

Article

Effect of the Forest-Mine Boundary Form on Woody Colonization and Forest Expansion in Degraded Ecosystems

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Abstract: We evaluated the ecological significance of the boundary form between two patches with contrasting vegetation (mine grassland and adjacent forest) on woody colonization and forest expansion in open-cast coal mines in Northern Spain. Woody colonization and browsing traces were measured on three mine sites, along 24 transects that were laid out perpendicular to the forest-mine boundary and classified according to their shape (concave, convex, straight). Mine sites were colonized from the close forest by woody species, whose colonization intensity depends on the boundary form. The overall colonization intensity decreased with increasing distance to the forest and differed depending on the boundary form. The more intense colonization was found in concave boundaries and the strongest decrease in convex boundaries close to the forest, whereas straight boundaries showed an intermediate colonization pattern. Concave boundaries reached higher woody cover in the basal strata of the mines than convex (up to 2 m) or straight boundaries (up to 1 m) from 11 m to the forest edge, mainly by the presence of dense patches of *Cytisus scoparius* (L.) Link, with a scattered overstory of *Genista florida* L. These shrubs might reduce the browsing intensity and act as nurse plants facilitating the establishment of *Quercus petraea* (Matt.) Liebl. in mine areas at greater distances from the forest edge. The forest-mine boundary form does not affect the forest vertical structure that is homogenous and does not help explain the woody colonization pattern in the mines. We conclude that edge characteristics have a strong potential to be used in the restoration of native forests based on natural processes. The implications of our results for sessile oak (*Quercus petraea* (Matt.) Liebl.) forest expansion along edges in fragmented Mediterranean forest landscapes were discussed.

Keywords: boundary form; browsing pattern; fragmentation; *Quercus petraea* forests; sub-Mediterranean climate; surface coal-mining; vertical structure; woody colonization

1. Introduction

The boundary form between different ecosystems or landscape elements can be widely varied [1], including concave, convex, and straight shapes. Convexities are characterized by a particular species and microenvironment composition because of the exposure on three sides to the surrounding matrix. On the contrary, concavities that are less exposed and have an ameliorated microclimate became areas with higher exchange rates due to colonization processes [2]. Such boundary forms doubtless affect important ecological

processes and dynamics in the vicinity [1,2], since the boundary form determines their roles as habitat, filter, or conduit [3]. As a result, the boundary form can determine patch expansion or contraction [4], because adjacent patch shapes interdigitate each other, and interact significantly with the orientation of directional forces in the landscape, such as wind and species dispersion from source areas [3]. Many of these effects emanate from the relation existing between the shape of patches, interactions with the surrounding matrix, and transport within a patch [3–5].

Therefore, edges created by habitat fragmentation mediate the rates of flow of energy, matter [6], and organisms [7]. How edges mediate these fluxes is determined by the edge permeability, which measures the tendency of an edge to inhibit or enhance the movement of organisms, material, or energy across it [6,8]. For example, the degree of permeability of a forest-grassland edge (with a high degree of vegetation contrast) could determine the movement of organisms, including seed mobility, and thus influence the invasion of woody species and forest expansion from the forest towards the inside of the grassland [9,10].

Although implications of edge permeability in terms of forest conservation, regeneration, and wildlife management are clear [6,9,11], few studies assess the influence of the boundary form on forest expansion, and particularly, in degraded areas such as those affected by opencast coal mining (but see [3]). In the Eastern USA, the forest-mine boundary form exerted a powerful control on woody colonization, resulting in opposite behaviors of concave vs. convex boundaries, with higher colonization intensity near concave boundaries and colonization reaching a higher distance [3]. Such a woody colonization pattern was related to the activity of animals through the quantification of herbivory intensity, although other hypotheses could be considered, such as different amounts of forest in the proximity that introduce differences in micro-environmental conditions on the mine [12,13]. Besides, the forest vertical structure on edges can influence the function of edges as barriers to seed flux [13], and it can become affected by the boundary form over time [14]. Thus, the boundary form as a spatial characteristic significantly affects several other variables; concavities or coves have an ameliorated microclimate, more adjacent cover for herbivores, and more potential propagule source in the forest per unit area of mine surface [15,16], all of which doubtless interact with the basic immigration process [3].

In Northern Palencia (Spain), as in other areas in the world, opencast coal mining plays an important role in the dynamics of landscape fragmentation [7]. In the reclaimed mining surfaces, herbaceous species are usually employed to favor soil stabilization since often there is a lack of soil seed bank in the topsoil [17]. The initial result is a patch of grassland in a forest matrix. The grassland is then colonized by woody species from the adjacent forest or dispersed by wind or animals from surrounding areas [7]. This process is strongly affected by interactions between the surrounding forest matrix and the grassland patch and is probably influenced by the geometry of the patch, which can be described as a combination of several boundary forms [3]. The forest matrix, as a seed source, partly determines the species composition of woody colonizers [7]. Browsing animals from the forest matrix selectively feed in the patch, retarding woody colonization, and additionally affecting species composition [18]. Grazing can directly limit the recruitment of woody species [11,19–21], and indirectly by specifically affecting the few seeds dispersed to the high-quality microsites [22,23].

In this context, our general aim was to evaluate the ecological significance of the boundary form between two patches with a high degree of vegetation contrast (forest and grassland) on woody colonization of reclaimed coal mines in Northern Spain. Specifically, we examined the following questions: (1) Are the intensity and colonizing distance of woody species higher in concave than in convex boundaries? (2) Does the forest vertical structure affect such a woody colonization pattern in the mines? (3) Does herbivore browsing play a key role in determining the colonization patterns? The resulting information may offer strong possibilities for landscape conservation [24] and restoration of disturbed sites, such as lands mined for coal all around the world, based on spontaneous processes such as colonization and succession [25,26].

2. Materials and Methods

2.1. Study Area

This study examines three close sites, all surface-mined for coal, in the province of Palencia (Northern Spain), near the village of Guardo (1110 m a.s.l.; see Figure A1). They lie at 42°47' N, 4°50' W in the “Montaña Palentina” area on predominantly limestone of Paleozoic age, with the presence of clay and to a lesser degree of sand [7]. The climate is sub-humid Mediterranean [27] with a mean annual rainfall of 973 mm, rainy seasons in autumn and spring, and acute summer droughts through July and August with only 8% of the annual rainfall [28]. The mean annual temperature is 9.2 °C, the mean minimum of the coldest month (January) is −2.7 °C, and the mean maximum of the warmest month (August) is 25.9 °C. Most of the area surrounding the sites is forested with relatively diverse vegetation associated with the sessile oak (*Quercus petraea* (Matt.) Liebl.) forests. The natural soils are mainly Inceptisols with a udic soil moisture regime and mesic soil temperature regime [29,30].

