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1 Forest and cone structure influence where crossbills forage in a managed Scots pine forest

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11 Abstract

12 The structure of forests is a fundamental attribute that impacts biodiversity and ecosystem
13 services and in turn is influenced by natural disturbances and management practices. Here, we
14 examine spatial variation in the interaction between a specialized predispersal seed predator,
15 common crossbills (*Loxia curvirostra*), and Scots pine (*Pinus sylvestris*) in relation to forest
16 structure and tree features in a managed Mediterranean forest. Crossbills preferred to forage
17 in pine stands that were more open, which correspond to older stands or regeneration stands
18 with scattered old seed trees. More open older stands with larger trees tend to produce more
19 cones that are attractive to crossbills, although their use was also consistent with crossbills
20 reducing their risk of predation. Within these patches, crossbills selectively foraged on trees
21 having many small, thin-scaled cones, which require less effort and time to extract the seeds.
22 Crossbills were apparently limited to only a very small subset of the closed Scots pine cones
23 because they have relatively small and ineffective bills for foraging on Scots pine. Given that
24 crossbills foraged on only a small subset of the cones within more open stands, a management
25 strategy that would aid common crossbills is to thin middle-aged stands. This would

accelerate the development of older stand structure, which would benefit crossbills by increasing the occurrence of suitably open woodlands, benefit other species that rely on older more open stand structure, and potentially decrease the vulnerability of the forest to fire and drought.

Keywords: foraging behavior, *Loxia curvirostra*, *Pinus sylvestris*, seed predation, Spain, tree thinning

Introduction

Forests are important for biodiversity conservation and as providers of ecosystem services (Ninan and Inoue 2013, Brockerhoff et al. 2017). Some of the components known to be linked to forest biodiversity and ecosystem services include forest structure and area, and tree species composition (Gao et al. 2014, Brockerhoff et al. 2017, Rocas-Díaz et al. 2021). For example, the abundance, composition, and diversity of forest birds are widely influenced by the vertical and horizontal structural complexity of the forest (McArthur and McArthur 1961, Cody 1985, Zellweger et al. 2017). Forest management often replaces natural disturbances and alters forest dynamics, and thus determines the structural characteristics of the different forest stands, with variable effects on species and forest functions depending on the type and intensity of forestry practices (Bengtsson et al. 2000, Wilson and Puettmann 2007, Hanle et al. 2020, Boucher et al. 2021). For example, short rotation ages increase the proportion of stands with younger trees, and clearcutting reduces canopy vertical heterogeneity compared to selective cutting (Hansen et al. 1991, Martin et al. 2020), with a general reduction in biodiversity and forest functions in young dense stands and with more intensive management (Koskela et al. 2007, Duncker et al. 2012, Angelstam et al. 2018, Rocas-Díaz et al. 2021).

Besides the structural characteristics of forest stands, forestry practices also have consequences for the spatial and temporal availability of seeds for natural regeneration and as a resource for seed-eating animals (Benkman 1993a, Carey 2000, Worthy et al. 2006). Natural regeneration is important to ensure forest sustainability and thus managing practices are directed to improve the production of viable seeds and seedling establishment (Barbeito et al. 2011, Chen et al. 2018). The impacts on seed-eating animals depends on their reliance on seeds and their capacity to use alternate resources (Smith and Balda 1979, Wauters et al. 2008). Perhaps the most specialized group of conifer-seed-eating vertebrates are medium-sized finches called crossbills (*Loxia* spp.), whose crossed mandibles are used first to form gaps between closed cone scales and then spread them apart providing crossbills access to the seeds at the base of the scales (Newton 1972, Benkman and Lindholm 1991). It is expected therefore that crossbill populations and habitat use are strongly influenced by natural disturbances or forestry practices that affect the abundance of cone-seed (Benkman 1993a, Mezquida and Benkman 2014, Behl and Benkman 2018).

