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Applying a continua landscape approach to evaluate plant response to fragmentation: *Primula vulgaris* in the Cantabrian mountains

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Abstract

Question: Continua landscape approaches conceptualize the effects of habitat fragmentation on the biota by considering fragmented landscapes as continuous gradients, departing from the view of habitat as either suitable (fragment) or unsuitable (matrix). They also consider the ecological gradients or the 'Umwelt' (species-specific perception of the landscape) to represent the processes that ultimately limit organisms' ability to colonize and persist within habitat remnants. Are these approaches suitable for evaluating the response of plant species to fragmentation?

Location: Fragmented mid-elevation temperate forests, Cantabrian range, Spain.

Methods: The presence, abundance and demographic structure of populations of the perennial herb *Primula vulgaris* were sampled across a continuous extent of 100 ha, subdivided into 400 50 m × 50 m sampling units. These variables were related to forest availability, forest subdivision and edge density, topography and the spatial clumpiness of populations (a measure of plant dispersal constraints and, hence, a major surrogate of plant Umwelt).

Results: Fragmentation processes, especially habitat loss, negatively affect *P. vulgaris*, with a stronger effect on presence than on abundance and demography. Despite the importance of habitat availability, *P. vulgaris* does not occupy all potentially suitable forest habitat, mostly owing to dispersal constraints. A positive effect of slope on plant presence also suggests some effect of habitat quality in determining establishment and occupancy of forest landscape.

Conclusions: Within-habitat dispersal constraints are as important as forest fragmentation in determining the landscape-scale distribution of *P. vulgaris*. By assessing the relative role of the diverse fragmentation processes, and of the species' landscape perception, a continua landscape approach proves to be a valuable tool for predicting plant response to landscape change.

Keywords: Habitat availability; Habitat suitability; Land use; Landscape change; Landscape ecology; Montane forests; Northern Spain; Perennial herbs; Plant dispersal.

Nomenclature: Castroviejo et al. (1986).

Introduction

Fragmentation of natural habitats caused by human activity is considered a major cause of plant biodiversity loss worldwide (Eriksson & Ehrlén 2001; Hobbs & Yates 2003; Honnay et al. 2005; Cousins 2009). Fragmentation includes three different, but interdependent, processes of landscape change (Fahrig 2003), each of which may lead to the extinction of plant populations through specific mechanisms: (1) Habitat loss: the area of original habitat decreasing because of destruction, may lead to direct reductions of population size (Jacquemyn et al. 2002; Leimu et al. 2006), (2) Habitat subdivision, habitat remnants becoming more and more isolated within a degraded matrix, can lead to indirect reductions of population size due to metapopulation disruption (Graae 2000; Dupré & Ehrlén 2002), (3) Edge increase, the perimeter to area ratio of habitat fragments increasing as a result of their smaller size and more irregular shape may result in fitness reduction in remnant habitat species because of percolation of harmful matrix conditions (i.e. edge effects; Jules 1998; Lienert & Fischer 2003). Although the effects of habitat fragmentation have been widely reported, the models aiming to conceptualize fragmentation effects are still weak on representing real-world landscapes and on integrating the diverse fragmentation processes (Haila 2002; Lindenmayer et al. 2008). The 'island' (Laurance 2008) and 'patch-matrix-corridor' (Forman & Godron 1986, see also Forman 1995) models defend a binomial classification of habitats, where the remnant patches of suitable habitat, sometimes connected by corridors, are equivalent to islands embedded in a dominant, highly contrasting matrix. However, most fragmented landscapes worldwide do not easily fit these models for several reasons. First, many landscapes are actually mosaics of patches, each subject to a different degree of habitat destruction (McIntyre & Barrett 1992; Bennett et al. 2006). Second, the boundaries between original and degraded habitats are frequently gradient-like rather than sharp transitions (McIntyre & Hobbs 1999). Third, the background matrix of many fragmented landscapes, otherwise classified as inhospitable, is frequently perceived as suitable habitat for many species (García & Bañuelos 2003; Murphy & Lovett-Doust 2004). Thus, McIntyre & Barrett (1992) advocated a 'variegation' model that classifies degraded landscapes within a continuum depending on the degree of habitat modification (i.e. intact, variegated, fragmented, or relictual landscapes). Nevertheless, all these landscape views emerge from human-defined landscape patterns, and ultimately consider that some original habitats are always suitable for some individual species, independently of the ecological processes underpinning species-specific distributions (Manning et al. 2004; Fischer & Lindenmayer 2007).

The 'continua' landscape approaches (continua and Umwelt approach, Manning et al. 2004; continuum approach, Fischer & Lindenmayer 2006, 2007) have been presented as an alternative to classic fragmentation models. They try to explain organisms' responses to fragmentation by representing fragmentation characteristics in the form of continuous gradients, a fact that makes it easier to discern the separate effects of habitat availability, isolation and edge density. More importantly, they highlight that other processes, apart from fragmentation, ultimately limit organisms' ability to colonize and persist within habitat remnants. These processes may be represented by means of life cycle or behavioural traits that condition the species-specific perception of the landscape (e.g. movement ability), and conceptualized as the species Umwelt (i.e. the environment that is perceived and used by each species; von Uexküll 1934; but see Manning et al. 2004). Alternatively, limiting processes may be expressed as species-specific ecological gradients such as resource availability or climatic constraints (Fischer & Lindenmayer 2006, 2007). Originally conceived for studying animal responses to fragmentation, continua approaches have not yet been applied to plants (but see other approaches in Dupré & Ehrlén 2002; Kolb & Diekmann 2004; Kunstler et al. 2007). It is widely accepted that seed dispersal may limit the extent to which the distribution of plants follows that of suitable habitats at local and regional scales (Primack & Miao 1992; Ehrlén & Eriksson 2000; Svenning & Skov 2002; McEuen & Curran 2004) thus dispersal potential together with the response to climatic, edaphic or topographic gradients should be considered a surrogate of Umwelt in plants.