Study sites were reclaimed around 16 years before our autumn sampling. They were regraded to approximately the original contour, and the surface was covered with 30 cm of fine-textured materials amended with cattle manure (30 t/ha) and fertilizer (8 N:15 P:15 K; 150 kg/ha). The fine-textured materials were a mixture of topsoil and sediments from deeper parts of the nearest opencast pits; this mixture had a clay loam texture, with a pH of 6.5, an electrical conductivity of 114.3 µS/cm, easily oxidizable carbon of 19.8 g/kg, available phosphorous of 9.7 mg/kg and an effective depth of 10–15 cm [30]. These soils can be classified as Lithic Udorthents (sensu [29]) and they have a very low water-holding capacity compared to the natural soil in the forest (1.0–3.4 vs. 19.87 ± 1.52) [30]. After topsoiling, mines were revegetated with a commercial seed mixture (210 kg/ha) of grasses and legume herbs (80:20 by weight). When sampled, the three sites were colonized by twelve native shrub species from the surrounding forests, mainly *Cytisus scoparius* (L.) Link and *Genista florida* L., two legume shrub species not especially abundant in the forest edge. The area was being grazed by wild animals from the surrounding landscape (deer, roe deer, and wild boar), and livestock (cattle and horses) [7].

The three reclaimed mine sites had similar geometry and slope: Site I: 325 × 185 m, eight transects sampled from northeast to east edges, slope varying from 20 to 28°; Site II: 100 × 100 m, six transects sampled from northeast to east edges, slopes 20–25°; Site III: 100 × 370 m, ten transects sampled from northwest to southwest edges, slope ca. 22°.

2.2. Vegetation Sampling

The sampling design followed that proposed by [3]. Transects 74 m long, extending 63 m onto the mine site and 11 m into the forest, were laid out perpendicular to the forest-mine boundary. Nineteen 2 × 2 m plots, centered at 4 m intervals along each transect, were sampled, i.e., three plots into the forest and 16 into the mine. An initial transect point was established at the southeasternmost corner of each mine site, and subsequent transects were established around the forested boundary in a clockwise fashion at 30 m intervals at larger sites, and at 15 m intervals at the smaller site. The initial transect point was omitted from sampling at each site to minimize a possible bias in the starting point selection. None of the selected transects crossed areas disturbed by erosion that could affect land recolonization (see Figure A2 for more sampling details).

At each transect, the forest-mine boundary form was recorded as concave, straight, or convex (i.e., a concave boundary is a projection of grass-vegetated mine into the forest). To determine the boundary form, a tangent was drawn at the midpoint of a smoothed arc connecting inflection points on each cove or lobe. Boundaries were defined as straight if the angle between the tangent and a line connecting the midpoint with the inflection point was <11°19' [3]. The 24 sampled transects included nine concave, eight convex, and seven straight boundaries.

Within each 2 × 2 m plot, the total cover of woody vegetation at seven strata (0–25 cm, 25–50 cm, 0.5–1 m, 1–2 m, 2–4 m, 4–8 m, and >8 m) was recorded to characterize the vertical

structure. The number of individuals of each woody species was also noted, recording the presence of browsing evidence; the size class was also recorded for individuals into the forest edge (11 m). Separate stems at ground level were registered as individuals. Five size classes were used: (1) ≤ 0.3 m height; (2) > 0.3 and ≤ 0.6 m height; (3) > 0.6 m and ≤ 2 m height; (4) > 2 m height, with a diameter at breast height (dbh) < 10 cm; (5) > 2 m height, with dbh ≥ 10 cm. The presence of a cut stem or twig was recorded as evidence of browsing [3]. Browsing intensity (percent of browsed stems to the total of colonizing stems) was then calculated.

2.3. Data Analysis

Linear Mixed Models (LMM) with the Restricted Maximum Likelihood method (REML; [31]) were used to assess the effect of boundary form on the vertical structure of woody vegetation in the forest edge (the 11 m strip of the forest close to mine), and in the mines considering the distance to the forest edge. In both cases, a null model considering the random effect of plots within transects was tested with the alternative model that, in the first case, included the fixed effect of the type of boundary, and, in the second case, the fixed effects of the type of boundary plus the distance to the forest edge. The Akaike information criterion (AIC; [32]) was used to verify whether the alternative model was more parsimonious, i.e., smaller values of AIC. The ANOVA was applied to test the significant differences between the null and the alternative models. Afterward, working over the model matrix, contrasts were carried out to test differences between fixed factor levels [33]. Consequently, the Bonferroni correction was used to adjust the significance level for each t-test [34,35].

Linear Mixed Models were also used to assess the influence of the boundary form and distance to the forest edge on global woody colonization intensity (stems/m²) and of the six more abundant species in the mines, as well as on browsing intensity in the mines. Then, we compared three different models: (i) a null model (without the variable “distance to the forest edge”); (ii) a model with a linear distance effect (density = $a \times \text{Distance} + b$); and (iii) a model with an exponential decay distance effect (density = $a \times \exp[-\text{Distance}] + b$). The best model was chosen by the lowest AIC, and the ANOVA was applied to test the significant differences between the null and the alternative models. The strength of the “edge effect” (how and by how much the abundance decreases towards the inside of mines) is described by the type of model supported (from no effect—null model, to moderate effect—linear model, or strong effect—exponential decay model) and, for a given type of model, by the values of the slope parameter estimates “a”.

Statistical analyses were implemented in the R software environment (version 4.0.3; [36]) using the nlme package for LMM (version 3.1–137; [37]).

3. Results

3.1. Vertical Structure and Composition of Woody Vegetation in the Forest Edge

Forest edge woody cover near to the mine was similar in the three boundary forms ($F_{[2,20]} = 1.33$, $p = 0.29$), but there was a significant vertical structure ($F_{[6,442]} = 28.91$, $p < 0.001$) slightly influenced by the boundary form (boundary form by stratum interaction; $F_{[12,442]} = 2.38$, $p < 0.01$; Figure 1). In concave boundaries, the lowest stratum (0–25 cm) showed the highest cover that was significantly higher than that in the next two strata (25–50 cm and 0.5–1 m). In straight boundaries, the highest cover was found in the stratum of 2–4 m and significantly differed from the remainder strata, except from the immediately higher (4–8 m) and the lowest (0–25 cm). In convex boundaries, the highest cover was found in the strata of 2–4 m and 4–8 m and significantly differed from the remainder strata, except from the lowest (0–25 cm).

Above 2 m high, *Quercus petraea* dominated (100% of stems with dbh ≥ 10 cm and 63% of stems with dbh < 10 cm) and *Crataegus monogyna*, *Rosa canina*, and *Genista florida* were the main accompanying species with dbh < 10 cm (see Table A1 in Appendix A). Between 60 cm and 2 m high, *Q. petraea* also dominated (72% of stems) with *Rosa can-*

ina, *Ligustrum vulgare* L., *Erica arborea* L., and *Rubus ulmifolius* as the main accompanying species. Below 2 m high, the percentage of stems of *Quercus petraea* was also important (ca. 26%), but closer to those of other shrub species, such as *Rosa canina* or *Cytisus scoparius*, and with several accompanying species.