Here, we examine common crossbill (*L. curvirostra*) habitat use in relation to Scots pine (*Pinus sylvestris*) forest structure and tree features in a managed Mediterranean forest. Scots pine occurs at high elevations in cold mountain areas in the Mediterranean (Barbéro et al. 1998, Castro et al. 2004), showing changes in forest structure along the elevational gradient as a result of variation in environmental conditions (Díaz 2006, Pascual et al. 2008). Crossbills in mountain pine (*Pinus uncinata*) forests in the Pyrenees preferred to forage at higher elevations where the canopy was more open (Génard and Lescourret 1987, Mezquida and Benkman 2014). More open forest patches may be preferred because it aids crossbills in their detection of approaching predators (Benkman 1987a, Summers and Proctor 1999). On the other hand, more open patches may be more profitable to crossbills because Scots pine in more open patches produce more and smaller cones (Summers and Proctor 1999), and

crossbills consistently prefer conifer trees that produce more cones (Holimon et al. 1998, Mezquida and Benkman 2014, Behl and Benkman 2018) and smaller cones (Benkman and Mezquida 2015).

Regardless of the natural variation in forest structure along the elevational gradient, forest structure is mainly determined by forestry practices in managed forests (Pascual et al. 2008, Uria-Díez and Pommerening 2017). Forest structure and cone production in different stands will depend on their developmental stage, from regeneration to mature and old-growth stands (Uria-Díez and Pommerening 2017). Crossbills are usually more abundant in older than in younger forests (Benkman 1993a, Holimon et al. 1998, Behl and Benkman 2018) presumably because older forests have more open canopies (Uria-Díez and Pommerening 2017) and the older, larger trees consistently produce more (Benkman 1993a, Holimon et al. 1998, Behl and Benkman 2018), and sometimes smaller, cones (Summers and Proctor 1999). However, the preference for individual trees by foraging crossbills is ultimately related to seed and cone traits that affect crossbill seed intake rates (Benkman 1987b, Benkman 1993b). Cone traits such as cone size and scale thickness are key traits that influence foraging crossbills (Benkman et al. 2003, Mezquida and Benkman 2014, Benkman and Mezquida 2015) because larger, thicker scales are more resistant to being spread apart so that the underlying seeds can be removed.

We characterized the structure of forest patches along a gradient of elevation and stand development, and quantified seed predation by crossbills to address the hypothesis that crossbills prefer to forage in more open forest patches. We also quantified seed predation by crossbills at individual trees to test whether crossbills preferences are determined by the structure of the forest patch, tree size, and cone structure. Because crossbills rely almost exclusively on seeds in conifer cones (Newton 1972), we assume that local variation in seed predation reflect variations in local crossbill abundance and habitat use (Benkman et al. 2013,

Behl and Benkman 2018). To further explore this relationship, we estimated crossbill abundance at each forest patch and tested whether the extent of seed predation was positively correlated with crossbill abundance.

Methods

Study area

The study was conducted in the forest of Valsain (7622 ha), located on the northern slope of the Guadarrama Mountains, central Spain (40° 51' N, 4° 3' W). The forest is mostly dominated by Scots pine, which occurs on acidic soils between elevations of 1200 and 2100 m. Pyrenean oak (*Quercus pyrenaica*) is more abundant at the lower elevations. The shrub layer is comprised of mainly *Genista florida*, *Cytisus scoparius*, *Juniperus communis*, *Rosa* sp., *Rubus* sp., and *Ilex aquifolium*. The climate is continental Mediterranean, with hot, dry summers and cold winters, annual precipitation ranging from over 900 to 1500 mm, depending on elevation, and mean annual temperature of around 10°C.

Management in this pine forest consists of harvesting timber while maintaining natural forest productivity and relying on natural regeneration. Using a group shelterwood method, old trees are gradually removed in a series of repeated partial harvests over a rotation period of 120 years to promote the establishment of a new stand under the shelter of the old one (Mason et al. 2004). This creates small gaps (0.1-0.2 ha) in the stand leaving groups of old trees that shelter the natural regeneration growing in the gaps (Barbeito et al. 2011). Part of the forest at higher elevations (3326 ha) was included in a National Park declared in 2013, where commercial cutting is forbidden (Ezquerro et al. 2019).