Perennial temperate and boreal herbs have been suggested to show specific forest habitat requirements (Dupré & Ehrlén 2002; Kolb & Diekmann 2004) and to be susceptible to habitat loss and edge effects (Jules & Rathcke 1999; Honnay et al. 2002). However, they also show low colonization capacity because of restricted dispersal even within undisturbed forest habitats (Ehrlén & Eriksson 2000; Honnay et al. 2005). Owing to the combination of forest disturbance susceptibility and dispersal limitation, they are a suitable group of plants for the evaluation of forest fragmentation effects under continua approaches. In this work, we study the primrose (*Primula vulgaris* L.) in the montane forest of the Cantabrian Range (N Spain), a habitat suffering a high degree of fragmentation (García et al. 2005). Our main objective is to apply a continua and Umwelt approach to discern how the presence, abundance and demographic structure of *P. vulgaris* are affected by habitat fragmentation. Specifically, we seek to answer the following questions: (1) Which process of landscape change (habitat loss, habitat subdivision, edge increase) affects *P. vulgaris* most? (2) Which ecological trait of *P. vulgaris* (presence, abundance or demographic structure) is the most sensitive to fragmentation effects at the landscape scale? (3) How important are the characteristics of the fragmented landscape in determining *P. vulgaris* distribution and demography in relation to the surrogates of species Umwelt, such as other landscape characteristics and dispersal constraints?

Methods

Study site

Our study was carried out in the Sierra de Peña Mayor, Asturias, Spain (43°17′N, 5°30′W, elevation 900 m a.s.l., Fig. 1), a mountain which is part of 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. As in many other parts of the Cantabrian Range (García et al. 2005), historical deforestation for cattle grazing has

