



Contrasting effects of different landscape characteristics on population growth of a perennial forest herb

Alicia Valdés, Daniel García, María B. García and Johan Ehrlén

A. Valdés (aliciavaldes1501@gmail.com) and D. García, Depto de Biología de Organismos y Sistemas, Univ. de Oviedo, and Unidad Mixta de Investigación en Biodiversidad (UMIB, CSIC-UO-PA), C/Catedrático Rodrigo Uría, s/n, ES-33071 Oviedo, Spain. Present address of AV: Unité 'Ecologie et Dynamique des Systèmes Anthropisés' (EDYSAN, FRE 3498 CNRS), Univ. de Picardie Jules Verne, 1 rue des Louvels, FR-80037 Amiens Cedex, France. – M. B. García, Inst. Pirenaico de Ecología (IPE, CSIC), Avda. Montañana, 1005, ES-50059 Zaragoza, Spain. – J. Ehrlén, Dept of Botany, Stockholm Univ., Lilla Frescativägen 5, SE-114 18 Stockholm, Sweden.

Anthropogenic changes in landscape structure, such as habitat loss, habitat subdivision and edge increase, can strongly affect the performance of plants, leading to population declines and extinctions. Many studies to date have focused on single characteristics of landscape structure or single life-cycle phases, but they poorly discern the different pathways through which landscape change influences plant population dynamics via different vital rates. In this study, we evaluated the effect of two structural characteristics (habitat quantity and edge length) on vital rates and population growth rates of a perennial forest plant (*Primula vulgaris*) in a historically managed landscape. Areas with higher amounts of forest habitat had higher population growth rates due to higher recruitment, survival and growth of seedlings, while increased forest edge length was positively associated with population growth rates primarily due to a higher survival of reproductive individuals. Effects were stronger during the first of the two transition intervals studied. The results demonstrate that changes in different landscape structural characteristics may result in opposing effects acting via different vital rates, and highlight the need for integrative analyses to evaluate the effects of rapid landscape transformation on the current and long term plant population dynamics.

Large-scale habitat degradation and fragmentation are among the major causes of biodiversity loss worldwide (Wilson 1985, Fahrig 2003, Sutherland et al. 2009). The alterations of landscape structure may negatively affect the performance of species in remaining habitat patches and lead to population declines and extinctions (Fischer and Stöcklin 1997, Hobbs and Yates 2003). The effects of landscape change may be the result of several simultaneous and interdependent processes, two of the most important being habitat loss, directly reducing population sizes (Swift and Hannon 2010) and edge increase, allowing potentially negative edge effects (Ries et al. 2004) to penetrate into the fragment and affect the viability of the occurring populations (Honnay et al. 2005).

The consequences of changes in landscape structure on individual plant fitness, population abundances and distributions have been extensively studied (Saunders et al. 1991, Bruna and Kress 2002, Fahrig 2003, Lienert 2004). However, most studies have considered only single characteristics of landscape structure, such as habitat quantity (Bruna and Oli 2005, García and Chacoff 2007, Cordeiro et al. 2009), or only a single phase of the life cycle, usually reproduction (Aizen and Feinsinger 1994, Cunningham 2000, Rabasa et al. 2009, Valdés and García 2011).

Understanding how changes in landscape structure affect plant population growth requires that specific landscape characteristics are explicitly linked to different vital rates. Several studies have shown that seed production and seedling survival are negatively affected by habitat loss and fragmentation (Steffan-Dewenter and Tscharrntke 1999, Kolb 2005), whereas individual growth has been demonstrated to be hampered due to the abiotic changes imposed by increases in habitat edges (Bruna et al. 2002). However, we also need to establish the extent to which such effects on vital rates are translated into effects on population dynamics. Populations of many perennial plants may persist over long periods, even when habitat fragmentation disrupts reproduction and seed production, if adult survival is sufficiently high (Colling and Matthies 2006, Kolb et al. 2010). To assess the effects of landscape structure we therefore need to combine the links between landscape characteristics and vital rates, with the links between vital rates and population viability (Bruna et al. 2009, Dahlgren and Ehrlén 2011). Such analyses are essential to fully understand the mechanisms by which changes in landscape structure may drive populations to extinction, but also to manage populations to avoid extinctions (Honnay et al. 2005, Vellend et al. 2006).

In this study, we assess the effects of landscape structure on population viability of a perennial forest plant (*Primula vulgaris*) in a historically managed landscape. We do this by linking variation in vital rates (survival, growth, reproduction and recruitment) and population growth rates to variation in two landscape characteristics (habitat quantity and edge length), in 15 sites within a fragmented landscape, and during two yearly intervals. We seek to answer the following questions: 1) how do both studied characteristics of landscape structure influence the different vital rates? 2) How do observed differences in vital rates translate into differences in population growth rate? 3) Which are the components of landscape structure and vital rates that most account for the response of population growth to landscape change?

Material and methods

Study species

Our study species, *Primula vulgaris* (Primulaceae), is a perennial, early-flowering herb. Although widespread in moist open habitats in Europe (Endels et al. 2002), it is mostly restricted to temperate forests in many parts of its range (Jacquemyn et al. 2009). In the study region (Cantabrian mountains in northwestern Spain), it mainly occurs in forests, although it is also found in some other semi-shaded locations, like roadsides and trails. Leaves are produced in basal rosettes, and vegetative spread through lateral rosettes is possible, but uncommon in the study area. Flowers are pale yellow and borne on separate stalks. Flowering in our

study area lasts from late winter (February) to late spring (June), peaking at the end of March–beginning of April (Valdés unpubl.). *Primula vulgaris* is distylous and normally only between-morph pollination (mainly by Hymenoptera and Diptera) results in seed production (Endels et al. 2002). Biased morph frequency in small populations therefore may lead to reduced reproductive output (Brys et al. 2004). Fruits (capsules containing 30–50 small seeds with elaiosome) are consumed by ungulates, rodents and Lepidoptera larvae. Seeds have been suggested to be dispersed mainly by barochory, but there is also some evidence of occasional dispersal by ants and slugs (Valverde and Silvertown 1995, Valdés and García unpubl.).

Study area

Our study was carried out in Sierra de Peña Mayor, Asturias, Spain (43°17'N–5°30'W, 900 m a.s.l.), within the Cantabrian Range. The climate of the region is Atlantic, with a mean annual temperature of 13°C and annual rainfall of ca 1300 mm. This area has suffered from historical deforestation for cattle grazing, as many other parts of the Cantabrian Range (García et al. 2005). As a result, the landscape has changed from continuous temperate forest to a heavily fragmented wood-pasture habitat.

