the region (Turó de l'Home and Les Agudes, 1712 and 1706 m, respectively). Below the beech forest in all areas of these mountains, the vegetation is Mediterranean, dominated by *Quercus ilex* (Peñuelas et al., 2007). The bed-rock consists mostly of metamorphic phyllites and schists (Avila et al., 2002) with some granodiorites areas at the northeastern ridge.

2.2. Data collection

Data collection was carried out during the spring of 2010. This year was a mast year in beech, therefore our fieldwork was conducted during a year of high seedling production. We selected 6 forest fragments investigated previously for population genetic structure by Jump and Peñuelas (2006). All of these forest fragments have *F. sylvatica* as the dominant tree species, just as it occurs in most of the local continuous beech forest. We characterized all investigated fragments according to their altitude, slope and aspect. This information was then used to select 6 continuous forest areas from the northeastern ridge as similar as possible to each one of the six fragments in order to allow us to compare seedling production, health status (defoliation index), tree mortality and forest demographic structure, between maximally similar fragmented and continuous beech forests. Details of fragments and their corresponding sampling sites from the continuous forest are shown in Table 1.

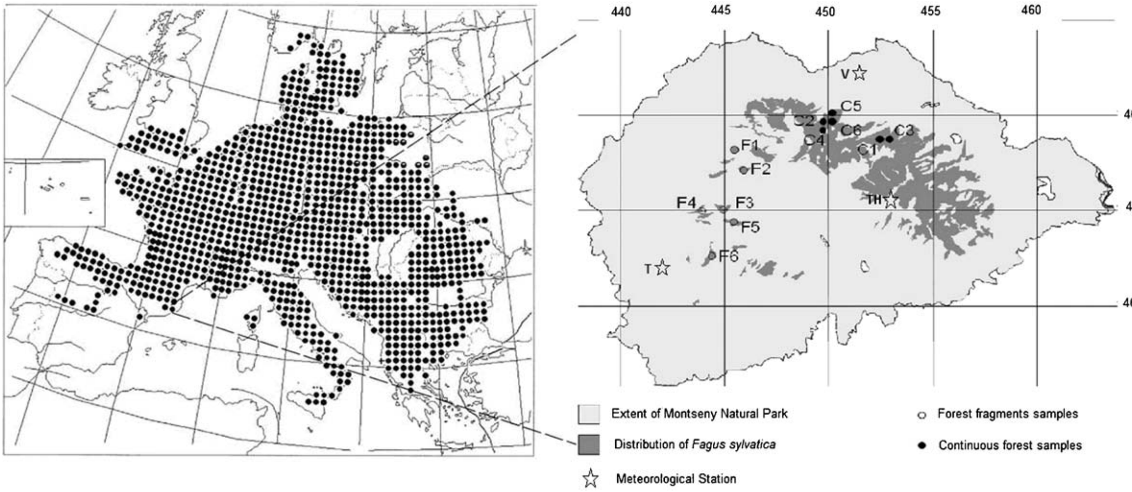

Fig. 1. Distribution of *F. sylvatica* in Europe and location of sample sites and meteorological stations within the Montseny natural Park, Catalonia, northeast Iberian Peninsula. Grid lines are marked with Universal Transverse Mercator coordinates in kilometers. V, Viladrau; T, Tagamanent; TH, Turó de l'Home meteorological stations.

In each fragment or zone of continuous forest, three 20 m × 20 m plots were established randomly but at least 50 m away from the forest edge, i.e., a total of 36 plots. Potential disturbance impacts by grazing were minimised by locating the plots distant from any paths or tracks. For each plot, we measured the diameter of the dominant stem of all individuals at 50 cm height and grouped them into 5 cm stem diameter range size classes in every plot. For multistemmed individuals, all stem diameters of each individual were measured at 50 cm height in order to derive the mean number of stems per individual of each plot. We also calculated the relative proportion of the number of individuals for each size class after measuring the density of each plot as the number of individuals per hectare. As *F. sylvatica* is a resprouting species, we also considered the cumulative basal area from all the stems for each individual. All beech current year seedlings were counted to consider seedling production (seedlings ha^{-1}). We calculated the population size structure (stem diameter distribution) both considering these seedlings and without considering them, as well as both taking the dominant stem diameter of each individual and its cumulative stem diameter. Finally, we estimated the seedling incorporation to the next size class (individuals with the largest stem between 0 and 5 cm), as the percentage of individuals of this 0–5 cm class (older than 1 year) relative to the current year seedlings, which was calculated plot per plot and then averaged for each sampling site. This approach gives a relative estimate of survival, which can be compared with total population structure, although we did not follow the fate of individual seedlings.

A visual evaluation of defoliation was used as indicative of tree health for each plot. Selected individuals were predominant, dominant and co-dominant individuals and without significant mechanical damage. Defoliation was defined as the percentage of leaf loss in the assessable crown, using a sliding scale of 5%. Ten randomly selected dominant individuals per plot were sampled. Percentage of dead trees was evaluated as the ratio between dead individuals and total individuals, without considering dead stems from otherwise living individuals, i.e., mortality was evaluated at the individual level, not at the stem level. The dominant stem diameter of dead individuals was also measured in order to calculate the size distribution and percentage of dead trees.