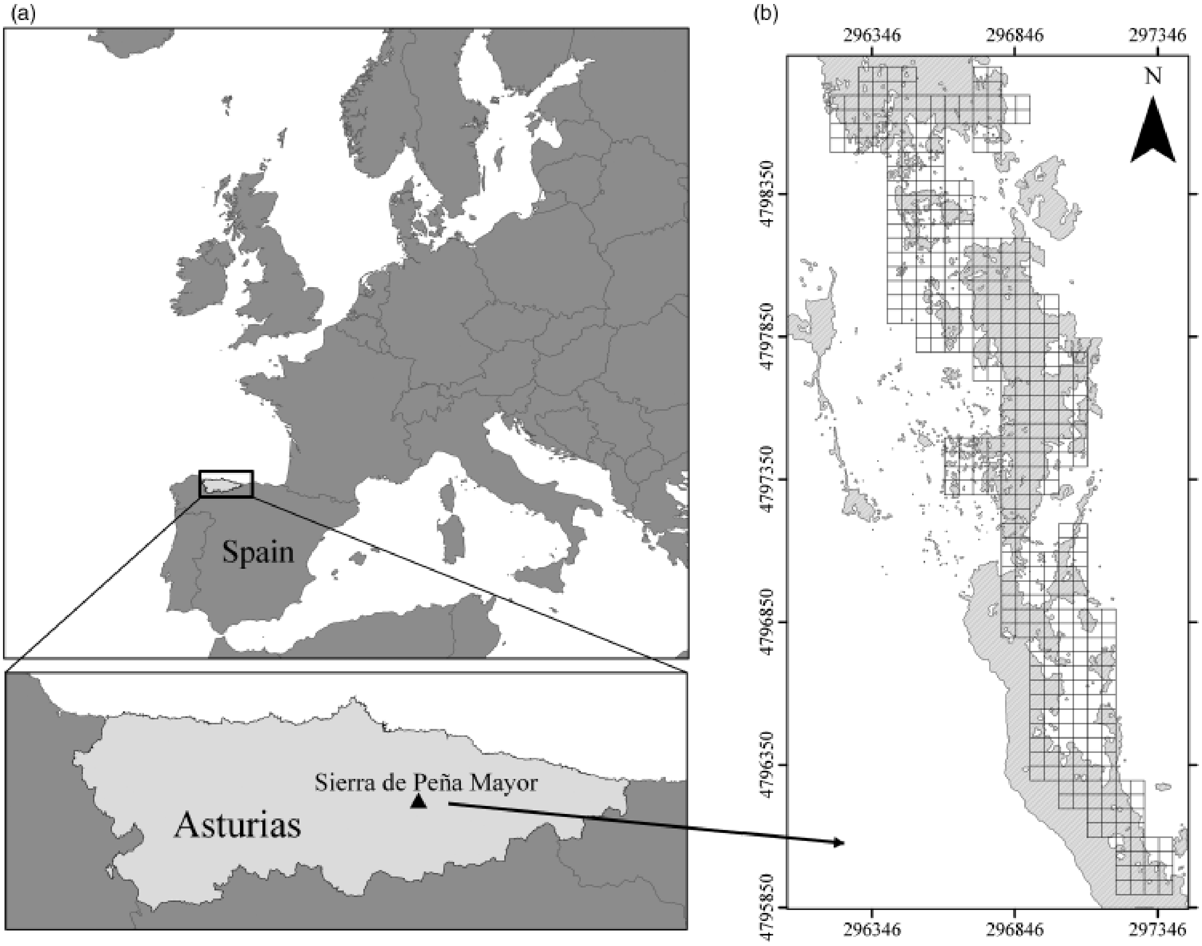

Fig. 1. (a) Geographic location of the study site, and (b) representation of the sampling extent (grid of 400 50 m×50 m sampling units, forest cover represented in grey, numbers are UTM coordinates).

transformed the once extensive temperate forests of the site into a heavily fragmented wood-pasture habitat. The topography might also partly determine forest configuration and fragmentation. For example, limestone rocky outcrops may prevent soil formation, negatively affecting forest development (García et al. 2005).

The spatial extent of the study was a continuous area covering 100 ha (over a surface approx. 3000 m long and 1000 m wide) along a N-S axis through the site, which was divided into 400 landscape sampling units (50 m×50 m square plots, Fig. 1). The physiognomy of the area is a highly variegated forest landscape (*sensu* McIntyre & Hobbs 1999). That is, it presents a mosaic composed of a few large forest fragments with hardwood species (beech, *Fagus sylvatica* L., and ash, *Fraxinus excelsior* L.), fringe fleshy-fruited, bird-dispersed trees (holly, *Ilex aquifolium* L., hawthorn, *Crataegus monogyna* Jacq., yew, *Taxus baccata* L., and rowan, *Sorbus* spp.) and hazel (*Corylus avellana*), as well as numerous small forest fragments mostly composed of fleshy-fruited trees, and a dominant (ca. 75% cover) matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.) with variable densities of scattered remnant trees (mostly hawthorns).

Study species

Our target species was *P. vulgaris* L. (Primulaceae), a perennial, early-flowering herb, typically living in moist open habitats in Europe (Endels et al. 2002a), but restricted to temperate forests in some parts of its range (Jacquemyn et al. 2009). In our region it behaves mainly as a forest species, although it can be also found in some other moderately shaded locations, such as road and path slopes. It grows producing basal rosettes of leaves every year, and vegetative spread is possible over very short distances through the production of lateral rosettes. Flowers are pale yellow and borne on separate stalks. Flowering in our study area lasts from late winter (February) to late spring (June), peaking in April. *P. vulgaris* is distylous and has a self-incompatibility system with two genetically determined floral morphs: 'pin', with anthers sunk in the corolla tube, and 'thrum', with anthers extending beyond the corolla tube. Only between-morph pollination is efficient for seed set, although the system allows for certain levels of self-fertilization (Endels et al. 2002b). Biased morph frequency in small populations leads to reduced reproductive output (Brys et al. 2004). The most common pollinators are Hymenoptera and Diptera. Fruits (capsules containing 30-50 small seeds with an elaiosome) are consumed by ungulates, rodents and Lepidoptera larvae. Seeds are thought to be dispersed mainly by barochory, but there is also some evidence of occasional dispersal by ants (Valverde & Silvertown 1995; authors' unpublished data).

Measures of fragmentation and other landscape characteristics

We developed a Geographic Information System (GIS) of the study area using ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA, USA), incorporating forest cover as a layer by carefully digitizing each of the forest patches revealed by digital orthophotographies (scale 1:5000). This allowed us to calculate, for each sampling unit, the following variables representing the degree of forest fragmentation: the percentage of forest cover, a measure of habitat availability and an inverse measure of habitat loss; the number of forest patches, a measure of habitat subdivision; and the density of forest perimeter, a measure of edge density. Moreover, we were interested in distinguishing to what extent the forest sampled was representative of the availability of mature, hardwood forest habitat, so, in March 2008, we performed field sampling to estimate the abundance of beech trees (*F. sylvatica*) with DBH (diameter at breast height) >30 cm in each sampling unit. A topographical map with level curves was incorporated as a layer into the GIS to build a digital elevation model (DEM) with cell size of 50 m. This provided us with a value of elevation, slope and aspect interpolated for each sampling unit.

P. vulgaris presence and abundance

In April-May 2007, during the peak of *P. vulgaris* flowering in the study site, the presence/absence of this species was determined in each sampling unit by carefully searching for individuals in a systematic zig-zag walk covering the whole surface. For those sampling units where the species was detected, a schematic map was drawn of all *P. vulgaris* patches representing their size and spatial arrangement, individual patches being defined as those clumps of plants clearly separated from each other by more than 20 m. Field maps were then used to create a digitized layer of *P. vulgaris* cover in the GIS, from which the per cent cover and the number of patches of *P. vulgaris* for each sampling unit were obtained. The per cent cover of the species was calculated by summing the areas of every patch, and then relating this to the total area of the unit. Those patches of *P. vulgaris* extending over more than one sampling unit in the field were drawn as a single patch in the GIS layer, but subsequently broken into different patches to calculate the cover corresponding to each sampling unit. The usefulness of percentage of *P. vulgaris* cover as a measure of abundance was validated by previous abundance sampling in 75 units containing the species, which showed that this percentage was strongly positively correlated to the abundance of all individuals per sampling unit (Pearson correlation coefficient $r=0.920$, $P<0.0001$; $N=75$). Thus, the percentage of cover of *P. vulgaris* was considered to be a surrogate for population size in further analyses, and the number of patches a measure of population subdivision.