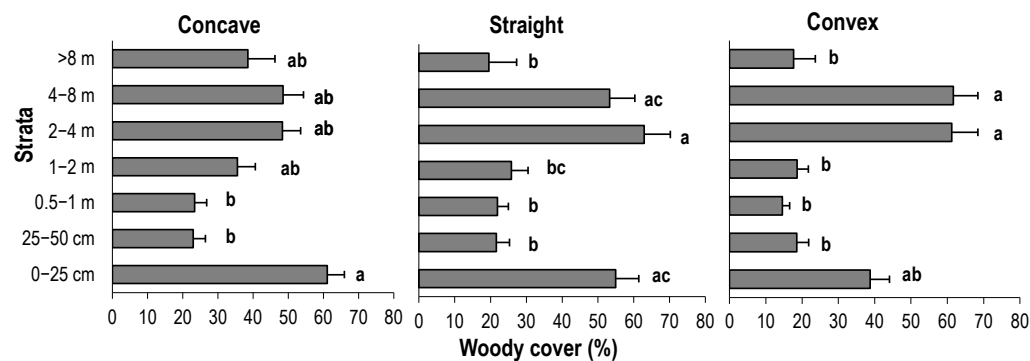


Figure 1. Vertical structure of woody vegetation in the forest edge next to the mine (mean cover and standard error in each stratum) according to the boundary form (concave, straight, or convex). Different letters indicate significant differences between all pairwise comparisons with Bonferroni's test ($p < 0.05$); i.e., among strata within each boundary form, and among boundary forms for each stratum.

3.2. Vertical Structure of Woody Vegetation in the Mines

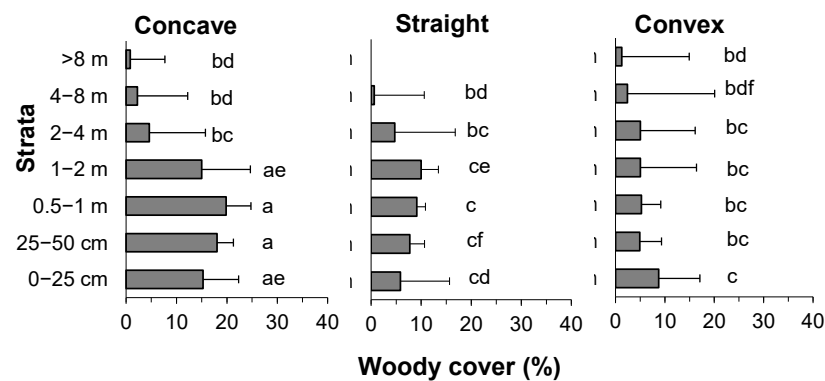
The LMM analysis of woody cover mines showed three significant two-way interactions (Table 1 and Figure 2). First, the vertical structure of woody vegetation in the mines depended on the forest-mine boundary form (Figure 2A). In concave boundaries, the cover was significantly higher in the lower four strata (0–2 m) than in the upper three. In straight boundaries, the cover of the strata between 25 cm and 2 m was higher only than that in the last stratum present (4–8 m) since no vegetation exceeding 8 m was found. In convex boundaries, the highest cover found in the lowest stratum only differed significantly from that in the last two. The cover in the first four strata (0–2 m) was significantly higher in concave than in straight or convex boundaries (intermediate values for the straight boundary form), whereas the cover was similar in the three boundary forms above 2 m.

Table 1. The summary results of linear mixed models testing the effect of boundary form (concave, straight, and convex), stratum (7 levels), and distance (16 levels) on the cover of woody vegetation colonizing the mines. The F-values of the fixed factors and their significance are presented.

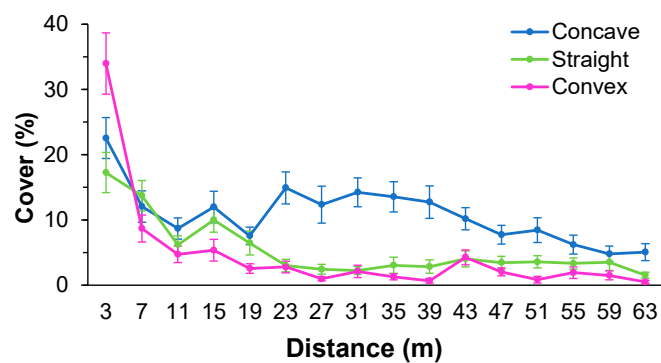
	df		F	p
Intercept	1	2220	284.03	<0.0001
Boundary form	2	20	21.51	<0.0001
Stratum	6	2220	61.56	<0.0001
Distance	15	2220	30.47	<0.0001
Boundary form × stratum	12	2220	11.90	<0.0001
Boundary form × distance	30	2220	5.00	<0.0001
Stratum × distance	90	2220	3.14	<0.0001
Boundary form × stratum × distance	180	2220	0.87	0.8833

Second, the forest-mine boundary form also influenced the colonization pattern of woody vegetation by increasing the distance to the forest edge (Figure 2B). The cover was significantly higher in convex than in concave or straight boundaries at 3 m. Between 3 and 7 m, there was a significant cover decrease in convex and concave boundaries (much stronger in convex boundaries) whereas it was gradual in straight boundaries. From 7 m, the cover did not differ with the distance for any boundary form. Nevertheless, the cover

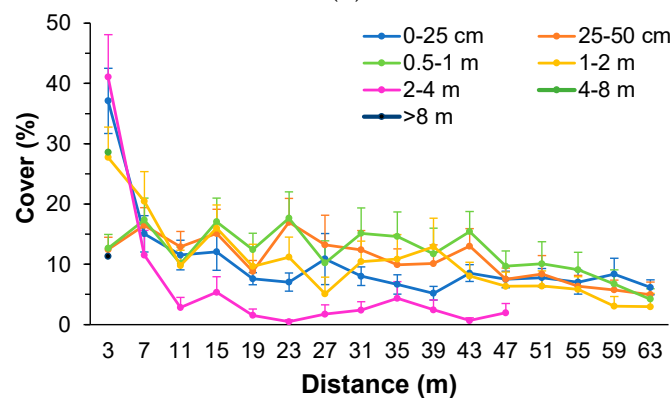
was significantly higher in concave than in straight or convex boundaries from 23 to 39 m, although the differences were not always significant.



(A)



(B)



(C)

Figure 2. (A) Vertical structure of woody vegetation in the mines according to the boundary form. (B) Woody cover in the mines along with the distance from the forest-mine limit according to the boundary form. (C) Vertical structure of woody vegetation in the mines according to the distance from the forest edge. Mean cover and standard error are shown. Different letters indicate significant differences between all pairwise comparisons with Bonferroni's test ($p < 0.05$).