The sampling sites (Fig. 1) are located along a north-south axis through the study area, which comprises a highly variegated forest landscape (sensu McIntyre and Hobbs 1999). That is, it presents a mosaic composed of a few large forest fragments with hardwood species (beech *Fagus*

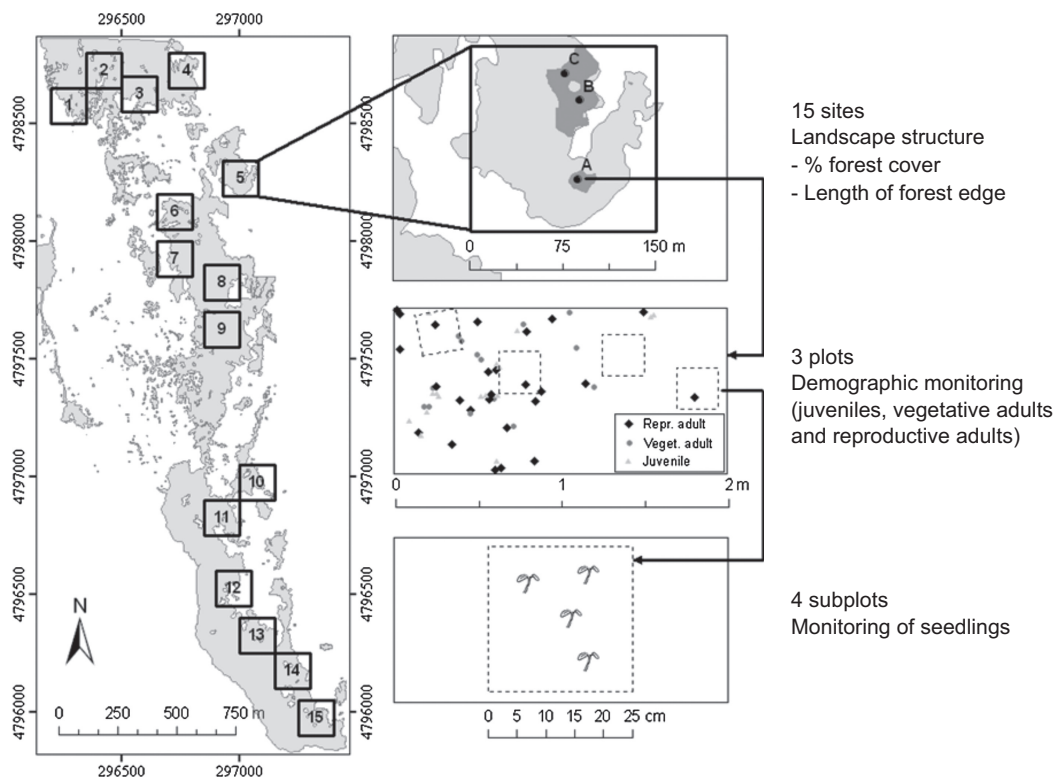


Figure 1. Outline of landscape structure sampling and estimation of demographic parameters of *P. vulgaris* along a gradient of landscape structure. Grey area represents forest cover.

sylvatica and ash *Fraxinus excelsior*), fringe fleshy-fruited, bird-dispersed trees (holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, yew *Taxus baccata*, rowan *Sorbus aucuparia* and whitebeam *Sorbus aria*) and hazel *Corylus avellana*, as well as numerous small forest fragments mostly composed of fleshy-fruited trees, and a matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus*), covering ca 60% of the area. A previous study (Valdés and García 2009) found that *P. vulgaris* is absent from highly deforested areas (forest cover < 20%), but it may also be absent from high-cover areas, and large forest patches may contain several groups of isolated plants. Within this area and with these patterns in mind, in 2008 we selected 15 sites (150 × 150 m, Fig. 1) containing *P. vulgaris*, and representing a landscape-scale gradient of habitat loss and fragmentation. At each site, we described landscape structure and followed the population dynamics of *P. vulgaris*. We selected this sampling site size (22500 m²) because 1) it represents a sampling scale that concentrates much of the variability in forest landscape structure (García et al. 2005, Valdés and García 2009) and most of the spatial heterogeneity in population features of our study species (Valdés and García 2009) and 2) it is also a scale suitable to represent the area covered by important interaction processes related to the life cycle of the species and its perception of the landscape, i.e. seed dispersal and pollination (Valdés and García 2009, 2011). The choice of the size of the sites was thus made by considering a trade-off between a size that was small enough to represent the perceptual scale of the species and big enough to represent spatial variability in population features and in forest landscape structure. From the point of view of our study species, and due to its small perceptual scale of landscape heterogeneity (mediated specially by its very restricted dispersal capacity, Jacquemyn et al. 2009, Valdés and García 2009), each of these sites can be considered as a different landscape.

Data collection

We represented the study area on a Geographic Information System (Hargis et al. 1998) using ArcGIS 9.1 (see Valdés and García 2009 for details). A layer of forest cover was incorporated, and for each 150 × 150 m site, we calculated two variables describing the landscape structure: the percentage of the area covered by forest was used as a measure of habitat quantity, and the length of forest perimeter was used as a measure of edge length. There was considerable variation in these parameters across the study sites (mean ± SD was 69.0 ± 16.5% for forest cover and 516.6 ± 205.8 m for edge length).

We carried out annual population censuses in three 2 × 1 m plots within each of the 15 sites (Fig. 1). These plots were randomly placed within the area covered by *P. vulgaris*. Censuses were performed at the beginning of July 2008, 2009 and 2010, just after fruit ripening and when seeds are being dispersed, but before germination. We distinguished four plant stages: 1) seedlings (with cotyledons still present, therefore less than one-year old), 2) juveniles (vegetative plants with one rosette with a diameter smaller than the average of reproductive individuals in the same plot), 3) vegetative adults (plants without flowers and with one or two

rosettes with a diameter equal to or larger than the average of reproductive individuals in the same plot, and often showing signs of overwintering leaves, hereafter vegetatives), and 4) reproductives (plants with flowers). We did not include a seed stage in our models because available information does not suggest the existence of a long-term seed bank in *P. vulgaris* (Thompson et al. 1997, pers. comm.).