As a surrogate of both the abundance of neighbour seed sources and the degree of clumpiness of the population at a spatial scale intermediate between the population patch and the landscape, we used the percentage of *P. vulgaris* cover in the neighbouring area. This percentage was estimated from the GIS for each sampling unit, the neighbourhood being the area covered by the eight $50\,\mathrm{m}\times50\,\mathrm{m}$ quadrats bordering the four sides of the targeted sampling unit. As *P. vulgaris* cover was exclusively sampled within the 100-ha extent, in those sampling units situated on the perimeter of the sample area, the percentage of *P. vulgaris* neighbouring cover was obtained from between three and seven quadrats, depending on location. The smaller sampling extent of these peripheral units had a negligible effect on the representativeness of the percentage of cover of *P. vulgaris* in the neighbourhood (a comparison of *P. vulgaris* cover values provided by, respectively, the eight neighbouring quadrats versus five, randomly chosen, neighbouring quadrats, around 50 central sampling units, showed no statistical differences between sampling extents). A positive response of *P. vulgaris* presence or population size to the percentage of cover in the neighbouring area (i.e. units showing a greater abundance of seed sources in their periphery had a stronger probability of containing the species or hosting greater abundances) would be indicative of significant dispersal constraints (for similar procedures see Svenning 2001; Svenning & Skov 2002).

P. vulgaris population structure

We were interested in estimating the demographic structure of *P. vulgaris* populations as a surrogate of the intensity of recruitment within the population. Therefore, in those units where the species was present, a systematic sampling protocol was set up. The group of plants that was nearest to the centre of the sampling unit was examined and the first 100 individuals assigned to one of the following developmental stages by size differences (rosette diameter) and other biological attributes (Valverde & Silvertown 1998; Endels et al. 2002a): (1) juveniles (i.e. immature plants without cotyledons and only one rosette of leaves – distinguished from vegetative adults with one rosette by means of size differences; an individual was considered an adult when its rosette diameter was similar to the average diameter of flowering adults in the same population); (2) vegetative adults (i.e. individuals without flowers and without cotyledons, often showing signs of overwintering leaves, and whose rosette diameter was comparable to that of reproductive adults in the same population); and (3) reproductive adults (i.e. plants showing one or more flowering stalks). Although present, we decided not to take into account individuals at the seedling stage (tiny individuals with cotyledons still present), owing to their low detectability. We considered that the proportion of juveniles relative to the total number of individuals sampled was a representative enough measure of the long-term cumulative demographic structure and recruitment potential of *P. vulgaris* in our site (see also Brys et al. 2003).

Morph imbalance in small populations negatively affects reproductive ability in this species (Endels et al. 2002b), so we wished to assess the effect of the proportion of floral morphs on demographic trends. To this end, the pin-thrum ratio was calculated as the quotient of the absolute difference between the number of pin and thrum individuals divided by the total number of flowering adults.

Statistical analyses

Multiple regression models were set up to analyse the response of *P. vulgaris* presence, abundance and population subdivision (response variables) to the predictor variables of landscape characteristics (fragmentation and topographic variables) and dispersal constraints (*P. vulgaris* cover in the neighbouring area). We also performed a regression model with the proportion of *P. vulgaris* juveniles as response variable and, as predictor variables, landscape characteristics, percentage of cover of the species (as a measure of abundance) and pin-hrum ratio. A combined stepwise multiple logistic regression was used for the model using presence, whereas combined stepwise multiple linear regressions were used for the rest of the models. The model for presence included all sampling units ($N = 400$) whereas the rest of the models were run exclusively with those units in which the species was present ($N = 120$).

Variation in habitat availability (in our case, the percentage of forest cover) through the landscape is known to inherently influence the patterns of variation of other fragmentation measures such as fragment isolation and edge density (Fahrig 2003). Thus, to statistically remove the effect of forest cover in the remaining fragmentation parameters, we fitted quadratic regression models considering the number of forest patches and the edge density as response variables and the percentage of forest cover as predictor variable. We then used the residuals of these regressions as predictor variables in the multiple regression models mentioned above (see similar procedures in Hargis et al. 1998; Villard et al. 1999), together with the percentage of forest cover. Furthermore, we were interested in distinguishing the effect of the forest cover accounted for by mature forest (i.e. beech) from that accounted for by secondary fringe forest dominated by other tree species (fleshy-fruited trees and hazel). Thus, we fitted the percentage of forest cover (response variable) to the abundance of beech (predictor variable) with a quadratic regression model. We then used the residuals of this model together with the abundance of beech in the multiple regression models rather than the raw percentage of forest cover. Prior to multivariate models, we checked for colinearity among the biological variables included as predictors (see the Supporting Information, Table S1). If two predictors were strongly correlated ($r > 0.70$), only the one that best fitted (based on R^2 values) the response variable in univariate models was included in the multiple regressions.