Seed predation by crossbills

We randomly selected 81 Scots pine trees along most of its elevational range (1273 to 2008 m), with a minimum distance of 250 m between them. The separation between trees was aimed to cover a wide range of forest structure. Young, non-reproductive trees or trees with signs of poor condition were avoided. We quantified seed predation by crossbills during late October and early November 2014, when cones were closed and mature and those foraged on by crossbills accumulate on the ground. Cones depredated by crossbills are easily recognized because crossbills bite off cones from branches, extract seeds by separating and usually shredding the cone scales, and then drop the cones (Mezquida and Benkman 2010, Summers et al. 2010). For each tree, we measured diameter at breast height (DBH) with a measuring tape and set up four 1-m wide and 25-m long transects at each of the four cardinal directions, starting at the base of the focal tree. Within each transect we counted the number of cones depredated by crossbills, using cone counts from the base of the focal tree to its canopy edge to estimate seed predation at the tree level, and cone counts beyond to estimate seed predation at the patch level. The ground was covered mainly by forbs, ferns, and mosses, with usually low shrub cover (9% on average; Jaime-González et al. 2017), so cones on the ground were generally easily located. We also recorded the number of cones depredated by European red squirrels (*Sciurus vulgaris*). However, they were scarce (E.T. Mezquida, pers. obs.) and because their depredated cones so few we do not present these data.

We were unable to count the number of cones on trees to estimate cone production because trees were tall (mean maximum tree height = 29.1 m, for the 81 patches) and the forest relatively closed. Instead, we estimated cone production by counting the number of cones on the ground the following summer (mid to late July 2015) after most of the cones had shed their seeds and fallen to the ground (Gibb 1958, Summers and Proctor 2005). We used the same four transects for each tree and patch where we counted the number of depredated cones. We counted the number of fallen cones in the transects from the base of the tree to the

canopy edge to estimate cone production for the focal tree. To estimate cone production at the patch level, we counted the number of fallen cones in five 1-m² separated sections of the 25 m transect between the canopy edge and the end of the transect for a total of 20 m² for each patch. We counted only brown cones corresponding to the current cohort and ignored old dark grey cones from previous cohorts (Summers and Proctor 2005) and did not attempt to distinguish cones foraged on by crossbills because our goal here was to provide a measure of total cone production.

In addition, we collected 10 cones from under the canopy of the focal trees to characterize cone traits (e.g., Benkman and Mezquida 2015). The assumption that these fallen cones are representative of the cones available and used by crossbills from the same tree is supported by earlier studies on crossbills foraging on closed Scots pine cones (Summers and Proctor 1999, Summers et al. 2010). For each cone, we measured maximum cone length and width after cones were reclosed with moisture. Then cones were opened by drying them in a 65°C oven for two days. Last, we measured maximum thickness at the distal end of five scales and length of three scales in the middle part of the cone to the nearest 0.01 mm with digital calipers, and cone mass to the nearest 0.1 mg with a digital scale (Benkman et al. 2003). Cone measurements were averaged for each tree.

Characterization of forest structure

Forest structure variables (horizontal and vertical) at the patch level (25-m radius circular plots surrounding the focal tree) were derived from Light Detection and Ranging (LiDAR) data collected in a Piper PA31 Navajo aircraft provided by Blom Sistemas Geoespaciales, S.L.U in 2009. The LiDAR sensor used was a Leica ALS 60 with a pulse density between 4.7 and 7.3 pulses m². Flight speed and altitude were 85 m/s and 891 m, respectively. The processing of the raw data from the LiDAR point cloud was made using the software

FUSION (McGaughey and Carson 2003). Because the year of characterization of habitat use and estimation of seed predation by crossbills (2014) differed from the acquisition of LiDAR data (2009), trees and patches were chosen according to the information provided by forest managers, and ground-truthed in the field, to avoid areas where silvicultural activities had occurred between 2009 and 2014 (see Marino et al. [2018] for similar structural values in 30 plots scattered across the Valsaín forest from forest inventories conducted in 2010 and 2016).