In July 2008, all the plants except new seedlings were located by means of X-Y coordinates within each plot, and their stage category was recorded. Seedlings were counted and mapped in 4 randomly distributed permanent subplots (25 × 25 cm) within each plot. In 2009 and 2010, each plot was again carefully inspected; previously mapped plants were relocated and their stage recorded. All new plants appearing in the plots were added to the study at their first recording.

Data analysis

Calculation of vital rates

From the census data, we calculated vital rates for each stage category in each site by pooling data from the 3 plots. The probabilities of survival of seedlings (Ss), juveniles (Js), vegetatives (Vs) and reproductives (Rs) were calculated as the proportion of individuals in each stage at t that were still alive at $t + 1$. The probabilities of transition to reproductive, given survival, of seedlings (Sr), juveniles (Jr), and vegetatives (Vr) were calculated as the proportion of all surviving individuals in each respective stage that were reproductive at the following census. The probability of reproductive stasis (i.e. reproductives remaining reproductive, given survival, Rr), was calculated as the proportion of surviving reproductive individuals that were reproductive at the following census. The probabilities of seedlings and juveniles growing to vegetatives, given survival (Sv and Jv, respectively), were calculated as the proportion of surviving non-reproductive seedlings and juveniles, respectively, that were vegetatives at the following census. The probability of seedlings growing to juveniles, given survival, was not calculated, as it is a combination of the probability of seedlings growing to vegetatives, given survival, and the probability of seedlings transitioning to reproductives, given survival (specifically, $(1 - Sv)(1 - Sr)$). Finally, the recruitment rate (i.e. average number of seedlings produced per reproductive individual) was calculated as the number of seedlings in one census divided by the number of reproductives in the previous census.

To get reasonably accurate estimates of vital rates for seedlings (probabilities of seedling survival, growth to vegetative and transition to reproductive), we only calculated them for sites that contained 10 or more seedlings (fewer were found in 9 and 3 sites out of 15 in 2009 and 2010 respectively). We evaluated the differences in vital rates between the two yearly intervals by means of paired t-tests.

Use of landscape characteristics as predictors

In our data set, forest edge length showed a high correlation with forest cover ($r = -0.71$, $p = 0.0028$). In order to avoid collinearity and test for the effects of edge length independent of forest cover, we fitted a quadratic regression model of length of edge against forest cover and extracted the residuals of this regression as estimates of the effects of length of edge

independent of the effect of forest cover (see Hargis et al. 1998, Villard et al. 1999 for similar approaches). Thus, in all regressions described above, 'length of forest edge' refers to the residual values of this quadratic regression. This method implies that effects of forest cover may be overestimated and effects of forest edge length underestimated (Koper et al. 2007, Smith et al. 2009). To investigate the magnitude of this potential problem, we performed a multiple regression model with type III sum of squares, using the raw landscape variables as predictors, and population growth rate (λ , see below) for each yearly interval as the response variable (Supplementary material Appendix 2). This type of regression model estimates the effect of each of both landscape characteristics, independent of the effects of collinearity among them.

Matrix construction and relationship between population growth rates and landscape characteristics

We constructed stage-classified matrix models according to the standard procedure (Caswell 2001); $n(t+1) = An(t)$, where A is a matrix describing how individuals in each stage class of a population with a given abundance of plants in each class $n(t)$ contribute to a new population structure $n(t+1)$. For each site, we constructed two matrices (2008–2009 and 2009–2010) from the estimated vital rates. Each matrix element was calculated as a combination of two or more vital rates (Supplementary material Appendix 1). For the sites without information on vital rates involving seedlings (see above), we used values of the most similar site in terms of forest cover.

We also constructed a set of predicted matrices based on the relationships between vital rates and landscape characteristics (cf. Kolb et al. 2007). We assessed the trends of variation in vital rates along the gradient of landscape structure by fitting linear regressions of every vital rate against each of the two landscape characteristics in each of the two yearly intervals. Our goal was not to detect strictly significant relationships or to reach the highest predictive value of the response based on the predictor, but to detect trends of correlation between vital rates and landscape characteristics, and build a model that realistically captured all the important effects of the landscape characteristics (i.e. we were not only concerned with type I errors but also with type II, as we did

not want to omit potentially important effects). Therefore, statistical significance level for these regressions was set at $\alpha = 0.1$ instead of the classic $\alpha = 0.05$, in order to allow us to detect a broader range of these trends (see Quinn and Keough 2002 for discussion on the choice of significance levels). For the 2008–2009 interval, five vital rates were related to forest cover, and four other vital rates were related to forest edge length (Table 1). For 2009–2010, three vital rates were related to forest cover and one vital rate to forest edge length (Table 1). Regression functions were used to assess the relationship between vital rates and forest cover (percent unit intervals from 40 to 100%) and length of forest edge (10-units intervals, from 47 to 807). For vital rates that were unrelated to the respective landscape characteristics, we used the across-site average value for all values of forest cover and forest edge length ($n = 15$). Predicted vital rates were used to calculate matrices for the entire range of observed values of forest cover and length of forest edge during both yearly intervals.

We calculated the deterministic population growth rates (λ , Caswell 2001) for matrices representing vital rates actually observed at the 15 sites, as well as for matrices representing vital rates predicted for each combination of forest cover and forest edge length. In the first case, 95% confidence intervals for λ were calculated using Monte Carlo simulations. First, we constructed an Excel worksheet (MS Office 2010) where the stage distributions for each population and year were resampled with replacement. The resampled values were used to construct transition matrices and calculate λ in each case. The Monte Carlo analysis recalculated this worksheet for 1000 replicates, with a new λ obtained for each replicate. Confidence intervals (95%) were calculated for the mean of these 1000 values of λ . Population growth rates and confidence intervals were calculated using the PopTools add-in for Microsoft Excel (Hood 2009).

We estimated the effects of forest cover and length of forest edge on population growth rate in two ways. For the 15 sites with direct observations in permanent plots, we regressed the estimated values of λ on the percentage of forest cover and on forest edge length for each yearly interval. For matrices representing predicted vital rates for different combinations of forest cover and forest edge length, we regressed the values

Table 1. Relationships between vital rates and landscape structure variables in the two yearly intervals studied. See text for abbreviations of vital rates. β , R^2 and p for significant linear regressions are shown ($\alpha = 0.1$).