Given the spatial structure of our sampling framework, the presence of spatial autocorrelation in the data may violate the assumption of independently distributed errors in the regression models

(Legendre & Legendre 1998). As a consequence, the effects of explanatory variables might be exaggerated (Legendre et al. 2002). In order to identify and control for the effect of large-scale spatial structures in the database, we applied a trend surface analysis (TSA; Legendre & Legendre 1998) that incorporated, as potential predictors in the linear models, spatial terms in the form of a third-order polynomial of the spatial Cartesian geographic coordinates X-Y of the centroid of the sampling units (extracted from UTM coordinates) and their cross-product terms. Moreover, the measure of cover of *P. vulgaris* in the neighbouring area incorporated in the models for evaluating the role of dispersal constraints was considered as a small-scale spatial autocorrelation term (Svenning 2001). Despite the incorporation of TSA and the cover of *P. vulgaris* in the neighbouring area in the models, we still checked for the presence of significant spatial autocorrelation in the residuals of all linear models by means of Moran's I correlograms (Legendre & Legendre 1998). Those linear models showing a significant spatial structure in their residuals were repeated by performing spatially explicit regression models (autologistic models and lagged autoregressions; Rangel et al. 2006) that incorporated additional spatial autoregressive terms accounting for spatial structures at all scales (see also Svenning & Skov 2007).

The fit of the models was evaluated on the basis of Akaike's information criteria (AIC; Akaike 1973), which allows the comparison of models with different numbers of parameters. Before running regression models, data were transformed to achieve normality and reduce heteroscedasticity (arcsine of square root for proportions, and $\ln(x+1)$ for the rest of the data). Statistical analyses were carried out with JMP 7.0.1 (SAS 2007) and SAM 3.0 (Rangel et al. 2006).

Results

P. vulgaris presence, abundance and demographic structure

P. vulgaris was present in 120 of the 400 sampling units (30%), and where it was present its percentage cover ranged from 0.9% to 100% (mean 40.0 ± 2.5 SE). The number of *P. vulgaris* patches varied between 1 and 7 (mean 1.6 ± 0.1 SE). Pin-thrum ratio) ranged between 0 and 1 (mean 0.23 ± 0.02 SE). The proportion of juveniles varied between 0 and 0.81 (mean 0.31 ± 0.01 SE). The proportion of vegetative adults relative to the total number of adults ranged between 0 and 0.78 (mean 0.48 ± 0.01 SE). Figure 2 shows the variation of some of these parameters along the study area and their frequency distributions.

Response of P. vulgaris to landscape characteristics and dispersal constraints

The multiple logistic model explained ca. 63% of the variance of the presence of *P. vulgaris* in the study area (Table 1). The probability of occurrence increased with the percentage of cover of the species in the neighbouring area, abundance of beech, forest cover of other trees and slope, and decreased with the number of forest patches within the sampling unit. Two of the TSA spatial terms (Y, Y^2) also had a significant positive effect on the probability of presence, indicating that the occurrence of *P. vulgaris* increased slightly moving northwards along the study site, while also showing a quadratic spatial trend, with larger occurrence probabilities at the centre of the study site (Table 1, Fig. 2). The importance of species cover in the neighbouring area and the TSA terms in this model suggested the existence of significant fine-scale and broad-scale spatial structures in our data. Despite the inclusion of these spatial parameters, we still detected a significant degree of spatial structure in the residuals of the multiple logistic model (significant Moran's I coefficients at several distance classes, data not shown). Therefore, the logistic model was repeated, incorporating a spatial auto-covariate term that accounted for this spatial autocorrelation, and this autologistic model showed a similar degree of fit, with all main effects remaining significant (Table 1). The one difference being that the effect of species cover in the neighbouring area was reduced in importance relative to landscape parameters (Table 1), suggesting that the importance of dispersal constraints on the presence of *P. vulgaris* was inflated by spatial autocorrelation in the database. In this spatially explicit model, the parameters related to forest habitat availability were revealed to be the main predictors.

The representation of the percentage of cover of *P. vulgaris* as a function of the amount of forest habitat revealed the absence of the species in sites with <20% forest cover (Fig. 3). Moreover, sites with moderate and high values of forest cover showed either presence or absence of *P. vulgaris*, and great variation in its abundance. A multiple regression model showed that abundance (response variable) was significantly positively related to species cover in the neighbouring area as well as to total forest cover (regression coefficients, respectively, $\beta = 0.63$,