Forest structure was characterized using 11 variables to describe four aspects of the forest structure at each patch: canopy cover, vertical structure plus its heterogeneity, and canopy height (see Table 1). Canopy cover was estimated from the percentage of first laser returns in the LiDAR point cloud at 5, 2 and 0.2 m, which is an indicator of canopy cover at each height. Canopy cover at 5 m indicates the cover of mature trees, whereas canopy cover at 2 m includes the cover of mature trees plus young trees (i.e., the regeneration layer). Canopy cover at 0.2 m includes trees plus shrub cover. Vertical structure was estimated for four forest layers: mature tree layer (>5 m), regeneration layer (2-5 m), shrub layer (0.2-2 m) and herbaceous layer (<0.2 m). The contribution of the four layers sums to 1. Thus, values close to one in the mature tree layer indicate dense tree crowns with limited presence of additional vertical structure at lower layers. On the other hand, values close to zero in the mature tree layer indicate open canopies with lower layers comprising most of the total vertical structure. We calculated the heterogeneity of canopy height for the mature tree layer (>5 m), for the mature plus regeneration layer (>2 m), and for the mature plus regeneration plus shrub layer (>0.2 m), as the standard deviation of height values for first returns up to 5, 2 and 0.2 m, respectively (Davies and Asner 2014). Finally, the maximum height of the vegetation was estimated.

Crossbill abundance and habitat use

In order to assess whether seed predation by crossbills indirectly reflects the abundance and overall habitat use by crossbills, we used data on a survey conducted in the same 81 patches (point counts) during the previous winter (late February to early March 2014); note that this represents a different cone crop year from when seed predation was measured. At each sampling point, we recorded the number of perched crossbills within a 75 m radius (grouped into three distance categories: 0-25, 25-50, 50-75 m) during a 5 min period within 3.5 h after dawn on days with no precipitation and no or low wind.

Statistical analyses

Variation in forest structure

The 11 forest structure variables derived from LiDAR were summarized using principal component analyses (PCA) from their respective correlation matrices. Varimax rotated components with eigenvalues >1 were retained in order to extract factors that represented major underlying gradients with ecological meaning.

Seed predation by crossbills at forest patches

We used the number of cones foraged on by crossbills at the patch scale as an estimation of seed predation. To assess whether seed predation by crossbills in forest patches was influenced by the structural characteristics of the forest patch, we used generalized linear models with a Poisson error structure. The principal components summarizing the 11 variables derived from LiDAR data were used as predictors in the model. Because the number of seeds depredated is usually linked to the number of seeds produced, we included the number of cones produced in each patch as a predictor (standardized to zero mean and unit variance) in the model so that we could determine the effect of forest structure while controlling for cone production. We checked for overdispersion in the model, and modelled

overdispersion as observation-level random effects (Harrison 2015). Tree number was included as a random effect in the generalized linear mixed model (i.e., a continuously varying value from 1 to 81 to increase the spread of the distribution; Harrison 2015).

Seed predation by crossbills at individual trees

We used the number of cones foraged on by crossbills at each tree as an estimation of seed predation at individual trees. To test whether seed predation by crossbills at individual Scots pines was determined by forest structure at the patch surrounding the tree, tree size, and cone structure, we used a generalized linear model with a Poisson error structure. Forest structure was included using the principal components extracted from the LiDAR-based variables (fPCs). Tree size was included in the model as DBH standardized to zero mean and unit variance. Cone structure was characterized using PCA based on the correlation matrix of the five cone traits, and the extracted principal components were used as predictors in the model (cPCs). The full model included the main effects and the interaction between cPCs. The number of cones produced by the tree (standardized to zero mean and unit variance) was also included in the model. We checked for overdispersion in the model and used generalized linear mixed models including the observation-level random effect, as explained above.