Climatic data (temperature and rainfall) for fragment and continuous forests sites was collected from the Climatic Digital Atlas of Catalonia (Pons, 1996; Ninyerola et al., 2000), ensuring that the main climatic variables, at least as modeled in this interpolation-based atlas, did not differ between the two sampled areas. Several landscape variables such as shortest distance to the continuous populations, fragment size and isolation levels (resulting from the average distance among the five closest beech forests) were determined with a GIS (Miramon 6, Barcelona). Distance of each plot to the top of the ridge was also measured. These characteristics might potentially influence the microclimatic conditions of the forest. Additionally, we collected meteorological data (temperatures and rainfall) from two stations within the Montseny Natural Park. Tagamanent station (marked with a T in Fig. 1) is located 2 km west of the southernmost sampling site of fragmented forests at an altitude of 1030 m, and Viladrau station (marked with a V in Fig. 1) is

Table 1
Physiographic conditions of fragments (labeled as F) and sampling sites at the continuous forest (labeled as C). UTM coordinates are given for the center of the three different plots sampled at each site. Altitude, aspect and slope are given as the range within each plot. Density is given as the mean of the three plots ± SEM.

Name	Code	UTM coordinates (*X*, *Y*)	Altitude (m)	Aspect	Slope (%)	Density (ind ha^{-1})
Collformic	F1	445,579, 4,627,860	1148–1173	N-NO	25–40	1667 ± 373
La Cortada	F2	445,682, 4,626,799	1191–1206	N-NE	15–30	1042 ± 55
Roca dels Corbs	F3	444,878, 4,624,728	1113–1139	N-NE	35–40	392 ± 29
Carena del Bofinar	F4	444,064, 4,624,855	1165–1183	NO	10–20	900 ± 154
Bac del Vilar	F5	444,876, 4,624,233	1229–1256	N	10–30	517 ± 57
Casanova de Vallfornés	F6	444,375, 4,622,461	1176–1231	NO	10–30	1358 ± 156
–	C1	452,752, 4,628,225	1145–1197	N-NO	15–30	700 ± 121
–	C2	449,225, 4,629,481	1128–1225	NE	25–40	1067 ± 54
–	C3	452,845, 4,628,248	1143–1156	N	20–40	667 ± 13
–	C4	449,855, 4,629,407	1128–1225	NO	5–20	942 ± 82
–	C5	450,482, 4,630,004	1180–1185	N	20–30	1283 ± 140
–	C6	450,348, 4,629,867	1145–1181	NO	10–40	1183 ± 101

Table 2
Landscape variables of each forest remnant (fragment). Distance to continuous forest was taken as the distance to the closest continuous beech forest population of Montseny Mountains' Northeastern ridge. Isolation is the mean distance among the closest five beech forest populations, either continuous or fragmented.

Code	Name	Area (m^2)	Distance to continuous forest (m)	Isolation (m)	Distance to ridge top (m)
F1	Fageda de Collformic	451605.6	1954.8	90.9	186.3
F2	La Cortada	148611.8	1677.1	174.4	139.3
F3	Roca dels Corbs	99335.5	3377.9	307.6	101.3
F4	Carena del Bofinar	148668.7	4382.9	99.9	608
F5	Bac del Vilar	320191.2	3423.5	307.6	226.7
F6	Casanova de Vallfornés	265392.6	5599	677.2	188.7

also located about 2 km but north from most of the continuous forest sampling sites at 953 m above sea level. Their data allowed us to compare growing season conditions that might affect reproductive capacity and tree health in the two sampling areas (Table 2).

2.3. Statistical analyses

We used Student's *t*-test analysis to compare recruitment rate, defoliation index and mortality of each fragment and continuous forest area. Mortality and defoliation were arcsin($\sqrt{x}$) transformed and seedling production logarithmically transformed prior to the test in order to meet assumptions of normality and homogenous variance. For forest size structure, we used non-parametric Kolmogorov–Smirnov tests to evaluate the differences in stem diameter distribution and tree frequencies of the different size classes. The percentage distribution of stem diameter classes (number of individuals of each class standardized by the total number of population trees) of *F. sylvatica* fragments and continuous forests were also tested by analyses of the variance. We carried out the tests for tree frequencies distribution with and without the current