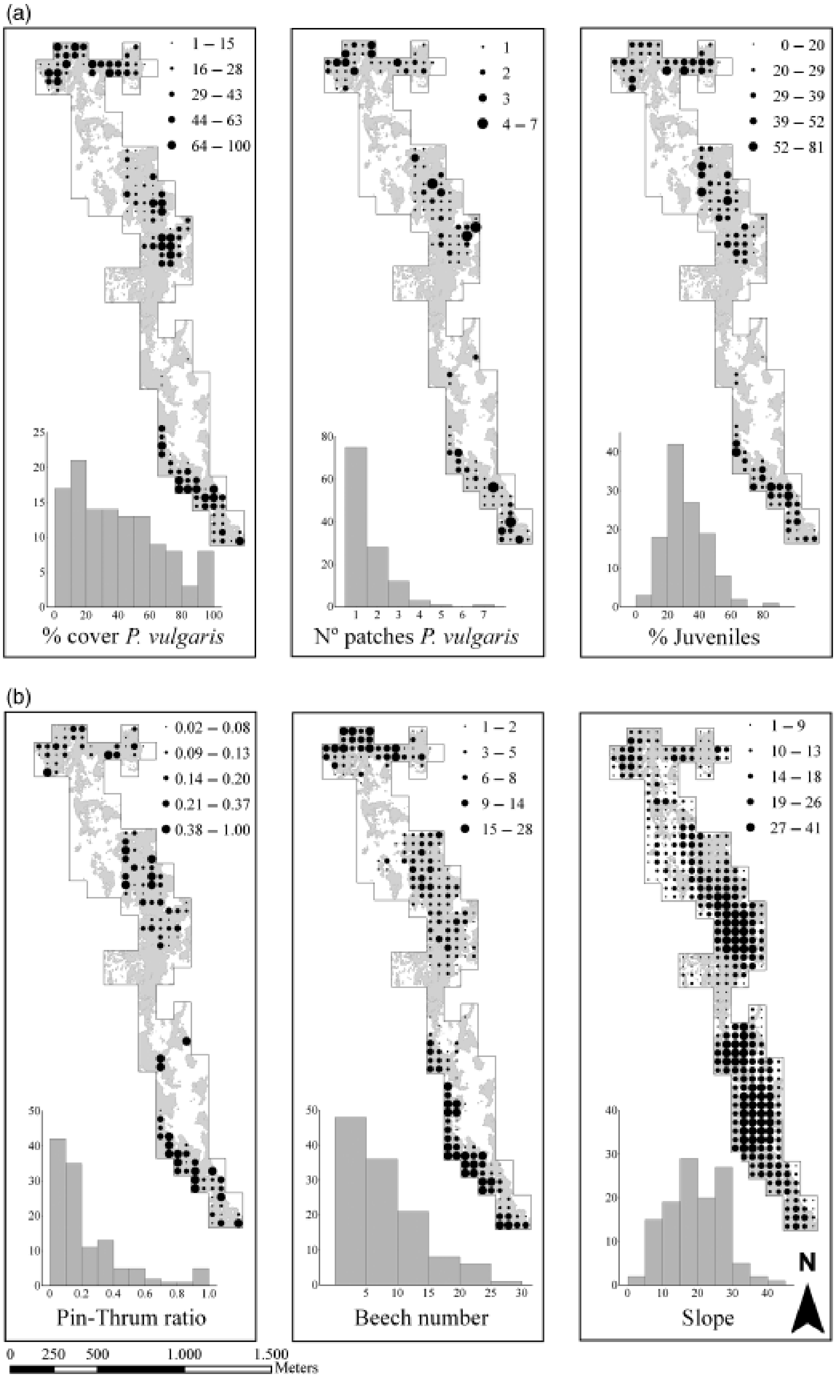

Fig. 2. Raw data values for some response variables (a) and predictor variables (b) across the sampling area. Grey background represents forest cover. The magnitude of the variables is represented by the size of the black dots according to their respective ranges. No dots means that the value is zero. Each map is accompanied by the histogram of frequencies (no. of sampling units) of the corresponding variable.

$P<0.0001$ and $\beta = 0.38$, $P = 0.0002$). This model explained ca. 28% of abundance variance ($N = 120$, $df = 2$, $F = 23.19$, $P<0.0001$). Other landscape characteristics were unrelated to the abundance of *P. vulgaris*. The residuals of the regression model for cover in the neighbouring area and forest cover showed a random spatial pattern (data not shown), so no further spatially explicit analysis was performed. The model for population subdivision, with the number of *P. vulgaris* patches as the response

Table 1. Summary of the best fit of the logistic and autologistic regression models for the presence of *Primula vulgaris* ($N = 400$, $R^2 = 0.633$, $\chi^2 \geq 309$, $P < 0.0001$, for both models; $df = 7$ and $\mathrm{df} = 8$, respectively). For each independent variable included in the models, the partial regression coefficients (β), and their associated statistics (Wald χ^2 in logistic regression and *t*-value in autologistic) and significance levels (*P*-values) are shown. [1]Residuals of the raw percentage of forest cover against the number of beech trees. [2]Residuals against the raw percentage of forest cover.