Interval	Vital rate	% Forest cover			Length of forest edge		
		β	R^2	p	β	R^2	p
2008–2009	Ss	0.0049	0.3430	0.0031			
	Sv				-0.0008	0.8927	0.0552
	Sr	0.0102	0.4630	0.0690			
	Jv				0.0009	0.3171	0.0288
	Jr	0.0048	0.2101	0.0858			
	Vr	0.0053	0.2356	0.0666			
	Rs				0.0003	0.3368	0.0233
	Rr				-0.0002	0.2740	0.0452
2009–2010	Re	0.0400	0.3101	0.0386			
	Ss	0.0030	0.5382	0.0066			
	Sr	0.0043	0.3539	0.0535			
	Vr	0.0035	0.1873	0.0911			
	Rs				0.0003	0.2652	0.0495

of λ obtained from predicted matrices ($n = 61$) on the two landscape characteristics.

Sensitivity and LTRE analyses

Originally used to determine how a discrete factor influences population growth rate via changes in different vital rates, LTRE (Life Table Response Experiment, Caswell 2001) may also be used to examine the effects of continuously varying factors, like herbivory (Knight et al. 2009) and time since last fire (Kesler et al. 2008). For our study, we used a regression-type LTRE to identify the vital rates that contributed most to the observed variation in λ along gradients of forest cover and forest edge length. We performed separate analyses for each yearly interval, using λ values obtained from the regressions of vital rates on forest cover or forest edge length (see above and Table 1). Analyses were carried out in three consecutive steps. First, we calculated the sensitivities of population growth rate to changes in vital rates for each of the predicted matrices (Ehrlén and Van Groenendael 1998, Morris and Doak 2002, Franco and Silvertown 2004). Second, we multiplied these sensitivities by the slope of the regression between the vital rate and, respectively, forest cover and forest edge length (β values in Table 1). These products estimate how λ changes in response to a change in the respective landscape structure variable through each of the vital rates. Third, we estimated the actual LTRE contribution of each vital rate to the differences in population growth rate along the landscape gradient, by multiplying the products of sensitivities per regression slopes by the values of forest cover or forest edge length, centered on their respective means. These contributions show the differences in population growth rate due to each particular vital rate between the populations with given values of forest cover and forest edge length, and populations located at the average value of these variables.

Results

Vital rates and population growth rates differed between the 15 sites and between the two yearly intervals. Population growth rates (λ) ranged from 0.71 to 1.30 (mean 0.97 ± 0.04 SE) during 2008–2009 and from 0.69 to 0.92 (mean

0.83 ± 0.02 SE) during 2009–2010. Confidence intervals for population growth rates were in all cases narrower than $\lambda \pm 0.002$.

Question 1: influence of landscape structure on vital rates

Forest cover was positively correlated ($\alpha < 0.05$) with the probability of seedling survival and with the recruitment rate in 2008–2009 (Table 1). Trends of positive correlation were also found between forest cover and the probabilities of seedlings, juveniles and vegetatives growing to reproductive ($\alpha < 0.1$). In 2009–2010 forest cover was positively correlated with probability of seedling survival, and trends of positive correlation were found between forest cover and the probabilities of transition of seedlings to reproductives and of vegetatives to reproductives. In 2008–2009, the probability of juveniles growing to vegetatives and probability of survival of reproductives were significantly higher in areas with longer forest edge, while probability of reproductives to remain reproductive was lower. There was also a trend in the probability of seedlings growing to vegetative to be lower in areas with longer forest edge. In 2009–2010, probability of survival of reproductives increased with increased forest edge length. Overall, more seedlings survived and grew to vegetatives, more individuals flowered, and recruitment rate was higher in 2008–2009 than in 2009–2010 (Table 2). However, more juveniles grew to vegetatives in 2009–2010 than in 2008–2009 (Table 2).

Question 2: influence of landscape structure on population growth rates

These differences in vital rates translated into differences in population growth rate along the gradients of landscape characteristics. λ values increased with increasing forest cover in both years (Fig. 2a, 2008–2009: $\beta = 0.009$, $F = 46.33$, $p < 0.0001$; 2009–2010: $\beta = 0.002$, $F = 5.70$, $p = 0.0328$). In 2008–2009, forest cover explained 78% of the variation in λ , and in 2009–2010 30%. There was no significant relationship between λ and forest edge length in any of the years (Fig. 2b). These results using residuals

Table 2. Mean values and coefficients of variation (CV) of the vital rates for each of the stages and intervals ($n = 15$ sites). Results of paired t-tests comparing each vital rate between intervals are also shown.

Stage		2008–2009		2009–2010		t	p > t
		Mean	CV	Mean	CV		
Seedling	Survival	0.18	0.75	0.11	0.73	-2.30	0.0375
	Transition to reproductive	0.04	2.22	0.20	1.21	2.12	0.0634
	Growth to vegetative	0.13	1.22	0.03	3.46	-2.28	0.0486
Juvenile	Survival	0.55	0.18	0.48	0.21	-2.06	0.0584
	Transition to reproductive	0.27	0.63	0.19	0.52	-1.94	0.0726
	Growth to vegetative	0.22	0.96	0.71	0.19	8.62	<0.0001
Vegetative	Survival	0.69	0.14	0.72	0.15	0.73	0.48
	Transition to reproductive	0.71	0.25	0.39	0.34	-7.06	<0.0001
Reproductive	Survival	0.82	0.07	0.82	0.08	0.06	0.9565
	Flowering	0.96	0.05	0.70	0.13	-11.48	<0.0001
	Recruitment rate	2.66	0.90	1.26	0.62	-2.35	0.0338