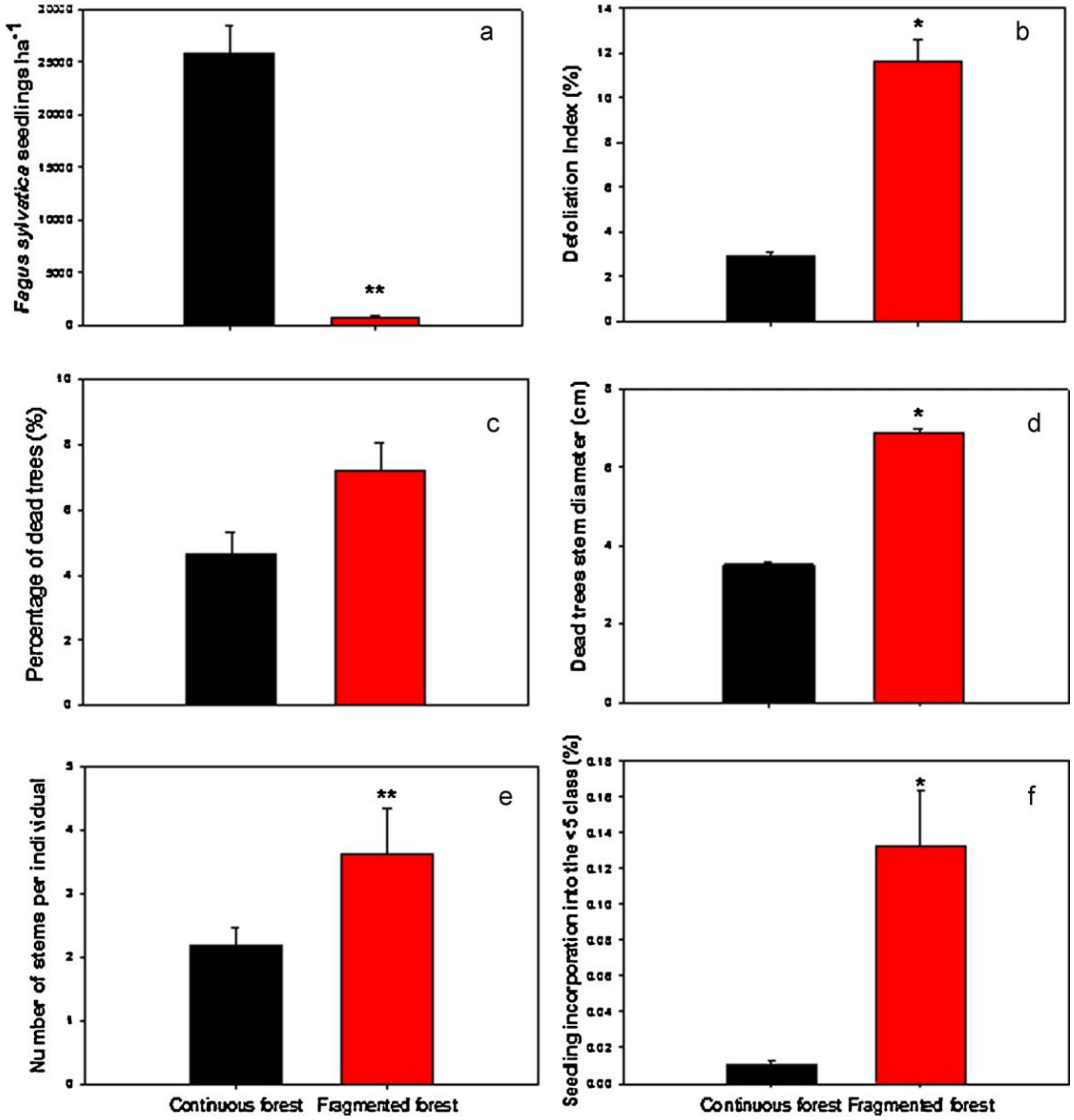

Fig. 2. (a) Seedling density, (b) defoliation index, (c) percentage of dead trees, (d) diameter of dead stems, (e) number of stems per individual, and (f) percentage of seedling incorporated into the next size class, for continuous and fragmented forests. The values are mean ± SEM of the 6 sampling sites. Significant differences are indicated with *($p < 0.05$) and **($p < 0.001$).

year seedlings. The differences in the stem diameter of dead trees between forest fragments and continuous forest plots were also evaluated with Kolmogorov–Smirnov tests as the data distribution did not fit normality. As an exploratory analysis, we tested the relationship of seedling production, defoliation, and tree mortality with landscape variables of each fragment with multiple regression analyses. Statistical analyses were conducted using Statistica (StatSoft, Tulsa, OK, USA).

3. Results

3.1. Density, seedling production, health status and percentage of dead individuals

Individual density was similar in both fragment and continuous areas (979 (mean) ± 81 (standard error) versus 974 ± 42 tree individuals ha^{-1}) (Student's *t*-test; $t = 0.02$, df = 10, $p = 0.98$). However, fragmented forests had more stems per individuals (3.63 ± 0.70) than continuous forests (2.20 ± 0.27) (Student's *t*-test, $p < 0.001$, $t = 3.80$, df = 1287) (Fig. 2e and Table 4).

Continuous forests showed a higher seedling density of *F. sylvatica*: the mean of the 18 plots was 25,917 ± 2623 seedlings ha^{-1} whereas for fragment forests it was 774 ± 88 seedlings ha^{-1} (Fig. 2a) (Student's *t*-test; $t = -5.42$, df = 10, $p < 0.001$). The defoliation index was higher in fragment forests (11.61% ± 1.04) than in the continuous forest (2.89% ± 0.22) (Fig. 2b) (Student's *t*-test, $t = 3.92$, df = 10 and $p < 0.01$). Seedling incorporation into the next size class was higher in fragmented forest (0.13% ± 0.03) than in the continuous forest (0.01% ± 0.003) (Fig. 2f) (Student's *t*-test; $t = 2.41$, df = 10, $p < 0.05$) (Table 4).

The percentage of dead individuals within a plot tended to be also higher in forest fragments (7.2% ± 0.82), although it did not differ significantly from continuous forest (4.67% ± 0.64) (Student's *t*-test, $t = 0.99$, df = 10, $p = 0.34$) (Fig. 2c). The dead trees of the fragment forests were slightly larger ($p < 0.05$, Kolmogorov–Smirnov) than the dead trees of the continuous forests (stem diameter average of 6.88 versus 3.52 cm) (Fig. 2d and Table 4).

3.2. Size structure

We censused 4743 trees (4226 *F. sylvatica* trees), split between fragment and continuous forests. Fragment forests plots had 2121 beech individuals, and continuous forests had 2013.

Size structure in both areas showed a similar shape, where smaller size classes contained more individuals and larger classes presented a progressive decrease of trees number. However, continuous forest size structure showed a slight trend towards two peaks, one for smaller classes and the other for class from 25 to 30 cm (Fig. 3a). This slightly bimodal size distribution is not present when using basal areas of each individual, i.e., when considering the cumulative diameter of all the stems of each individual (Kolmogorov–Smirnov test) (Fig. 3b). The variances of all these size distribution variables in the different plots were not different in the fragments than in the continuous forest.

3.3. Climatic data

Climatic conditions collected from the Climatic Digital Atlas of Catalonia (Pons, 1996; Ninyerola et al., 2000) were very similar both in fragments and continuous forests. Annual rainfall in the fragment forests ranges between 982 and 1044 mm, whereas it ranges between 1017 and 1100 mm in continuous forest sites, slightly more rainy (Student's *t*-test, $p < 0.05$, $t = 3.14$, df = 10). Average temperature did not differ between both zones as it ranges between 9.1 and 9.5 °C in fragment forests and between 8.9 and 9.6 °C in continuous forest (Student's *t*-test, $p = 0.73$, $t = -0.34$, df = 10). Summer rainfall ranges between 217 and 224 mm in fragment forests, whereas it ranges between 188 and 219 mm in continuous forests, which are slightly dryer during these months (Student's *t*-test, $p < 0.01$, $t = -3.59$, df = 10).