Third, the vertical structure of woody vegetation in the mines also depended on the distance from the forest edge (Figure 2C). At 3 m of distance from the forest edge, the cover was similar in the first (0–25 cm), fifth (2–4 m), and sixth (4–8 m) strata but higher than that in the second (25–50 cm), third (0.5–1 m) and seventh (>8 m) strata; the cover was intermediate in the fourth stratum (1–2 m). At 23 m, the cover in the fifth stratum (2–4 m) was significantly lower than that in the second (25–50 cm) and third (0.5–1 m) strata; the cover was intermediate in the first (0–25 cm) and fourth (1–2 m) strata. The cover was similar in all the strata for the remaining distances.

3.3. Boundary Form Effect on Total Woody Colonization (Density) in the Mines

We found that woody density declined exponentially with an increasing distance from the forest edge towards the inside of mines ($F_{[1,342]} = 32.45$, $p < 0.0001$; Table 2); forty-one percent of all colonizing stems were within 13 m from the forest edge. Such an edge effect was evident in the three boundary types (Table 2; Figure 3) but its magnitude varied depending on the boundary form. In all cases, the null models (no edge effect) or the linear models (linear decrease in abundance towards the interior of mines) were the least supported (Table 2). There was also a significant boundary form $\times$ exp[distance] interaction ($F_{[2,342]} = 6.09$, $p = 0.0025$). The slope parameter that estimates comparisons among boundary types indicated that the exponential decay in woody colonization intensity in the mines with increasing distance to the forest edge was stronger in convex (slope $\pm$ SE: 2.16 ± 0.35) than in straight boundaries (1.23 ± 0.39) but it was not significant in concave boundaries. In general, woody density in concave boundaries (4.18 ± 0.32 stems/m²) was 1.4 times greater than in straight boundaries (2.89 ± 0.35 stems/m²; $t = 2.59$, $p = 0.0175$), and 2.1 times greater than in the convex boundaries (2.03 ± 0.34 stems/m²; $t = 4.33$, $p = 0.0003$).

Table 2. Results of Linear Mixed Models (LMM) describing how woody density in mines varied with increasing distance to the forest edge. The best models (lowest AICs) are highlighted in bold. p indicates the significant differences between the null and the alternative models after the ANOVA.

	Model	d.f.	AIC	Δ AIC	p
Global	Null	3	2030.24	35.54	
	Lineal	8	2016.43	21.73	<0.0001
	Exp. decay	8	1994.70	0.00	<0.0001
Boundary type					
	Concave				
	Null	3	802.36	8.49	
	Lineal	4	807.52	13.65	0.079
	Exp. decay	4	793.87	0.00	0.049
	Convex				
	Null	3	608.36	46.85	
	Lineal	4	598.55	37.04	<0.001
	Exp. decay	4	561.51	0.00	<0.001
	Straight				
	Null	3	612.17	13.10	
	Lineal	4	612.97	13.90	0.007
	Exp. decay	4	599.07	0.00	0.010

3.4. Boundary Form Effect on Main Woody Colonizers of Mines

The *Quercus petraea* (Figure 4A) and *Crataegus monogyna* (Figure 4D) density declined exponentially with increasing distance to the forest edge (Table 3) but with different intensity depending on the boundary form (Table A2 in Appendix A). The *Quercus petraea* decay was stronger in convex (slope $\pm$ SE: 1.49 ± 0.21) than in concave (0.56 ± 0.12) and straight boundaries (0.71 ± 0.29). The *Crataegus monogyna* decay was the strongest in concave boundaries (slope $\pm$ SE: 0.40 ± 0.12), intermediate in the convex (0.16 ± 0.04), and not significant in the straight.

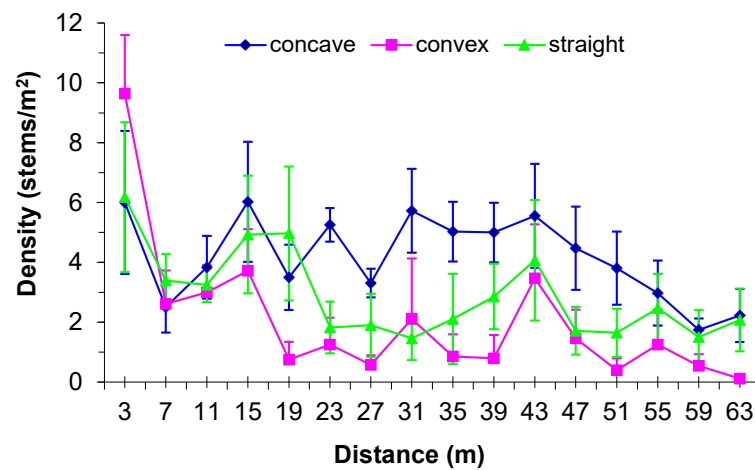


Figure 3. Average woody density (stems/m²) and standard error according to the distance from the forest edge (m) in the three boundary types (concave, convex, and straight).