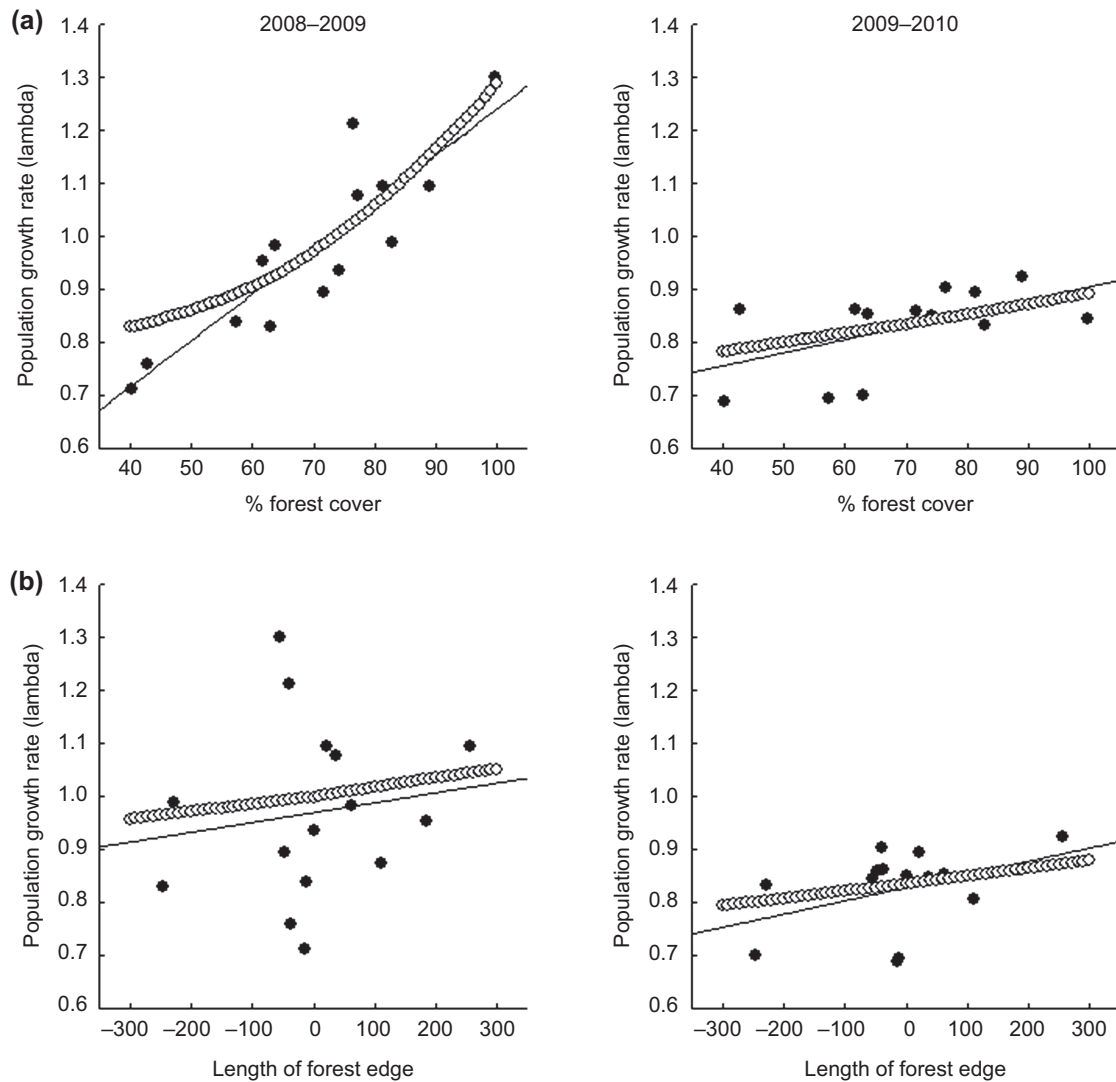


Figure 2. Relationships between population growth rate (λ) and forest cover (a) and the length of forest edge (residuals from quadratic regression against forest cover, (b)) for the two intervals studied. Filled circles are values from matrices based on original data (lines from fitted regressions are shown), and open circles are the values from matrices based on fitted vital rates.

were corroborated by type III multiple regressions using original values (Supplementary material Appendix 2).

Question 3: components of landscape structure and vital rates accounting for the response of population growth to landscape change

The estimates of LTRE contributions of vital rates showed that, in 2008–2009, the positive relationship between population growth rate and forest cover was mainly due to a higher probability of seedlings surviving and developing into reproductives, and a higher recruitment rate in high-cover areas (Fig. 3a). Although λ was not very sensitive to changes in recruitment rate, this vital rate shows the largest differences along the gradient of forest cover (high β value in Table 1). In 2009–2010, the effects of forest cover on vital rates were smaller, resulting in smaller contributions (Fig. 3a). The LTRE contributions also indicated that in both yearly intervals, the increase in λ with forest edge

length was mainly due to a higher probability of survival of reproductives in edge-rich areas (Fig. 3b).

Discussion

In this study, we have shown that landscape structure affects the population dynamics of *P. vulgaris* in the highly fragmented forests of the intensively managed Cantabrian Range, by applying an integrative approach considering different components of landscape structure and their respective effects on all phases of the life cycle. Different characteristics of landscape structure influenced population dynamics of this species in opposed ways. Less forest cover was associated with lower vital rates but the intensity of these effects differed among vital rates and years. As a result, populations inhabiting highly deforested areas showed negative trends of population growth, whereas populations in highly forested sites showed increasing trends. However, longer forest edges, which are also associated with habitat fragmentation,