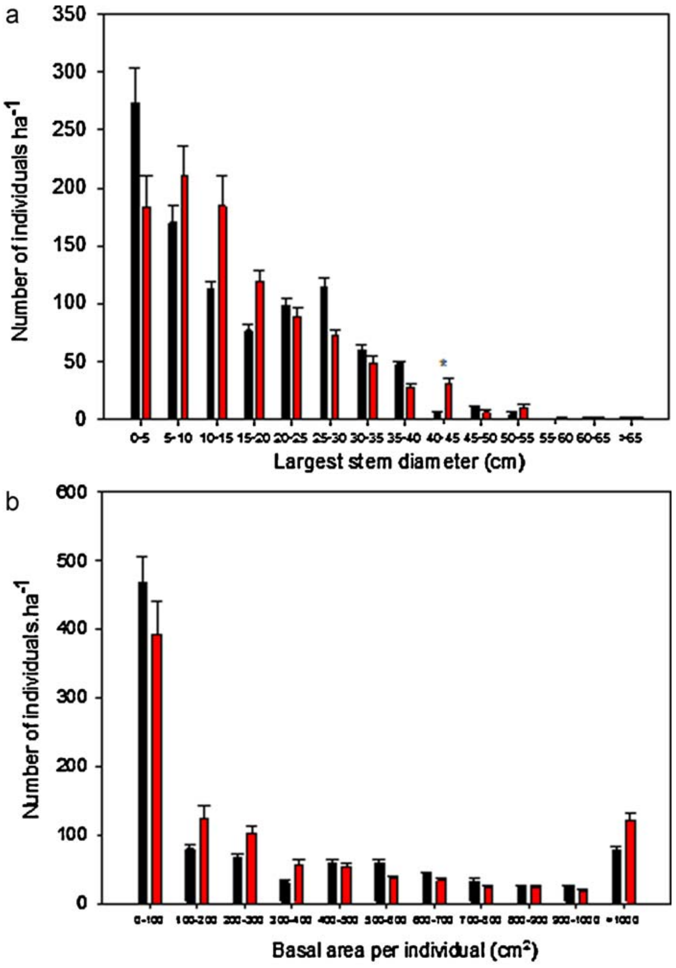

Fig. 3. (a) Number of *F. sylvatica* individuals per hectare distributed per size classes. (b) The distribution of the cumulative basal area per individual considering all the stems of each individual. Seedlings of the current year were not included. Significant differences are marked with *($p < 0.05$).

Local instrumental meteorological data taken from the stations at Viladarau and Tagamanent (Fig. 1) show similar mean temperature and monthly rainfall across the study area during the seedling growing season, when water availability is likely to be critical for seedling germination and survival. Precipitation was slightly higher in March and April at Viladarau station (near the continuous forest) whilst, in May, precipitation was highest at Tagamanent station near the fragmented populations. Monthly mean temperature is higher throughout the spring at the Viladarau station, which is situated at a lower altitude that that at Tagamanent (953 m versus 1030 m). Extreme temperatures, both maximum and minimum are hotter and colder, respectively, for Viladarau station (Table 3).

4. Discussion

Fragment populations of *F. sylvatica* showed noticeable differences in health and seedling recruitment with the continuous beech forest. Seedling recruitment was more than 30 times lower in fragment forests, trees were more than 4 times more defoliated, and the percentage of dead trees tended to be higher in fragment forests. Furthermore, the growth form of individual trees

Table 3
Meteorological data from the two stations near the sampling sites. Tagamanent is closer to the fragmented forests and Viladrau to the continuous forest.

	Altitude (m)	Mean temperature (°C)	Mean of daily maximum temperatures (°C)	Mean of daily minimum temperatures (°C)	Absolute maximum temperature (°C)	Absolute minimum temperature (°C)	Monthly rainfall (mm)	Maximum rainfall in 24 h (mm)
March								
Tagamanent	1030	5.1	9.4	2.0	19.4	−8.6	81.6	38.8
Viladrau	953	5.7	11.6	1.2	21.3	−9.6	91.6	48.1
April								
Tagamanent	1030	9.2	13.1	6.3	19.3	1.3	60.8	21.4
Viladrau	953	9.5	15.4	4.7	23.4	−0.2	70.3	24.2
May								
Tagamanent	1030	10.5	14.4	7.4	23.0	0.6	240.2	70.0
Viladrau	953	11.4	17.3	6.2	25.8	0.3	197.6	65.0

differed on average between the two forest types, since trees had more stems per individual in the forest fragments when compared with the continuous forest (Fig. 2e). However, although seedling recruitment was significantly lower in the forest fragments, this reduction in seedling production has not been translated into differences in stand structure, since the size class distribution of the two forest classes remains similar (Fig. 3 and Table 4). This similarity appears to be due to demographic compensation, since substantially reduced mortality occurs in the forest fragments when compared with the continuous forest (0.13% of seedlings are incorporated into the next size class in the fragments whereas only 0.01% are incorporated into the next largest size class in continuous forest) thereby counteracting initially much lower seedling production in the forest fragments. Seedling production is, however, likely to vary significantly between years, along with the proportion of these seedlings that survive to be incorporated into larger size classes. However, the similar size profiles between the continuous and fragmented forest suggests that such a demographic compensation may be a persistent phenomenon.