Independent variables	Logistic regression			Autologistic regression		
	β	Wald χ^2	*P*	β	*t*	*P*
Per cent cover *P. vulgaris* in the neighbourhood	5.64	26.49	<0.0001	5.40	3.23	0.001
Number of beech trees	1.43	30.49	<0.0001	1.43	5.52	<0.001
Per cent forest cover (other trees)[1]	2.83	17.52	<0.0001	2.81	4.13	<0.001
Number of forest patches[2]	– 1.76	6.05	0.0139	– 1.74	–2.42	0.015
Slope	6.35	8.18	0.0042	6.32	2.84	0.005
Y	8.94e-4	7.86	0.0051	<0.001	2.61	0.009
Y^2	1.24e-6	9.46	0.0021	<0.001	2.48	0.013
yW (spatial auto-covariate term)	–	–	–	0.955	0.19	0.847

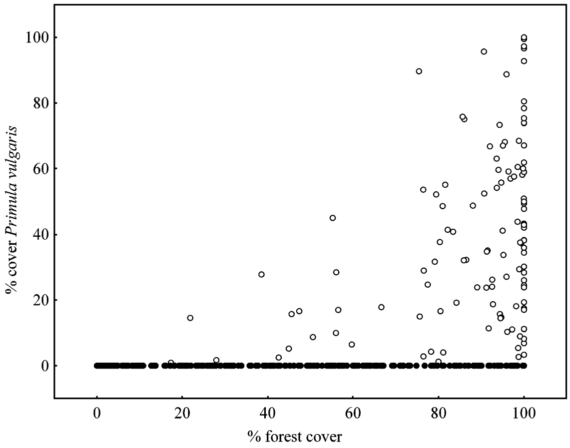

Fig. 3. Percentage cover of *Primula vulgaris* as a function of percentage of forest cover in the 400 sampling units.

variable, did not indicate a significant effect of any predictor variable.

A small amount of variance (9%) of the proportion of *P. vulgaris* juveniles was accounted for by total forest cover ($\beta = 0.18$, $P = 0.0007$). The proportion of juveniles was lower in areas of low forest cover, but it was highly variable where higher levels of suitable habitat were available. No significant spatial autocorrelation was detected for the residuals of this model.

Discussion

The aim of this work was to predict the presence, abundance and demographic structure of *P. vulgaris* as a function of continuous gradients of habitat fragmentation, other landscape characteristics, and the spatial clumpiness of populations. The response of *P. vulgaris* to the availability of forest cover and to the number of forest patches indicated that this species responds to both habitat loss and habitat subdivision at the landscape scale. As judged by the degrees of fit and the number of fragmentation parameters included in the regression models, fragmentation effects were, nevertheless, stronger on presence than on abundance, abundance in turn suffering a stronger effect than demographic structure. This response to fragmentation, however, does not mean that the species occupies all the potentially suitable remnant habitat: there was only a partial match between the spatial distribution of *P. vulgaris* and that of the potential forest habitat. This may happen because the species is unable to reach all remnant habitat, because of dispersal limitation or, alternatively, because some habitat sectors, despite colonization, are unsuitable for the long-term persistence of the species.

Effects of forest fragmentation on P. vulgaris

In the montane areas of the Cantabrian range, *P. vulgaris* behaves as a strict forest species, being fully dependent on the presence of forest cover. As this species has also been found to occur in undisturbed, non-forested habitats in central Europe (Endels et al. 2002a), it seems that its requirements for forest conditions are indirect and relatively unrelated to shade tolerance or vernal habit. In this sense, the avoidance of non-forest habitats in our site may relate to the low abundance of highly competitive graminoids on the forest floor (Jacquemyn et al. 2003) or to the lower risk of browsing and trampling damage by domestic cattle than in the pasture-heathland matrix (García & Ehrlén 2002; Leimu et al. 2002: both with *P. veris*).

We found a positive response of *P. vulgaris* presence, abundance and demographic structure to forest habitat availability, suggesting habitat loss has a pivotal role as a major driver of negative fragmentation effects. This agrees with previous research that suggested a correlation between habitat loss and decreased population viability, conditioned by the biased flower morph ratios, and hence reduced seed production, in small populations (Endels et al. 2002a, b; Brys et al. 2004). This does not, however, seem to be the case for our populations, in which no effect of morph imbalance was detected and thus, we would expect a direct link between habitat loss and actual population size.

In relation to habitat availability, our results suggest the existence of a critical amount of forest cover (ca. 20%) below which *P. vulgaris* seems unable to occur (Fig. 3). This cover value is notably similar to the theoretical threshold below which the effects of fragmentation become exponential – a result of the emergence of the disrupting effects of habitat subdivision (Fahrig 2003). Our study also shows a negative effect of habitat subdivision on the presence of *P. vulgaris*, although weaker than that of habitat loss. Conversely, we failed to detect any potential independent edge effect, as none of the species parameters measured were affected by edge density. This contrasts with previous studies demonstrating a clear negative response of other perennial herbs to the proximity of forest edges (e.g. Jules 1998; Lienert & Fischer 2003). These contrasting results may be partly explained by the scale differences between studies (small-scale distance to the edge gradient versus the large-scale landscape gradient considered in our study). Thus, there is a need for complementary multi-scaled approaches enabling the interpretation of edge effects within a landscape context (Ewers et al. 2007).

Our results suggest that the effects of habitat fragmentation were not equally strong for all of the ecological traits analysed: there was a decrease in the magnitude of fragmentation effects, from presence to abundance to demography. This difference could be partly attributable to sampling effects, namely, a smaller sample size and a narrower gradient of sampled landscape in the models for abundance and demography relative to the presence model. In addition, we found that the proportion of juveniles was low in areas of low forest cover, but along a broad portion of the gradient of habitat availability it was highly variable. This suggests that small-scale environmental factors and stochasticity, not detected by our sampling grain, may be accounting for a large proportion of the variability in the abundance and the demographic structure of *P. vulgaris*. For example, it is known that the demography of *Primula* sp. depends on the presence of small gaps in the forest canopy (Valverde & Silvertown 1995, 1998), as well as on ground-level disturbance (Ehrlén et al. 2005).