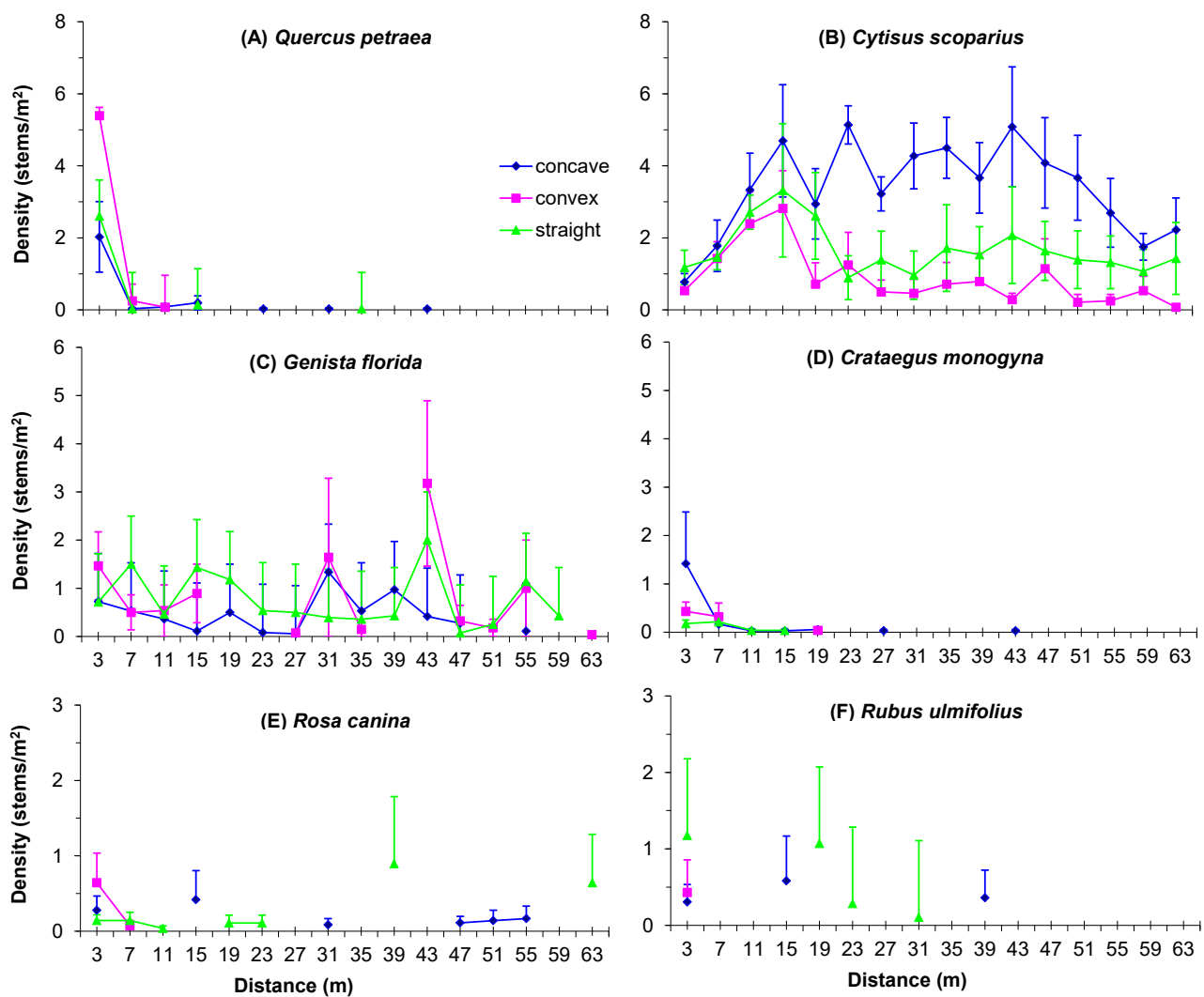


Figure 4. Average woody density (stems/m²) and standard error (SE) of six main woody species (A–F) colonizing the mines (those that accounted for more than 2% of all the colonizing stems), according to the distance to the forest edge (m) in the three boundary types (concave, convex, and straight).

Table 3. Results of Linear Mixed Models (LMM) describing how the density of main woody colonizers of the mines varied according to boundary form, distance to the forest edge, and their interaction. F-values of fixed effects and their significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) for the best model (lowest AIC; see Table A2 in Appendix A) are shown.

	Best Model	Boundary Form	Distance	Boundary Form $\times$ Distance
<i>Quercus petraea</i>	Exp. decay	1.17	119.19 ***	13.36 ***
<i>Cytisus scoparius</i>	Exp. growth	13.47 ***	7.23 **	2.57 *
<i>Genista florida</i>	Exp. decay	0.68	1.58	0.52
<i>Crataegus monogyna</i>	Exp. decay	0.63	29.94 ***	8.70 ***
<i>Rosa canina</i>	Exp. decay	0.88	7.31 **	2.84
<i>Rubus ulmifolius</i>	Exp. decay	1.54	9.67 **	2.12

Unlike previous species, the *Cytisus scoparius* density increased exponentially with increasing distance to the forest edge (Table 3; Figure 4B; Table A2 in Appendix A) but with different intensity depending on the boundary form (Table A2 in Appendix A). The increase was only significant in concave boundaries, whereas it was not significant in convex and straight boundaries. So, from a certain distance (23 m), differences in density were found between concave and convex or straight boundaries (Figure 4B). The *Genista florida* density was similar regardless of boundary form and distance (Table 3; Figure 4C). The *Rosa canina* (Figure 4E) and *Rubus ulmifolius* (Figure 4F) density declined exponentially with increasing distance to the forest edge regardless of the boundary form (Table 3). As a whole, *Quercus petraea* showed the most extreme pattern with 94% of the stems within 3 m from the forest edge. In addition, *C. monogyna* was particularly restricted to the near the forest edge (60% of the stems within 7 m from the forest edge). *R. canina*, and *R. ulmifolius* were particularly abundant near the forest edge, and at farther distances (*Rosa canina* at 39 m or 63 m, and *Rubus ulmifolius* at 19 m). Nevertheless, overall colonization beyond 11–15 m from the forest edge was predominantly by *C. scoparius* and *G. florida*.

3.5. Influence of Browsing

Only $2.2 \pm 0.5\%$ of the stems colonizing the mine showed evidence of browsing compared to $25.6 \pm 2.6\%$ in the forest, the difference being statistically significant ($F_{[1,414]} = 214.96$, $p < 0.0001$). *Quercus petraea*, *Cytisus scoparius*, and *Crataegus monogyna* were the most browsed species (67%, 28%, and 5% of all browsed stems, respectively) with similar browsing intensity in forest and mines and regardless of the boundary form (statistical analysis results are omitted for simplicity).

Overall browsing intensity (percent of browsed stems to the total of colonizing stems) in the mines declined exponentially with the distance to the forest edge ($F_{[1,229]} = 22.55$, $p < 0.0001$). Particularly, 52% of the browsed stems were within the first 7 m from the forest edge, and evidence of browsing was considerably reduced beyond 15 m. There was also a significant boundary form $\times$ exp[distance] interaction ($F_{[2,229]} = 4.48$, $p = 0.0123$; Figure 5). In all cases, the null models (no edge effect) or the linear models (linear decrease in abundance towards the interior of mines) were the least supported (Table A3 in Appendix A). The exponential decay was stronger in convex (slope $\pm$ SE: 5.90 ± 1.58) than in concave boundaries (2.88 ± 1.36), and it was not significant in straight boundaries.

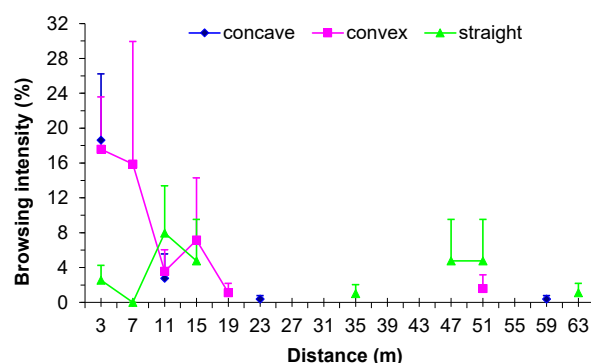


Figure 5. Average browsing intensity (percent of browsed stems to the total of colonizing stems) and standard error according to the distance to the forest edge (m) in the three boundary types (concave, convex, and straight).

4. Discussion

Our results showed how the natural woody colonization of the mines was concentrated in the proximity of the forest edge and decreased exponentially with increasing distance. This pattern of colonization depends on the forest-mine boundary form and particularly on the opposite form of concave vs. convex boundaries (the straight boundaries occupying an intermediate position), which allows us to accept our first hypothesis (research question 1). A similar colonization pattern was found in surface coal mines under different environmental conditions in the Eastern USA [3]. However, the effect of boundary form affected woody colonizers differently, probably because of their different tolerance to environmental stress [38,39].