Our results nonetheless suggest that chronic habitat fragmentation entails a reduction of reproductive and vegetative capacity of populations. Decreased seedling establishment and plant health is indicative of reduced habitat quality in the fragmented populations (Saunders et al., 1991; Harper et al., 2005). This proposed impact of reduced habitat quality in generating differences in plant performance between continuous and fragmented populations is further supported by the identified alterations to stem morphology, since increased stem branching also occurs in response to elevated environmental stress (Kramer and Kozlowski, 1979), although this differential branching could also be the result of different management (e.g., charcoal versus timber). Unfortunately, we do not have information on historical management of these sites earlier than 40 years ago.

However, whilst in the short term, major differences in plant performance are evident, the effects of such differences when integrated over time may be less significant for population persistence, since, overall, the size profiles between the two forest classes do not differ significantly. This reduced impact of differences in seedling production over time highlights the importance of rare reproduction events in populations of woody species on longer timescales (Mejías et al., 2007; Pulido et al., 2008) and demonstrates the necessity of taking more than single year 'snapshot' measures of plant performance in long-lived species. Fig. 3 does, however, indicates that the relative proportion of plants in the smallest age class tends to be reduced in forest fragments, which might be an indication of future decline. Given that these populations occur at the very edge of the distribution of this species in southern Europe, the ongoing increase in temperature in this region is likely to progressively decrease the frequency of successful seedling establishment in these populations (Mejías et al., 2007; Pulido et al., 2008).

Although we believe that the differences in plant performance that we report occur principally as a response to differences in habitat quality, they might also be indicative of reduced plant fitness, or inbreeding depression (Lienert et al., 2002), given the elevated inbreeding levels reported by Jump et al. (2006) for these forest patches. Declining reproductive success can be a response to reduced pollination and seed production, and higher seed abortion rates. Paschke et al. (2002) found a positive correlation between reproductive performance and allelic variation as inbred plant populations produced fewer flowers and seeds, whilst Aizen and Feinsinger (1994) reported decreased pollen and seed production in several species in fragmented forests. Furthermore, with decreasing fragment areas reduced seed production has been related to self-fecundation, as Wang et al. (2010) have recently described on *Pinus tabulaeformis* fragmented forests, and as was similarly shown in *Pinus sylvestris* (Robledo-Arnuncio et al., 2004), where fragmented forests showed a higher abortion rate than continuous ones.

Inbreeding is typically higher in seeds and seedlings than adult trees (Naito et al., 2005; Fuchs and Hamrick, 2010), an observation confirmed by Jump and Peñuelas (2006) for the *F. sylvatica* populations studied here. However, whereas inbreeding is effectively zero in adult trees in the continuous forest, levels of inbreeding remain higher for adult trees in the forest fragments than population genetic models based on population size predict (Jump and Peñuelas, 2006). The results that we present in the current paper raise the intriguing possibility that reduced mortality of seedlings in the forest fragments might contribute to the elevated inbreeding recorded in adult trees. Such an effect is possible if density dependent selection against inbred individuals is lower in the forest fragments than the continuous forest, a condition highly possible based on the data that we present here. Whereas we cannot test such a possibility directly from the present work, it remains an exciting possibility for future research.

The differences in plant health, structure and demography that we report are unlikely to be related to differences in macroclimatic, or physiographic conditions, management practices or stand densities, since these are similar in fragment and continuous forests. In effect, average temperatures for all plots were estimated to be all in the same range with little variation (±0.7 °C). The rainfall was also estimated to be very similar and although continuous forests could receive a very slightly higher amount of water annually, summer rainfall would even be higher for fragment forests. Summer is the season when *F. sylvatica* is likely to suffer drought, which is critical both for growth of adult trees and seedling survival (Jump et al., 2007). The meteorological data of the spring of 2010 from surrounding stations also showed little difference between ridges (Table 3), as accumulated rainfall is similar during the growing season of seedlings and even the most important rainfall events coincided in time at both sites. However, microclimatic conditions

Table 4
Summary of results by sampling site. The values are mean ± SEM of the three plots of each site (fragments labeled as F and continuous forest sites as C).

	F1	F2	F3	F4	F5	F6	C1	C2	C3	C4	C5	C6
Seedlings ha^{-1}	1167 ± 547	1500 ± 722	33 ± 33	925 ± 788	550 ± 279	467 ± 109	43,250 ± 18,242	30,417 ± 17,567	23,917 ± 11,812	41,583 ± 15,277	12,583 ± 3110	3750 ± 1090
Seedling incorporation to the next size class (%)	0.08 ± 0.04	0.05 ± 0.03	0.03 ± 0.03	0.19 ± 0.16	0.1 ± 0.09	0.4 ± 0.14	0.001 ± 0.0004	0.004 ± 0.001	0.01 ± 0.003	0.002 ± 0.0005	0.003 ± 0.0005	0.04 ± 0.01
Percentage of dead trees (%)	0.02 ± 0.02	0.06 ± 0.03	0.08 ± 0.04	0.14 ± 0.04	0.02 ± 0.02	0.12 ± 0.02	0.01 ± 0.03	0.01 ± 0.01	0.05 ± 0.01	0.07 ± 0.02	0.03 ± 0.02	0.11 ± 0.05
Defoliation index (%)	0.06 ± 0.004	0.07 ± 0.02	0.15 ± 0.04	0.20 ± 0.08	0.05 ± 0.03	0.17 ± 0.11	0.04 ± 0.002	0.02 ± 0.005	0.02 ± 0.01	0.02 ± 0.01	0.05 ± 0.02	0.02 ± 0.01
Dead trees stem diameter (cm)	2.26[a]	4.32 ± 0.38	24.64	7.17 ± 1.35	8.19 ± 3.04	6.90 ± 0.3	4.13 ± 1.67	3.11 ± 0.41	5.16	15.50	4.03 ± 0.94	2.36
Stems per individual (branchiness)	4.81 ± 3.62	4.51 ± 2.87	2.17 ± 2.16	2.31 ± 1.40	5.83 ± 5.48	2.13 ± 1.70	1.23 ± 1.18	2.70 ± 3.91	2.41 ± 2.48	1.60 ± 2.15	2.14 ± 1.67	3.12 ± 5.28