Crossbill abundance, forest structure, and seed predation

We used the number of crossbills recorded in point counts to estimate crossbill abundance at each patch after accounting for potential variation in detection probability. Thus, we fitted a hierarchical distance sampling model using the data for the three distance classes (Kéry and Royle 2016). We used a half-normal detection function, which was the function that best fitted the data, and used forest structure (fPCs) as covariates in the detection and abundance part of the model. Because crossbill abundance was estimated using wider forest patches, we

characterized forest structure at 75-m radius patches using the same 11 structural variables derived from LiDAR data, and summarized in principal components (fPCs) using PCA, as explained above. We used the `distsamp` function in the R package *unmarked* (Fiske and Chandler 2011) that fits a Poisson abundance model. We simplified models using the Akaike's Information Criterion (AIC) and checked for overdispersion in the model. Because the Poisson model showed overdispersion, we used the `gdistsamp` function in *unmarked* that allows the fitting of negative binomial abundance models. We used the best negative binomial abundance model to compute the best unbiased predictor of local abundance at the sample points (Kéry and Royle 2016).

To assess whether seed predation by crossbills at the patch and tree scale reflects the relative local abundance of crossbills, we used generalized linear mixed models with a Poisson error structure. Crossbill abundance at each patch (standardized to zero mean and unit variance) was the predictor variable in both models, the number of cones produced at the patch or tree scale (standardized to zero mean and unit variance) was included as predictor in the model for each scale, and the observation-level effect was included as a random factor to model overdispersion. We note that crossbill abundance was estimated during a different cone year than when seed predation was measured.

Models were fit using base packages in R 3.6.1 (R Core Development Team) and the *lme4* package (Bates et al. 2015). Variance inflation factor scores were <1.5 for all predictor variables included in the models. We used the *visreg* package (Breheny and Burchett 2017) to visualize regression models using partial residual plots.

Results

Seed predation by crossbills in relation to forest patch structure

The first three components from the principal component analysis using the 11 LiDAR-derived forest structure variables accounted for 91% of the variance (Table 1). The first component was positively associated with canopy cover at different heights (5, 2, and 0.2 m) and the relative contribution of the tree layer, and negatively correlated with the contribution of the herbaceous layer (Table 1). This component was interpreted as a gradient of forest openness, with closed canopies and a low herbaceous layer at one extreme and more open patches with better developed herbaceous layers at the other. The second component was positively associated with the heterogeneity of canopy height at the three levels and with maximum canopy height (Table 1). Thus, this component was interpreted as a gradient of increasing complexity in vertical structure. Finally, the third component was positively correlated with the contribution of the regeneration and shrub layers, and negatively correlated with the contribution of the tree layer (Table 1). This component was interpreted as a gradient of patches with increasing development of lower layers and less contribution of the tree layer.

Forest structure	fPC1	fPC2	fPC3
Canopy cover at 5 m	0.80	-0.04	-0.59
Canopy cover at 2 m	0.92	-0.02	-0.35
Canopy cover at 0.2 m	0.99	0.04	-0.10
Contribution of the tree layer	0.81	0.07	-0.57
Contribution of the regeneration layer	-0.10	0.10	0.90
Contribution of the shrub layer	-0.21	0.20	0.78

Contribution of the herbaceous layer	-0.92	-0.27	-0.19
Heterogeneity of the canopy height (>5 m)	0.06	0.92	0.15
Heterogeneity of the canopy height (>2 m)	0.02	0.92	0.27
Heterogeneity of the canopy height (>0.2 m)	-0.04	0.94	0.17
Maximum canopy height	0.28	0.86	-0.29
Explained variance (%)	37.30	31.40	22.44

Table 1. Principal component loadings from the 11 forest structure variables derived from LiDAR at 81 circular patches (25 m radius) in the Valsaín pine forest. Loadings after varimax rotation for the three extracted components (eigenvalue > 1) are shown.