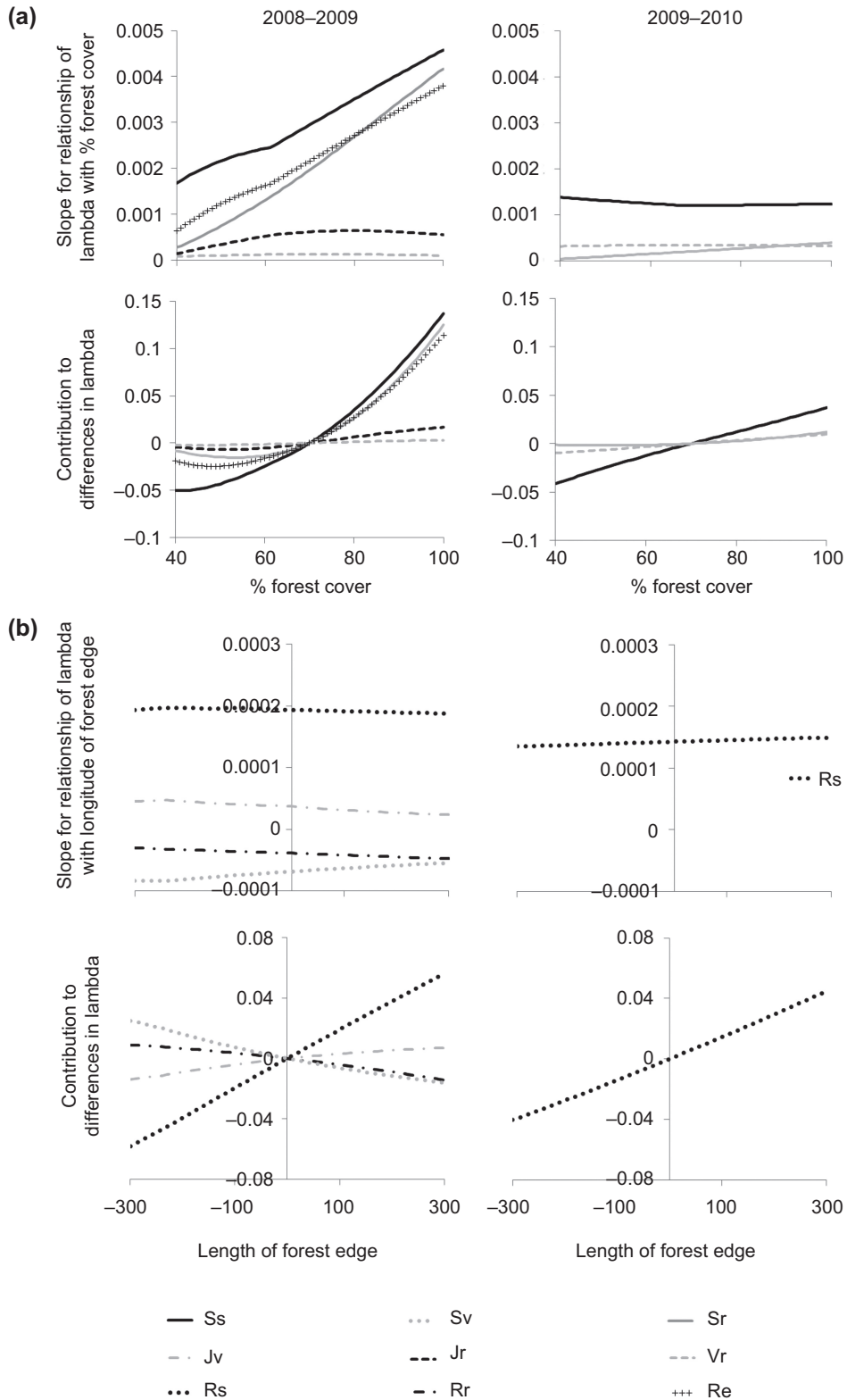


Figure 3. Contributions of vital rates to the differences in population growth along the gradients of forest cover (a) and length of forest edge (residuals from quadratic regression against forest cover, (b)), for each of the two yearly intervals studied. At a given point of the landscape gradient, the value of the contribution is either negative or positive depending on whether habitat quantity is below or above its mean value and on the sign of the slope coefficient of the relationship between population growth rate and habitat quantity. Note the different scales used in the y-axis. Only vital rates significantly related to landscape structure variables were used for the analysis. See text for abbreviations of vital rates.

led to increases in some vital rates. The effects of landscape characteristics on population growth rates varied between the two study years and were larger in the year with higher growth rates.

Landscape structure and vital rates

Landscape structure affected several vital rates, particularly through the effects of forest cover, which increased the probability of seedling survival, the probability of transition to reproductive from all stages, and the recruitment rate. Lower seedling survival probabilities in forest fragments compared to continuous forest have been observed also for a tropical understory herb (Bruna 2002), and high forest cover has also been demonstrated to offer an improved environment for seedling survival and recruitment in Mediterranean ecosystems (Ramírez et al. 2006). Soil moisture, a factor limiting seedling survival (Albrecht and McCarthy 2009), may be higher in more forested areas. Besides, areas with less forest cover harbor smaller populations of *P. vulgaris* (Valdés and García 2009), where lowered seedling survival may also be the result of increased inbreeding and increased genetic load (Kolb 2005, Van Geert et al. 2008). Small populations of *P. vulgaris* can also suffer from a biased morph ratio which leads to reduced reproductive output (Brys et al. 2004), although this is not the case in our study area, as we failed to detect a biased morph ratio in any of the populations studied (unpubl.). In *P. vulgaris*, seedlings, and also juveniles and vegetatives in one year, reached the reproductive state more frequently in high- than in low-cover areas. This may be associated with the same environmental conditions favoring growth and development; more water and nutrients for reproducing and growing in more forested areas (Jacquemyn et al. 2009). Fast transitions from seedlings to reproductive adult individuals have been observed in other *Primula* species (*P. farinosa*, Toräng et al. 2010). Finally, recruitment rate was also higher in high-cover areas in the first study year. Previous research in our study area demonstrated that populations in low-cover areas had lower reproductive output (i.e. flower, fruit and seed production) during this first year than those in highly forested areas (Valdés and García 2011). Such differences in reproductive output may be largely responsible for the differences in recruitment rate observed along the forest cover gradient in the first year. The relationship of reproductive output with habitat quantity was also positive in the second study year, although not significant (Valdés and García 2011), resulting in recruitment rate being unrelated to forest cover in this year. Taken together, the results of this study suggest that the amount of forest cover can have strong effects on multiple vital rates of individuals and growth rates of populations.

The effects of forest edge length on vital rates were not as strong as those of forest cover. Still, edge length affected the probability of growth of several stages, and the probabilities of survival and stasis in reproductives. These effects varied between the two study years. Positive effects of edges have previously been documented for plant growth (Bach et al. 2005) and reproduction (Burgess et al. 2006). We found that forest edge length increased the probability of juvenile growth, but decreased the probability of seedling growth

and the probability of flowering of reproductives in the first year. However, we also found an increased probability of survival of reproductive adults in edge-rich sites. The larger light availability in these sites could favor resource acquisition and accumulation by adults in these areas (Schmucki and De Blois 2009), enhancing their re-growth ability and long-term survival. Overall, the effects of increased edge length tended to have a positive effect on vital rates. This implies that effects of fragmentation via decreased forest cover and increased edge length can have partly opposed effects on vital rates.

We found considerable differences in vital rates and their relationships with landscape characteristics between the two study years. The most plausible explanation for these differences is the variation in climatic conditions. For example, mean precipitation was higher for the first year (Valdés unpubl.), and some studies have found a positive relationship between this variable and recruitment and seedling survival in tropical and temperate forests (Clarke 2002, Engelbrecht et al. 2005). On the other hand, the winter of the first year was mild, with higher-than-average temperatures and a shorter snow cover period, which enabled an early start of the growing season. This resulted in a larger reproductive output per adult than in the second year (Valdés and García 2011), which was possibly due to more opportunities for pollination during this longer flowering period. Since recruited seedlings observed in the field emerged from seeds produced in the previous year, the differences in seed production between 2008 and 2009 are consistent with the larger recruitment rates observed in 2008–2009 compared with 2009–2010.