[a] There is no SEM for “Dead trees stem diameter” in those sites where only one out of the three plots presented mortality.

associated with the small area of the fragments such as wind speed or air moisture could still be playing an important role, especially in fragmented forests where these microclimatic conditions might vary (Ferreria and Laurance, 1997). In any case, although micrometeorological differences cannot be totally discarded, there was not any significant correlation between physiographic variables such as distance to the top of the ridges and seedling density, defoliation index or percentage of dead trees. It is unlikely that other site characteristics such as air or soil quality could explain our results. Soils are silicieous, rocky and scheletic in both sampling areas, so edaphic determinants of water and nutrient availability should be similar. Tropospheric ozone mixing ratios within the study area range from 95 μg m^{-3} in winter to 125 μg m^{-3} in summer (XVPCA, Network for Vigilance and Forecast of Atmospheric Pollution, Catalan Government). Locally elevated tropospheric ozone is unlikely to be responsible for the observed defoliation since sampling sites are all at 1150–1250 m above sea level, also ozone mixing ratios are expected to be similar as they increase with altitude (Díaz-de-Quijano et al., 2009) and the geographical scale of this study is not large enough to define different areas of ozone mixing ratios.

Regarding management, forest owners state that neither the fragments nor the sites of the continuous forests here studied had been managed for at least 40 years, although some exploitation may still have been carried out near our continuous forest's plots (personal communication from the owners). Beech forests of this area were managed in the first half of the 20th century in order to obtain timber and charcoal, although the steepness of most of these studied forests only permitted low intensity exploitation. However, the indication of a slight bimodal structure in the size profile for the continuous forest might be an indication of past management activity (Fig. 3a and b). The lower seedling density in fragments cannot be attributed to a reduced number of maternal trees or to an altered size structure since the number of individuals and their relative proportion did not reveal large differences for the following larger size-classes, and tree density did not differ.

2010 was a mast year for the *F. sylvatica* forests in Montseny. The forest plots that we investigated are separated by a maximum distance of 5.5 km, therefore, differences in timing of masting between populations are highly unlikely to be responsible for the differences in observed seedling density given the known climatic triggers for masting in beech (Piovesan and Adams, 2001; Drobyshev et al., 2010) and that temperature and moisture interannual variations are similar across the geographical scale of this study. Alvarez-Aquino and Williams-Linera (2002), reported *F. grandiflora* seedling intensities 6 times higher in a mast year and Masaki et al. (2008) identified mast years as those with a seeding density higher than 169.8 seeds m^{-2}, whereas modest or poor seeding years ranged between 0 and 169.8 seeds m^{-2}. Seedling production 30 times higher for continuous forest versus fragments in our study is well outside these limits and is therefore highly likely to be a response to other factors, such as those described above. However, Burgos et al. (2008) reported stronger interannual variations in seed production for *Nothofagus glauca* continuous forests than in fragmented ones that may indicate a higher occurrence of mast events in continuous populations, thereby raising the possibility that fragmentation might itself reduce seedling production through less frequent masting. Seed and seedling predation by livestock, might be higher in the fragments, as the high plain located above forest fragments is dominated by pastures and shrublands (Laurance, 1994; Santos and Tellería, 1994; Wethered and Lawes, 2003). Despite the presence of livestock, it is unlikely to expect impacts on seedling density due to grazing or trampling, as these herbivores rarely forage in the forest and nowadays the intensity of pasture is low. Furthermore, similar seedling density was found in fragments with more visual evidence of animal movement through nearby paths as in those with apparently less animal movement. Moreover, plots were located far enough from the paths in order to minimize grazing impacts.

Negative effects of habitat fragmentation on tree health, such as increased defoliation, have been attributed to edge and area effects (Harper et al., 2005; Ferreria and Laurance, 1997), which could affect forest microclimatic conditions through an increased exposure to the prevailing climate of the forest exterior. The negative effects could be also explained by the fact that inbred populations may reduce their capacity to ward off pathogens, and that small populations are also more sensitive to negative climatic episodes such as droughts (Lienert, 2004). Aridity and windspeed are expected to be higher on the upper areas close to the ridge top, affecting tree health through drought and mechanical damage. Thus, increasing mortality and defoliation index would be expected for these more exposed locations; however, we did not find such an increase either in the fragments or in the plots of the continuous forest, which showed a homogenous response.

In summary, there were significant differences in forest reproduction, tree structure (number of stems per individual) and health between continuous and fragmented *F. sylvatica* populations. However, since size structures remain similar between the two forest types, it appears that the differences in seedling density that we report have not yet been translated into long-term decrease in fitness of the studied populations. Despite the apparent absence of differences between the forest classes when integrated over time, our results provide clear evidence of the demographic and ecological impacts of forest fragmentation. Furthermore, two aspects of our results might give immediate cause for concern with regards to future decline in these fragments, the apparently reduced proportion of individuals in the youngest age class is shown in Fig. 3 and the increased defoliation of adult trees. Given the previously demonstrated negative impacts of rising temperatures on the growth and reproduction of this species in the region (Jump et al., 2007; Peñuelas et al., 2007, 2008) further increases in temperature and drought stress are likely to significantly reduce adult growth and viability and seedling survival whilst elevated crown damage might, in turn, reduce future seed production.