Seed predation (number of cones foraged on) by crossbills was variable among forest patches (mean \pm SE: 28.1 ± 7.3 , $n = 81$ patches, range = 0-342). Mixed models indicated that seed predation decreased with canopy closure (fPC1) (Table 2; Fig. 1) and increased in regeneration patches (fPC3) (Table 2), implying crossbills preferentially foraged in more open forests and regeneration stands with scattered old trees remaining. Seed predation also increased as the number of cones produced in the patch increased (Table 2). Although cone production did not correlate with canopy closure ($r = 0.10$, $P = 0.39$), cone production relative to the amount of tree cover in the patch (i.e., divided by canopy cover at 5 m) decreased with canopy closure ($r = -0.28$, $P = 0.012$), indicating that more open patches produced more cones relative to the amount of pine canopy.

Variables	Estimate	SE	Z	P
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Intercept	1.680	0.190	8.9	<0.001
fPC1	-0.664	0.190	-3.5	<0.001
fPC2	0.228	0.182	1.3	0.209
fPC3	0.465	0.217	2.1	0.032
Number of cones	1.092	0.213	5.1	<0.001

Table 2. Estimates and SE from generalized linear mixed models for seed predation by crossbills in Scots pine patches in the Valsaín forest ($n = 81$) showing that seed predation decreased as the forest canopy became more closed (fPC1), increased in regeneration patches (fPC3), and increased with increasing cone abundance.

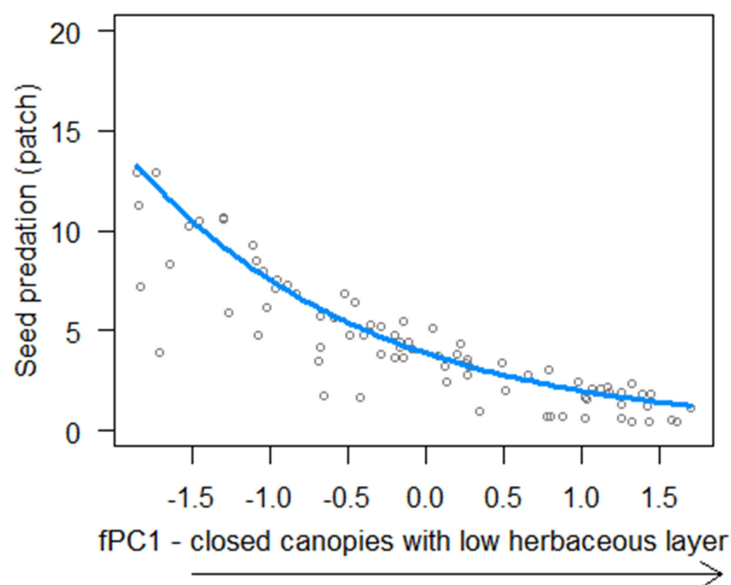


Figure 1. Seed predation by crossbills (number of cones foraged on) decreased with increasing canopy closure at the patch scale (fPC1), as estimated by a generalized linear mixed model. Trend line and partial residuals fitted to data from 81 Scots pine patches in the Valsaín forest.

Seed predation by crossbills in relation to cone traits, tree size, and patch structure

The five cone traits (Table A.1) were summarized in two principal components extracted from the PCA. The first principal component (cPC1) accounted for 62.3% of the variance in cone structure, and represented variation in cone size, with positive factor loadings for most characters (cone length = 0.89, cone width = 0.84, cone mass = 0.95, scale length = 0.84). The second principal component (cPC2) accounted for 21% of variation and represented variation in scale thickness (factor loading: 0.99).