Landscape structure and population growth rates

Our study for the first time jointly analyzed two components of landscape structure and multiple vital rates integrated in a population model. Landscape structure influenced *P. vulgaris* population growth rate, the most important effect being that of habitat quantity. We did, however, not find a significant relationship between population growth rate and forest edge length. This agrees with most empirical studies to date (reviewed by Fahrig 2003), which suggest that the negative effects of changes in landscape structure on biodiversity are mostly due to habitat loss, and not to habitat fragmentation. It is possible that our approach may have overestimated the net effect of habitat quantity per se, as our estimates include the joint variance explained both by forest cover and edge length (Koper et al. 2007). Likewise, the effect of edge length could have been underestimated, as our residual variable accounts only for the independent effects of edge, but not for its joint effect with forest cover. However, the results of the multiple regression (Supplementary material Appendix 2) showed that the amount of variance explained by habitat quantity was larger than the variance explained by forest edge length, and thus confirmed the dominant effect of habitat quantity over edge length on population dynamics.

We found considerable differences in population growth rates between the two study years, and in the magnitude of the effects of forest loss on population growth. This sort of

temporal inconsistency in the effects of landscape structure has been documented previously for reproduction in this study system (Valdés and García 2011), and also in other studies (Rabasa et al. 2009). Population growth rates in sites with low habitat quantity remain consistently low regardless of year, but in sites with high habitat quantity, there is considerable variation among the two years. Hence, according to our results, it seems that habitat loss drives populations into a deterministic decline, and makes them scarcely unable to respond to favorable climatic conditions. However, studies spanning several more years (Nicolè et al. 2011) are needed to confirm this hypothesis.

Influence of vital rates on the response of population growth to landscape structure

Population growth of *P. vulgaris* was strongly favoured by the amount of forest cover, and our LTRE analysis showed that this effect was mostly the result of increased probabilities of recruitment, seedling survival, and growth of seedlings to the reproductive state in sites with high forest cover. This means that in our study system, the effects of habitat loss on early stages of the plant life cycle were most important for population growth. According to previous studies using prospective perturbation analysis (elasticity) on this species (Valverde and Silvertown 1998), population growth would be strongly dependent on the persistence of adult stages in closed canopy areas. However, using LTRE analysis in *Primula veris*, Lehtilä et al. (2006) showed that processes of large elasticity, (survival of largest individuals) contributed little to differences in population growth between different habitats compared to other with much lower elasticity values (seed production and growth of small individuals). Thus, the importance of adult persistence for population growth in perennial plants varies not only among species, but also among habitats within the same species.

The lack of significant relationship between population growth rates and increased forest edge length was mostly the result of a higher probability of survival of reproductive adults in edge-rich sites. However, due to the non-significant effect of forest edge length on population growth rate, the survival of reproductive adults was less important for population dynamics than other vital rates. This suggests again that the persistence of adults, contrary to other forest perennial herbs (Silvertown et al. 1993), had a low contribution to the observed variation in population growth. Hence, no long-term demographic inertia against landscape change (i.e. extinction debts; Honnay et al. 2005) would be expected in this species under the current environmental scenario.

Conclusions

Changes in landscape structure are expected to affect sizes, isolation and dynamics of populations of understory herbs (Honnay et al. 2005). We have shown for *P. vulgaris* that changes in landscape structure affect demography, either vital rates (habitat loss, edge increase) or population growth rate (habitat loss), and that habitat loss, and

not habitat fragmentation per se, is the main process influencing population dynamics in the fragmented forest of the Cantabrian range. However, we have also shown that two different aspects of landscape change, habitat loss and increased edge length, may have opposite effects on vital rates in our system. Overall, our study suggests the importance of disentangling different components of landscape structure, and that although their effects may differ between years, strong population declines and ultimately local extinctions are expected in response to landscape alteration. Our results highlight the importance of separately considering the different characteristics of landscape structure and of assessing the effects of landscape structure on the whole set of vital rates constituting the life-cycle of a species. Only by considering all phases of the life cycle we will be able to identify the key processes responsible for population declines along the gradients of landscape structure and therefore, to discern the appropriate management measures for avoiding species extinction.

Acknowledgements – We thank J. Rodríguez, D. Martínez, V. Rivera, J. Rodríguez-Pérez, E. Vigón and I. Peñacoba for their help in field and lab work. We acknowledge funding from a FPU grant (MICINN-European Social Fund) to AV and the projects CGL2008-1275/BOS (MICINN) and IB08-039 (PCTI-FICYT) to DG, and CGL2010-21642 to MBG.

References

- Aizen, M. A. and Feinsinger, P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. – *Ecology* 75: 330–351.
- Albrecht, M. A. and McCarthy, B. C. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. – *J. Ecol.* 97: 1037–1049.
- Bach, C. E. et al. 2005. Forest edges benefit adults, but not seedlings, of the mistletoe *Alepis flavida* (Loranthaceae). – *J. Ecol.* 93: 79–86.
- Bruna, E. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. – *Oecologia* 132: 235–243.
- Bruna, E. and Kress, J. 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). – *Conserv. Biol.* 16: 1256–1266.
- Bruna, E. M. and Oli, M. K. 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. – *Ecology* 86: 1816–1824.
- Bruna, E. M. et al. 2002. Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. – *J. Ecol.* 90: 639–649.
- Bruna, E. M. et al. 2009. Habitat fragmentation and plant populations: is what we know demographically irrelevant? – *J. Veg. Sci.* 20: 569–576.
- Brys, R. et al. 2004. Reduced reproductive success in small populations of the self-incompatible *Primula vulgaris*. – *J. Ecol.* 92: 5–14.
- Burgess, V. J. et al. 2006. Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae). – *N. Z. J. Ecol.* 30: 179–190.
- Caswell, H. 2001. Matrix population models. Construction, analysis and interpretation. – Sinauer Associates.