Our results do not yet allow us to fully disentangle the genetic impacts of reduced population size and increased isolation from those of decreased habitat quality. Indeed, they raise the interesting possibility that ecological-genetic feedbacks in forest fragmentation might be more complex than had previously been envisaged. Further research is therefore necessary to tease apart the contribution of genetic and environmental factors contributing to the differences we observe. Such research must include greater understanding of the microclimatic differences between plots and long time series of reproductive output and success, in combination with controlled environment studies aimed at identifying the impact of elevated inbreeding on establishment success and demographic–genetic modeling. In combination with the data that we present here and those reported previously, such research will substantially increase our understanding of both the short and long-term impacts of forest fragmentation.

Acknowledgements

This research was supported by the Spanish Government projects CGL2006-04025/BOS, CGC2010-17172 and Consolider Ingenio Montes (CSD2008-00040), by the Catalan Government project SGR 2009-458 and via a Natural Environment Research Council (NERC) grant for ERA-net BiodivERsA project, Beech Forests for the Future. Special thanks to Carlos Rodríguez for field assistance during the course of this research.

References

Adriaens, D., Jacquemyn, H., Honnay, O., Hermy, M., 2009. Conservation of remnant populations of *Coclhium autmnale* – the relative importance of local habitat quality and habitat fragmentation. Acta Oecol. 35, 69–82.

Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination and plant reproduction in a Chaco dry forest, Argentina. Ecology 75, 330–351.

Alvarez-Aquino, C., Williams-Linera, G., 2002. Seedling bank dynamics of *Fagus grandifolia* var. Mexicana before and after a mast year in a Mexican cloud forest. J. Veg. Sci. 13, 179–184.

Avila, A., Rodrigo, A., Rodà, F., 2002. Nitrogen circulation in a Mediterranean holm oak forest, La Castanya, Montseny, northeastern Spain. Hydrol. Earth Syst. Sci. 6 (3), 551–557.

Bacles, C.F.E., Lowe, A.J., Ennos, R.A., 2006. Effective seed dispersal across a fragmented landscape. Science 311, 628.

Bacles, C.F.E., Jump, A.S., 2011. Taking a tree's perspective on forest fragmentation genetics. Trends Plant Sci. 16, 13–18.

Broadhurst, L.M., Young, A.G., 2006. Reproductive constraints for the long-term persistence of fragmented *Acacia dealbata* (Mimosaceae) populations in southeast Australia. Biol. Conserv. 133, 512–526.

Bruna, E.M., 1999. Seed germination in rainforest fragments. Nature 402, 139.

Burgos, A., Grez, A.A., Bustamante, R.O., 2008. Seed production, pre-dispersal seed predation and germination of *Nothofagus glauca* (Nothofagaceae) in a temperate fragmented forest in Chile. Forest Ecol. Manag. 255, 1226–1233.

Comps, B., Gömöry, J., Letouzey, J., Thiébaut, B., Petit, R.J., 2001. Diverging trends between heterozygosity and allelic richness during postglacial colonization in the European beech. Genetics 157, 389–397.

Cordeiro, N.J., Henry, J., Ndangalasi, J.P., McEntee, J.P., Howe, H.F., 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. Ecology 90 (4), 1030–1041.

Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proc. Natl. Acad. Sci. U.S.A. 24 (100), 14052–14056.

Díaz-de-Quijano, M., Penuelas, J., Ribas, A., 2009. Increasing interannual and altitudinal ozone mixing ratios in the Catalan Pyrenees. Atmos. Environ. 43 (38), 6049–6057.

Drobyshev, I., Övergaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M., Sykes, M.T., 2010. Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. Forest Ecol. Manag. 259, 2160–2171.

Ellstrand, N.C., Elam, D.R., 1993. Population genetic consequences of small population size: implications for plant conservation. Ann. Rev. Ecol. Syst. 24, 217–242.

Ferreria, L.V., Laurance, W.F., 1997. Effects of forest fragmentation on mortality and damage of selected trees in Central Amazonia. Conserv. Biol. 11, 1797–1801.

Frankham, R., 1996. Relationship of genetic variation to population size in wildlife. Conserv. Biol. 10, 1500–1508.

Fuchs, E.J., Hamrick, J.L., 2010. Spatial genetic structure within size classes of the endangered tropical tree *Guaiacum sanctum* (Zygophyllaceae). Am. J. Bot. 97, 1200–1207.

Ghazoul, J., McLeish, M., 2001. Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. Plant Ecol. 153, 335–345.

Hamrick, J.L., 2004. Response of forest trees to global environmental changes. Forest Ecol. Manag. 217, 323–335.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.A., 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. 19, 768–782.

Heithecker, T.D., Halpern, C.B., 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in eastern Washington. Forest Ecol. Manag. 287, 163–173.

Henríquez, C.M., 2004. Efecto de la fragmentación del hábitat sobre la calidad de las semillas en *Lapageria rosea*. Rev. Chil. Hist. Nat. 77, 177–184.

Howe, H.F., 1977. Bird activity and seed dispersal of a Tropical wet forest tree. Ecology 58 (3), 539–550.

Jump, A.S., Marchant, R., Peñuelas, J., 2009. Environmental change and the option value of genetic diversity. Trends Plant Sci 14 (1), 51–58.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. Ecoscience 14 (4), 507–514.

Jump, A., Hunt, J., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Glob. Change Biol. 12, 2163–2174.

Jump, A.S., Peñuelas, J., 2006. Genetic effect of chronic habitat fragmentation in a wind-pollinated tree. Proc. Natl. Acad. Sci. U.S.A. 103 (21), 8096–8100.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. P. Roy. Soc. Lond. B Biol. Sci. 270, 955–961.

Kramer, A.T., Ison, J.L., Ashley, M.V., Howe, H.F., 2008. The paradox of forest fragmentation genetics. Conserv. Biol. 22, 878–885.