Forest availability and habitat suitability

In our study site, *P. vulgaris* occupied only a part of its potential distribution area, as judged by the distribution of the fragmented forest cover (Figs. 2 and 3). The species only appeared when forest cover was $>20\%$, but there were also many sites with moderate or high levels of forest cover in which it was absent or very scarce.

Incorporation in the analytical models of a term explicitly representing the degree of clumpiness of the populations suggests that dispersal constraints have an important effect on habitat occupancy, irrespective of the increased dispersal limitations imposed by habitat subdivision. In other words, as shown for other perennial herbs of temperate and boreal forests (Primack & Miao 1992; Ehrlén & Eriksson 2000), *P. vulgaris* cannot establish in many forested sites because seeds are unable to reach and colonize them. The dispersal mode (barochory and/or myrmecochory) of this species probably prevents seeds from being deposited more than a few metres away from the mother plant (Valverde & Silvertown 1995). Long-distance dispersal events carried out by ungulates have been demonstrated in other perennial herbs (Vellend et al. 2006) but, if they exist at all, they seem to be very rare in the case of *P. vulgaris* judging by the aggregated structure of the populations at the landscape scale. At the same time, dispersal limitation is expected to inhibit the filling of potentially suitable habitats even in a scenario of progressive recovery of historically fragmented forest habitats, as currently happens in many forest landscapes of Europe (Honnay et al. 2005). In such a case, the distribution of herbs sensitive to fragmentation may represent the distribution of suitable habitat at the moment of lowest forest availability (Cousins et al. 2006; Helm et al. 2006). Our results suggest, however, that this was not the case of *P. vulgaris* in the Cantabrian range, since it was as equally affected by the availability of mature forest as by the availability of secondary-growth and fringe forest.

This study also suggests some effect of establishment limitation, in addition to dispersal constraints, on the partial occupancy of the fragmented forest by *P. vulgaris*. In other words, low habitat quality in some sections of the landscape may prevent population establishment, despite the presence of viable seeds. In this sense, the significant effect of other landscape characteristics, namely the slope, in the species' occurrence was indicative of habitat suitability playing such a role. We may expect a direct, positive effect of slope on forest suitability if steep areas are less frequented by natural enemies of this species, such as domestic and wild ungulates (enemy-free-sites hypothesis; Haig et al. 2000). Steep slopes may also exert an indirect, positive effect by enhancing dispersal and concomitant colonization and persistence: the tiny *P. vulgaris* seeds (mean weight in mg from sample of seeds from our study area is 0.81 ± 0.02 SE) may have some degree of secondary dispersal by wind, downhill rolling or dragging by superficial water (Oshawa et al. 2007). Finally, although our regression models showed an effect of slope independent of the role of fragmentation, there may also be some indirect effect accounted for by the correlation between forest cover and slope, as less fragmented forests occur in steeper areas which are inherently more difficult to exploit from a human perspective, (Fig. 2; García et al. 2005; see also Silva et al. 2007).

Concluding remarks

This work provides evidence that dispersal constraints and some landscape characteristics that determine habitat suitability are almost as important as forest fragmentation in determining the landscape-scale distribution of *P. vulgaris* in the Cantabrian range. This is equivalent to acknowledging that fragmentation is a spatially non-random process and that not all fragmented forest habitat is suitable for this perennial herb. Moreover, it illustrates the advantages of applying a continuum landscape view to explain plant response to fragmentation, compared with other approaches relating life-history traits and dispersal syndromes to fragmentation response (Hewitt & Kellman 2002; Kolb & Diekmann 2004; Kunstler et al. 2007). First, the continuum landscape approach highlights the fact that plants are affected by the continuous gradients of landscape modification caused by different, although simultaneous, fragmentation processes. Second, it enables the incorporation and explicit evaluation of the relative role of the Umwelt, or perceptual landscape, of plant species in fragmented scenarios. In our case, we propose that the Umwelt of *P. vulgaris* in Cantabrian fragmented landscapes was represented primarily by dispersal ability, as seed dispersal determined the range of environmental heterogeneity actually perceived by the plant, and, complementarily, by topography, which may determine to some extent the persistence by fostering establishment limitations. In summary, by looking at the landscape as spatial and environmental continua, and by discerning the relative roles of fragmentation processes, dispersal constraints and habitat quality, the continua landscape approach overcomes the weakness of classic fragmentation models and proves itself to be a more robust and integrative tool for predicting future plant responses to landscape degradation caused by human activity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Landscape of the study site (Sierra de Peña Mayor, Asturias, Spain) showing a large fragment of mature hardwood forest together with many small patches of secondary forest, both immersed in a matrix of stony pastures and heathlands.

Table S1. Correlation matrix showing Pearson correlation coefficients (r) for all pairs of biological variables initially entered as predictors in the stepwise regression models for presence, abundance and population subdivision. Correlations higher than $r = 0.7$ are shown in bold type.

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