- Clarke, P. J. 2002. Experiments on tree and shrub establishment in temperate grassy woodlands: seedling survival. – *Austral Ecol.* 27: 606–615.
- Colling, G. and Matthies, D. 2006. Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzoneria humilis*). – *J. Ecol.* 94: 959–972.
- Cordeiro, N. J. et al. 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. – *Ecology* 90: 1030–1041.
- Cunningham, S. A. 2000. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. – *Conserv. Biol.* 14: 758–768.
- Dahlgren, J. P. and Ehrlén, J. 2011. Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. – *Oikos* 120: 1183–1190.
- Ehrlén, J. and Van Groenendael, J. 1998. Direct perturbation analysis for better conservation. – *Conserv. Biol.* 12: 470–474.
- Endels, P. et al. 2002. Temporal changes (1986–1999) in populations of primrose (*Primula vulgaris* Huds.) in an agricultural landscape and implications for conservation. – *Biol. Conserv.* 105: 11–25.
- Engelbrecht, B. M. J. et al. 2005. Drought effects on seedling survival in a tropical moist forest. – *Trees* 19: 312–321.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 34: 487–515.
- Fischer, M. and Stöcklin, J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. – *Conserv. Biol.* 11: 727–737.
- Franco, M. and Silvertown, J. 2004. A comparative demography of plants based upon elasticities of vital rates. – *Ecology* 85: 531–538.
- García, D. and Chacoff, N. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. – *Conserv. Biol.* 21: 400–411.
- García, D. et al. 2005. Fragmentation patterns and protection of montane forests in the Cantabrian range (NW Spain). – *For. Ecol. Manage.* 208: 29–43.
- Hargis, C. D. et al. 1998. The behaviour of landscape metrics commonly used in the study of habitat fragmentation. – *Landscape Ecol.* 13: 167–186.
- Hobbs, R. J. and Yates, C. J. 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. – *Aust. J. Bot.* 51: 471–488.
- Honnay, O. et al. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. – *New Phytol.* 166: 723–736.
- Hood, G. M. 2009. PopTools version 3.1.1. – <www.cse.csiro.au/poptools>.
- Jacquemyn, H. et al. 2009. Biological flora of the British Isles: *Primula vulgaris* Huds. (*P. acaulis* (L.) Hill). – *J. Ecol.* 97: 812–833.
- Kesler, H. et al. 2008. Demographic responses of *Pinguicula ionantha* to prescribed fire: a regression-design LTRE approach. – *Oecologia* 156: 545–557.
- Knight, T. M. et al. 2009. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. – *For. Ecol. Manage.* 257: 1095–1103.
- Kolb, A. 2005. Reduced reproductive success and offspring survival in fragmented populations of the forest herb *Phyteuma spicatum*. – *J. Ecol.* 93: 1226–1237.
- Kolb, A. et al. 2007. Environmental context influences the outcome of a plant–seed predator interaction. – *Oikos* 116: 864–872.
- Kolb, A. et al. 2010. Population size affects vital rates but not population growth rate of a perennial plant. – *Ecology* 91: 3210–3217.
- Koper, N. et al. 2007. Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. – *Landscape Ecol.* 22: 811–820.
- Lehtilä, K. et al. 2006. Habitat change and demography of *Primula veris*: identification of management targets. – *Conserv. Biol.* 20: 833–843.
- Lienert, J. 2004. Habitat fragmentation effects on fitness of plant populations – a review. – *J. Nat. Conserv.* 12: 53–72.
- McIntyre, S. and Hobbs, R. J. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. – *Conserv. Biol.* 13: 1282–1292.
- Morris, W. F. and Doak, D. F. 2002. Quantitative conservation biology. Theory and practice of population viability analysis. – Sinauer Associates.
- Nicolé, F. et al. 2011. Interdependent effects of habitat quality and climate on population growth of an endangered plant. – *J. Ecol.* 99: 1211–1218.
- Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. – Cambridge Univ. Press.
- Rabasa, S. et al. 2009. Temporal variation in the effects of habitat fragmentation on reproduction of the Mediterranean shrub *Colutea hispanica*. – *Plant Ecol.* 200: 241–254.
- Ramírez, J. M. et al. 2006. Altitude and woody cover control recruitment of *Helleborus foetidus* in a Mediterranean mountain area. – *Ecography* 29: 375–384.
- Ries, L. et al. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. – *Annu. Rev. Ecol. Evol. Syst.* 35: 491–522.
- Saunders, D. A. et al. 1991. Biological consequences of ecosystem fragmentation: a review. – *Conserv. Biol.* 5: 18–32.
- Schmucki, R. and De Blois, S. 2009. Population structures and individual performances of *Trillium grandiflorum* in hedgerow and forest habitats. – *Plant Ecol.* 202: 67–78.
- Silvertown, J. et al. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. – *J. Ecol.* 81: 465–476.
- Smith, A. et al. 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. – *Landscape Ecol.* 24: 1271–1285.
- Steffan-Dewenter, I. and Tschamtkke, T. 1999. Effects of habitat isolation on pollinator communities and seed set. – *Oecologia* 121: 432–440.
- Sutherland, W. J. et al. 2009. One hundred questions of importance to the conservation of global biological diversity. – *Conserv. Biol.* 23: 557–567.
- Swift, T. L. and Hannon, S. J. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. – *Biol. Rev.* 85: 35–53.
- Thompson, K. et al. 1997. The soil seed banks of north west Europe: methodology, density and longevity. – Cambridge Univ. Press.
- Toräng, P. et al. 2010. Linking environmental and demographic data to predict future population viability of a perennial herb. – *Oecologia* 163: 99–109.
- Valdés, A. and García, D. 2009. Applying a continua landscape approach to evaluate plant response to fragmentation: *Primula vulgaris* in the Cantabrian mountains. – *Appl. Veg. Sci.* 12: 504–515.
- Valdés, A. and García, D. 2011. Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb. – *J. Appl. Ecol.* 48: 1422–1431.
- Valverde, T. and Silvertown, J. 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. – *Funct. Ecol.* 9: 942–950.
- Valverde, T. and Silvertown, J. 1998. Variation in the demography of a woodland understory herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. – *J. Ecol.* 86: 545–562.

- Van Geert, A. et al. 2008. Genetic diversity in adult and seedling populations of *Primula vulgaris* in a fragmented agricultural landscape. – *Conserv. Genet.* 9: 845–853.
- Vellend, M. et al. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. – *Ecology* 87: 542–548.
- Villard, M.-A. et al. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. – *Conserv. Biol.* 13: 774–783.
- Wilson, E. O. 1985. The biological diversity crisis. – *BioScience* 35: 700–706.

Supplementary material (Appendix ECOG-00216 at www.oikosoffice.lu.se/appendix). Appendix 1–2.