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, New York.

Kunstler, G., Thuiller, W., Curt, T., Bouchaud, M., Jouvie, R., Deruette, F., Lepart, J., 2007. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean Landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. Divers. Distrib. 13, 799–807.

Lande, R., 1988. Genetics and demography in biological conservation. Science 241, 1455–1460.

Laurance, W.F., 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biol. Conserv. 69, 23–32.

Lienert, J., 2004. Habitat fragmentation effects on fitness of plant population – a review. J. Nat. Conserv. 12, 53–72.

Lienert, J., Diemer, M., Schmid, B., 2002. Effects of habitat fragmentation on population structure and fitness components of the wetland specialist *Swertia perennis* L. (Gentianaceae). Basic Appl. Ecol. 3 (2), 101–111.

Lowe, A.J., Boshier, D., Ward, M., Bacles, C.F.E., Navarro, C., 2005. Genetic resource impacts of habitat loss and degradation; reconciling empirical evidence and predicted theory for neotropical trees. Heredity 95, 255–273.

Masaki, T., Oka, T., Osumi, K., Suzuki, W., 2008. Geographical variation in climatic cues for mast seeding of *Fagus crenata*. Popul. Ecol. 50, 357–366.

Mejías, J.A., Arroyo, J., Marañón, T., 2007. Ecology and biogeography of plant communities associated with post Plio-Pleistocene relict *Rhododendron ponticum* subsp. *baeticum* in southern Spain. J. Biogeogr. 34, 456–472.

Naito, Y., Konuma, A., Iwata, H., Suyama, Y., Seiwa, K., Okuda, T., Lee, S.L., Muhammad, N., Tsumura, Y., 2005. Selfing and inbreeding depression in seeds and seedlings of *Neobalanocarpus heimii* (Dipterocarpaceae). J. Plant Res. 118, 423–430.

Nazareno, A., de Carvalho, D., 2009. What the reasons for no inbreeding and high genetic diversity of the neotropical fig tree *Ficus arpazusa*? Conserv. Genet. 10 (6), 1789–1793.

Ninyerola, M., Pons, X., Roure, J.M., 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. Int. J. Climatol. 20, 1823–1841.

Paschke, M., Abs, C., Schmid, B., 2002. Relationship between the population size, allozyme variation, and plant performance in the narrow endemic *Cochlearia bavarica*. Conserv. Genet. 3, 131–144.

Peñuelas, J., Hunt, J., Ogaya, R., Jump, A., 2008. Twentieth century changes of tree-ring δ13C at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. Glob. Change Biol. 14, 1076–1088.

Peñuelas, J., Ogaya, R., Boada, M., Jump, A., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia. Ecography 30, 830–838.

Petit, R.J., Latouche-Halle, C., Pemonge, M., Kremer, A., 2002. Chloroplast DNA variation of oaks in France and the influence of forest fragmentation on genetic diversity. Forest Ecol. Manag. 156, 115–129.

Piovesan, G., Adams, J.M., 2001. Relation between beech masting events and climate fluctuations the role of drought. Can. J. Bot. 79, 1039–1047.

Pons, X., 1996. Estimación de la radiación solar a partir de modelos digitales de elevaciones. Propuesta metodológica. A. VII Coloquio de Geografía Cuantitativa, Sistemas de Información Geográfica y Teledetección. In: Juaristi, J.i, Moro, I. (Eds.) Vitoria-Gasteiz.

Pulido, F., Valladeres, F., Calleja, J.A., Moreno, G., González-Bornay, G., 2008. Tertiary relict trees in a Mediterranean climate: abiotic constraints on the persistence of *Prunus lusitanica* at the eroding edge of its range. J. Biogeogr. 35, 1425–1435.

Rathcke, B.J., Jules, E.S., 1993. Habitat fragmentation and plant–pollinator interactions. Curr. Sci. India 65, 273–277.

Robledo-Arnuncio, J.J., Alía, R., Gil, L., 2004. Increased selfing and correlated paternity in a small population of a predominantly outcrossing conifer, *Pinus silvestrys*. Mol. Ecol. 13, 2567–2577.

Santos, T., Tellería, J.L., 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper (*Juniperus thurifera*). Biol. Conserv. 70, 129–134.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation. Conserv. Biol. 5, 18–32.

Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetation 108, 15–29.

Tomimatsu, H., Ohara, M., 2002. Effects of forest fragmentation on seed production of the understory herb *Trillium camschatcense*. Conserv. Biol. 16 (5.), 1277–1285.

Turner, M.G., Romme, W.H., Reed, R.A., Tuskan, G.A., 2005. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landscape Ecol. 18, 127–140.

Young, A., Boyle, T., Brown, T., 1996. The population genetic consequences of habitat fragmentation for plants. Trends Ecol. Evol. 11 (10), 413–418.

Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., Sagheb-Talebi, K., 2010. Beech regeneration research: from ecological to silvicultural aspects. Forest Ecol. Manag. 259, 2172–2182.

Wang, T., Liang, Y., Ren, H., Yu, D., Ni, J., Ma, K., 2004. Age structure of *Picea schrenkiana* forest along an altitudinal gradient in the central Tianshan Mountains, northwestern China. Forest Ecol. Manag. 196, 267–274.

Wang, H., Sork, V.L., Wu, J., Ge, J., 2010. Effect of patch size and isolation on mating patterns and seed production in an urban population of Chinese pine (*Pinus tabulaeformis* Carr.). Forest Ecol. Manag. 260, 965–974.

Wethered, R., Lawes, M.J., 2003. Matrix effects on bird assemblages in fragmented Afromontane forests in South Africa. Biol. Conserv. 114, 327–340.