The homogeneity in the vertical structure of the adjacent forest (regardless of the forest-mine boundary form) indicates that this is not a plausible explanation for such a colonization pattern (research question 2). Perhaps the time elapsed after mine rehabilitation in our study is not enough that the structure of this anthropogenically created forest edge became affected by the forest-mine boundary form and, consequently, to affect woody colonization in the mines [13,14].

The herbivory on colonizing stems seems to be more explanatory of the colonization pattern and explains the opposite results for concave and convex boundaries (research question 3), but together with the differences in the immigration process (dispersal mode, dispersal distance, and establishment). Differences in microenvironmental conditions on the mines because of different amounts of forest in their proximity [2] determine a different vertical structure of woody vegetation in the mines as a function of the forest-mine boundary form and the distance to the forest edge.

Microclimatic conditions are supposed ameliorated in concavities that are less exposed, whereas convexities are exposed on three sides to the surrounding matrix [2]. As a result, concave and convex edges might have a different floristic composition [3]. In our study, we found evidence of this, since more variety of colonizing species were found near concave boundaries. Particularly, *Euonymus europaeus*, *Ligustrum vulgare* and *Sorbus aucuparia* only colonized the mine sites near concavities; the *Crataegus monogyna* density was the highest near concave boundaries and decreased strongly with distance; the *Cytisus scoparius* density increased exponentially with increasing distance to the forest edge only significantly in concavities and maintains up to 63 m. The density of other species such as *Rosa canina* and *Rubus ulmifolius* was independent of the boundary form, although it declined exponentially with increasing distance to the forest edge, whereas the *Genista florida* density was independent of both the boundary form and the distance.

Cytisus scoparius and *Genista florida* are two Mediterranean species well adapted to stressful environments [7,40]. Both species actively colonize coal mines in Northern Spain [20,41], probably because of their ballistic dispersion mode, i.e., explosive dehiscence [42,43], and being long-distance dispersed by a wide range of wild herbivores, e.g.,

ants [44], birds [42]; mammals [45]; livestock [46]. *Genista florida* showed also vegetative reproduction in the study area [47], which has been considered the most successful means of colonization in reclaimed mines of Germany [48] and the USA [3]. In turn, the massive spread of *Cytisus scoparius* colonizing open areas has been closely linked to specific traits of invasive species such as the production of high amounts of seeds forming a long-lasting seed bank [49], a capacity to establish in areas immediately after a disturbance and fast initial growth [40,50,51].

On the contrary, the *Quercus petraea* colonization was mostly concentrated in the mines close to convex boundaries, although its colonization reached a longer distance in concavities. Difficulties in colonizing the mine area for species that are forest specialists, such as *Q. petraea*, could be explained by lower phenotypic plasticity to light and lower acclimation potential to increasing light which is associated with late-successional species [52]. *Q. petraea* is a typical Eurosiberian species adapted to wet and cold locations where resources are abundant, but it endures badly stressful conditions, such as high radiation, water deficit, or above-ground disturbances [52]. In the study area, *Q. petraea* is at its southernmost distribution limit [53], which could also contribute to its relatively narrower wide niche in comparison with most active colonizer shrub species [54]. Moreover, the natural establishment of *Quercus* on Mediterranean mine sites is a complex process limited by ecological filters, such as (i) migration barrier produced by seed dispersal mechanisms (i.e., barochory and zoochory; [19,55,56]), (ii) summer drought being increased in reclaimed mined sites by a lack of soil structure such as in forest systems [30] and (iii) herbivory which can occur through trampling and browsing by livestock and wild ungulates [20,57]. These ecological filters determined that 94% of the *Quercus* seedlings colonizing the mines under study were found in the first 3 m from the forest edge, probably by its primary mechanism dispersion (i.e., barochory), whereas beyond 5 m from the forest edge, seedling arrival was mainly due to a secondary dispersal mechanism by animals (i.e., zoochory). Moreover, most *Q. petraea* seedlings in the mine area were located under the influence of the two main shrubby colonizers (*Cytisus scoparius* and *Genista florida*), suggesting that even if acorns overcome the dispersal barrier, they have to reach inside the mine suitable microsites under shrubs for effective germination and growth [41,58]. This fact can explain why the *Quercus petraea* density was the highest close to convex boundaries, where the cover of both shrubby colonizers was also the highest (results not shown here), whereas reached longer distances in concave boundaries where their cover was then the highest.

Although the abundance of *Q. petraea* in the mine was lower than in the forest edge [41,47], its estimated density is near or even above 7000–15,000 seedlings per hectare, recommended as minimum initial stocking to provide a total of at least 250 potential crop oaks of reasonable stem quality and acceptable crown form in Germany [59]. Therefore, such a density would probably be enough to ensure the natural regeneration of *Q. petraea* in reclaimed coal mines in Northern Spain, whenever they establish under shrubs protection [41,58].

Woody vegetation in the mines close to the forest edge (the highest cover and density) can act as perches favoring seed deposition from birds [60], thus allowing the seed dispersion of *R. canina*, *R. ulmifolius* and *C. monogyna* and explaining the presence of scattered individuals of them beyond 7 m.

Stems of colonizing species extended up 63 m in the three boundary forms, although they are more numerous in concave than in convex boundaries. In the coal mines of the Eastern USA, stems of colonizing species extended >61 m from concave boundaries, but rarely >13 m from convex boundaries [3]. Perhaps the different time elapsed after reclamation at the time both studies were conducted (16 years here vs. 10 years in USA) could partially explain the longer-distance woody colonization found in our study regardless of the boundary form. In addition, the intrinsic characteristics of the main colonizers could help understand such a colonization pattern. The main colonizers in our mines, *Genista florida* and *Cytisus scoparius*, were shrub species with ballistic dispersion and being long-distance dispersed by a wide range of wild herbivores, as previously mentioned,

whereas in the coal mines of the Eastern USA the main colonizers produced clonal clusters of stems (vegetative reproduction) and have not explosive dehiscence that can affect the lower speed of dissemination and distance reached in a similar period.

Woody colonization shortage in the mines under study could be explained, in part, by the intrinsic characteristics of the potential colonizer species, as mentioned above, but also by the properties of the mine soils, especially concerning their nutritional deficiencies [7], barely depth and very low water holding capacity [30]. In addition, success in the colonizing species establishment greatly depends on good germination and the pre-reproductive mortality [61] that, at the same time, is strongly conditioned by abiotic factor variability [62]. Therefore, it is possible that the species that are active colonizers of the mines have broad niches, due to their tolerance to different light regimes and because they occupy disturbed habitats with variable and changing environments [63,64].

Finally, the browsing intensity was significantly greater in convex boundaries than in concave boundaries, contrary to that found in the reclaimed coal mines in the Eastern USA [3]. It is argued that herbivores prefer concavities due to the coverage of the adjacent forest which generates a favorable microclimate and predator avoidance [2]. This conflicting pattern can be explained taking into account that most of the browsed stems in our mines were those of *Q. petraea*, and that *Q. petraea* stems are mostly concentrated near convex boundaries where the density of *Cytisus scoparius* was lower and thus its protective role against herbivory on sessile oak.

We also found that the browsing intensity decreases exponentially with distance from the forest edge, whereas browsing intensity did not increase or decrease significantly with distance from the forest edge in the reclaimed coal mines in the Eastern USA [3]. Our results are consistent with the argument that, in large clear-cuts, herbivores tend to forage near the perimeter of the harvested area, despite the high nutritional value of browse in the open [65]. Feeding in the middle of such large openings requires that herbivores move long distances away from the escape cover afforded by the intact forest stands surrounding the clear-cut [66].

The browsing intensity pattern found in our study is consistent with the pattern of the overall woody colonization intensity that showed an exponential decay with increasing distance from the forest edge, stronger adjacent to convex boundaries than next to other boundary forms. Thus, herbivory could be considered as a secondary cause of the overall pattern of woody colonization in the mines, despite the woody colonization intensity was the highest in the concave boundaries except in the first 3–7 m from the forest edge.

On the other hand, *Q. petraea* was the larger browsed species even though *C. scoparius* was the most abundant in the mine sites. This result suggests that herbivores prefer some woody species, especially those with soft leaves [67], and these species are positively selected by browsers regardless of their abundance. *Quercus* spp. are more palatable than other deciduous species [68]; therefore, spatial association with unpalatable plants that offer protection against herbivory might be a key mechanism for oak regeneration [69]. In this sense, cattle reject *Genista florida*, probably because it is considered non-palatable and even of some toxicity to ungulates [46,67], and horses mainly graze herbaceous species [46].

5. Conclusions

We conclude that the forest-mine boundary form exerts a powerful control on woody colonization and explains the opposite results for concave vs. convex boundaries in Northern Spain sixteen years after coal mining reclamation. The woody colonization intensity decreases exponentially as distance increases from the forest edge, with the highest colonization occurring in concave boundaries, the lowest in convexities (except at 3–7 m from the forest) and being intermediate in the straight boundaries. The effect of boundary form also affects woody colonizers differently, probably because of their different tolerance to environmental stress.

These conspicuously different colonization patterns appear to be primarily the result of the immigration process, interacting directly with the forest-mine boundary form as a

spatial characteristic that significantly affects several other variables such as environmental conditions and browsing intensity. Herbivory seems to be a secondary contributing factor, whereas the homogeneity in the forest vertical structure on the edges does not help explain such a colonization pattern.

In summary, mine areas by concavities experienced more woody colonization than those by straight boundaries or convexities. Sixteen years after revegetation, concavities had dense patches of *Cytisus scoparius* with a scattered overstory of *Q. petraea* in mine areas at greater distances from the forest edge. Therefore, edge characteristics have a strong potential to be used in the restoration procedures of native forests, in mined or other degraded lands, based on natural processes. Planting shrubs along the forest edge to produce concavities, and accentuate those less marked, could favor the expansion of sessile oak forests into the mines.

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Appendix A

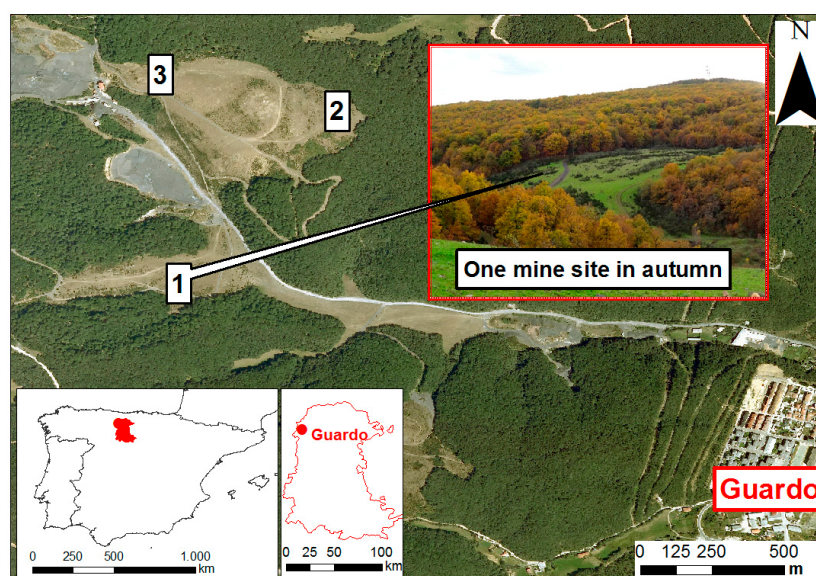


Figure A1. Location of the study sites in Northern Spain.

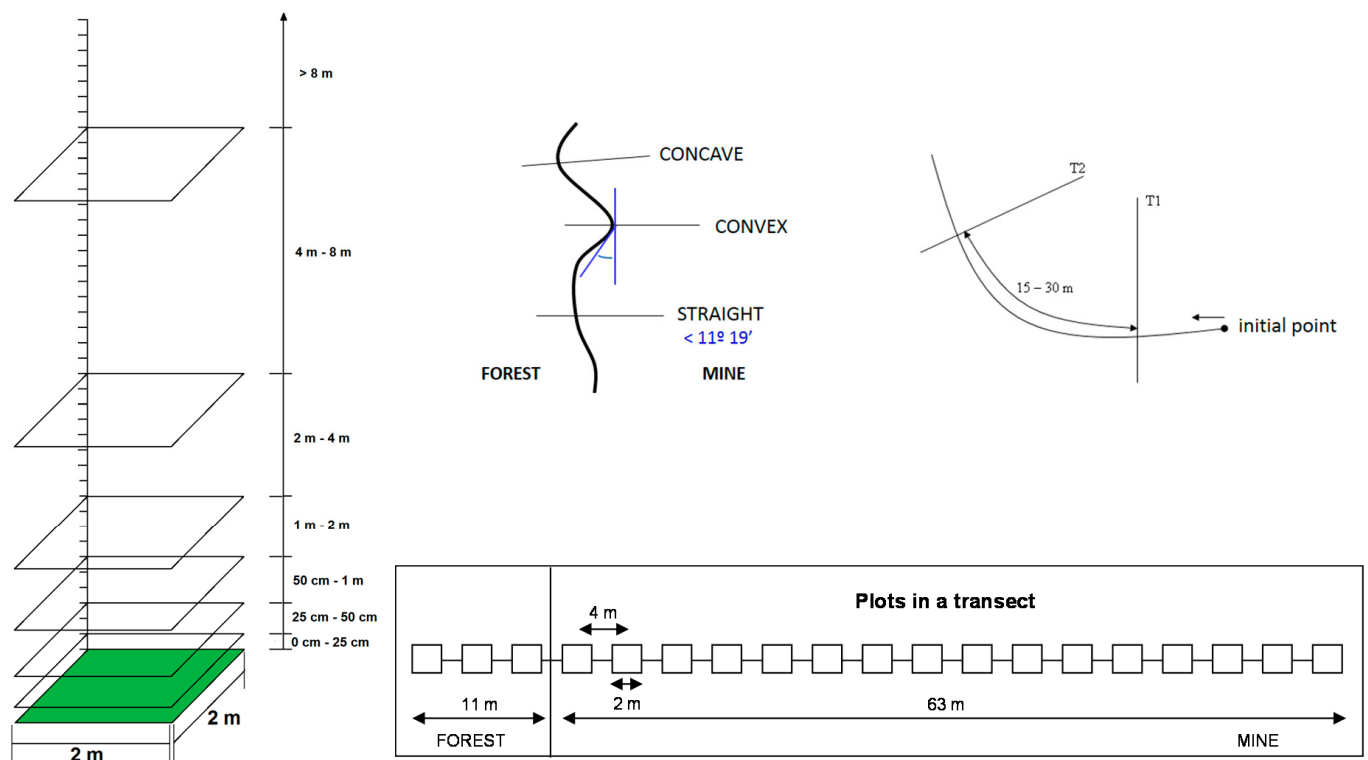


Figure A2. Details of vegetation sampling using transects (T).

Table A1. Percentage of individuals (stems) of woody species in the forest edge (the nearest 11 m of the forest close to the mine sites) according to their size class; dbh = diameter at breast height (1.3 m); the five last species did not colonize the mines.

Species	≥ 2 m ≥ 10 cm dbh	≥ 2 m <10 cm dbh	≥ 60 cm y < 2 m <10 cm dbh	≥ 30 cm y < 60 cm <10 cm dbh	<30 cm <10 cm dbh
<i>Quercus petraea</i> (Matt.) Liebl.	100	62.85	71.89	27.86	24.63
<i>Rosa canina</i> L.	0	8.97	5.79	33.22	15.84
<i>Ligustrum vulgare</i> L.	0	0	4.72	8.30	3.52
<i>Crataegus monogyna</i> Jacq.	0	12.82	2.87	6.27	12.32
<i>Rubus ulmifolius</i> Schott.	0	0	3.83	8.49	3.23
<i>Cytisus scoparius</i> (L.) Link	0	1.28	1.44	4.06	19.36
<i>Genista florida</i> L.	0	11.54	0.59	1.85	7.04
<i>Euonymus europaeus</i> L.	0	1.28	1.47	1.29	1.76
<i>Ilex aquifolium</i> L.	0	1.28	0.59	0.92	0.29
<i>Lonicera xylosteum</i> L.	0	0	0.15	0.55	0.29
<i>Lonicera periclymenum</i> L.	0	0	0	0	0.29
<i>Sorbus aria</i> (L.) Crantz	0	0	0.26	0	0.59
<i>Erica arborea</i> L.	0	0	4.39	4.61	7.04
<i>Prunus spinosa</i> L.	0	0	0.18	0.92	2.64
<i>Malus sylvestris</i> Mill.	0	0	0.37	1.66	1.17
<i>Vaccinium myrtillus</i> L.	0	0	1.40	0	0
<i>Viburnum lantana</i> L.	0	0	0.07	0	0
Total	100	100	100	100	100

Table A2. Results of Linear Mixed Models (LMM) describing how woody density in mines varied with increasing distance to the forest edge. The best models (lowest AICs) are highlighted in bold. *p* indicates the significant differences between the null and the alternative models after the ANOVA.

	Model	d.f.	AIC	ΔAIC	<i>p</i>
(1) <i>Quercus petraea</i>					
Global	Null	3	975.11	75.56	
	Lineal	8	977.55	78.00	<0.0001
	Exp. decay	8	899.55	0.00	<0.0001
Boundary type					
Concave	Null	3	295.97	39.33	
	Lineal	4	296.71	40.07	0.2629
	Exp. decay	4	256.64	0.00	<0.0001
Convex	Null	3	317.87	100.67	
	Lineal	4	309.63	92.43	0.0014
	Exp. decay	4	217.20	0.00	<0.0001
Straight	Null	16	333.11	16.49	
	Lineal		338.49	21.87	0.0662
	Exp. decay		316.62	0.00	<0.001
(2) <i>Cytisus scoparius</i>					
Global	Null	3	1729.98	35.54	
	Lineal	8	1736.56	50.91	0.6360
	Exp. growth	8	1685.65	0.00	<0.0001
Boundary type					
Concave	Null	3	736.64	13.23	
	Lineal	4	745.23	21.82	0.0102
	Exp. growth	4	723.41	0.00	<0.0001
Convex	Null	3	429.86	5.19	
	Lineal	4	429.98	5.31	0.1693
	Exp. growth	4	424.67	0.00	0.0073
Straight	Null	16	502.35	5.86	
	Lineal		510.26	13.77	0.015
	Exp. growth		496.49	0.00	0.005
(3) <i>Genista florida</i>					
Global	Null	3	1401.70	13.00	
	Lineal	4	1432.27	43.57	0.001
	Exp. decay	4	1388.70	0.00	0.0003
(4) <i>Crataegus monogyna</i>					
Global	Null	3	513.05	5.27	
	Lineal	4	538.34	30.58	0.0092
	Exp. decay	4	507.78	0.00	<0.0001
Boundary type					
Concave	Null	3	290.07	20.88	
	Lineal	4	294.85	25.66	0.0956
	Exp. decay	4	269.19	0.00	0.0001
Convex	Null	3	40.18	14.4	
	Lineal	4	42.73	16.95	0.4584
	Exp. decay	4	25.78	0.00	0.0001
Straight	Null	16	83.15	−9.15	
	Lineal		96.20	−13.05	0.0642
	Exp. Decay		92.30	0.00	0.0008
(5) <i>Rosa canina</i>					
Global	Null	3	534.30	10.22	
	Lineal	4	577.09	53.01	<0.0001
	Exp. decay	4	524.08	0.00	0.0011
(6) <i>Rubus ulmifolius</i>					
Global	Null	3	544.33	17.76	
	Lineal	4	575.18	48.61	0.0009
	Exp. decay	4	526.57	0.00	<0.0001

Table A3. Results of Linear Mixed Models (LMM) describing how browsing intensity in mines varied with increasing distance to the forest edge. The best models (lowest AICs) are highlighted in bold. *p* indicates the significant differences between the null and the alternative models after the ANOVA.

	Model	d.f.	AIC	ΔAIC	<i>p</i>
Global					
	Null	3	1999.93	57.41	
	Lineal	8	2002.52	60.00	0.192
	Exp. decay	8	1942.52	0.00	<0.0001
Boundary type					
Concave	Null	3	792.76	24.75	
	Lineal	4	797.77	29.76	0.008
	Exp. decay	4	768.01	0.00	<0.0001
Convex	Null	3	644.06	16.8	
	Lineal	4	641.37	14.11	0.0304
	Exp. decay	4	627.26	0.00	<0.0001
Straight	Null	16	545.25	8.05	
	Lineal		551.61	14.41	0.0368
	Exp. decay		537.20	0.00	0.0015

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