Seed predation by crossbills at individual trees ranged from 0 to 171 cones (7.8 ± 2.8 , $n = 81$ trees). Mixed models indicated that cone traits rather than forest structure were the main predictors of seed predation at individual trees. Crossbills preferentially foraged on trees with more and smaller cones (Table 3), especially those with thin scales (Fig. 2; significant interaction between cone size [cPC1] and scale thickness [cPC2] in Table 3; Table A.1). Cone size was only weakly correlated with tree size (cPC1 and DBH: $r = -0.16$, $P = 0.15$; cone length and DBH: $r = -0.16$, $P = 0.19$) and canopy closure (cPC1 and fPC1: $r = 0.18$, $P = 0.11$; cone length and fPC1: $r = 0.20$, $P = 0.072$).

Variables	Estimate	SE	Z	P
Intercept	-0.601	0.353	-1.7	0.089
fPC1	0.024	0.311	0.1	0.938
fPC2	-0.231	0.286	-0.8	0.419
fPC3	0.167	0.285	0.6	0.559
DBH	0.281	0.342	0.8	0.411
Cone size (cPC1)	-1.388	0.363	-3.8	<0.001
Scale thickness (cPC2)	0.503	0.295	1.7	0.088
cPC1 \times cPC2	0.795	0.347	2.3	0.022

Number of cones	0.911	0.321	2.8	0.005
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Table 3. Estimates and SE from generalized linear mixed models for seed predation by crossbills on Scots pines in the Valsain forest ($n = 81$ trees) showing that seed predation increased as cone size decreased and as scale thickness decreased for the smallest cones (see Fig. 2), and as the number of cones produced by the tree increased.

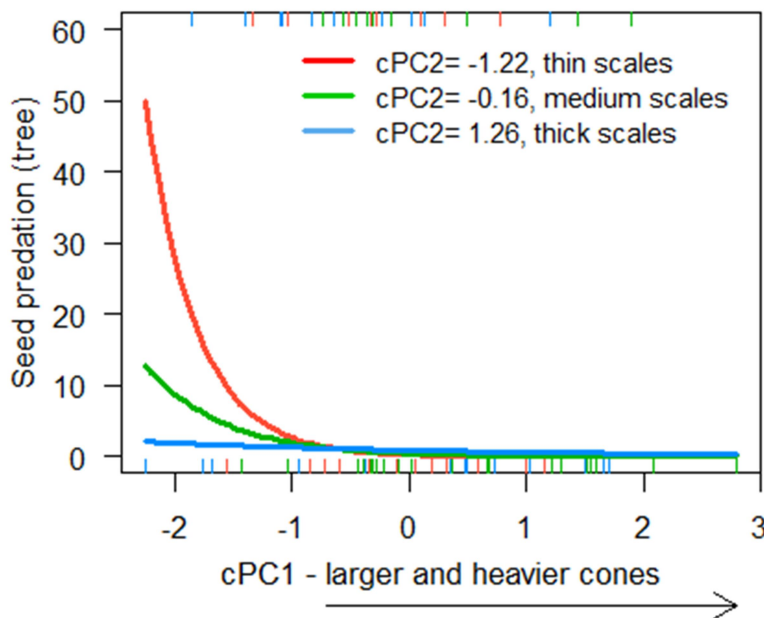


Figure 2. Cross-sectional plot depicts the interaction between Scots pine cone size (cPC1) and scale thickness (cPC2), and its effect on seed predation by crossbills (number of cones foraged on) showing that seed predation by crossbills was concentrated on trees having the smallest cones, and especially those with the thinnest scales. Trend lines based on generalized linear mixed models fitted to data from 81 Scots pine trees in the Valsain forest. Lines are cross-sections at the 10th (red line), 50th (green line) and 90th (blue line) percentiles of scales thickness (cPC2; positive values indicating thicker scales). Rugs represent observations with positive (top) or negative (bottom) residuals.

Crossbill abundance, forest structure, and seed predation

The three principal components extracted from the PCA of 11 structural variables derived from LiDAR data at wider patches (75-m radius) accounted for 93% of variance (Table A.2) and represent structural gradients similar to those summarized at 25-m radius patches (Table 1; correlations between factor loadings from the first, second, and third fPCs at both scales: $r = 0.81, 0.93, \text{ and } 0.87$, respectively; $P < 0.001$, in all cases).

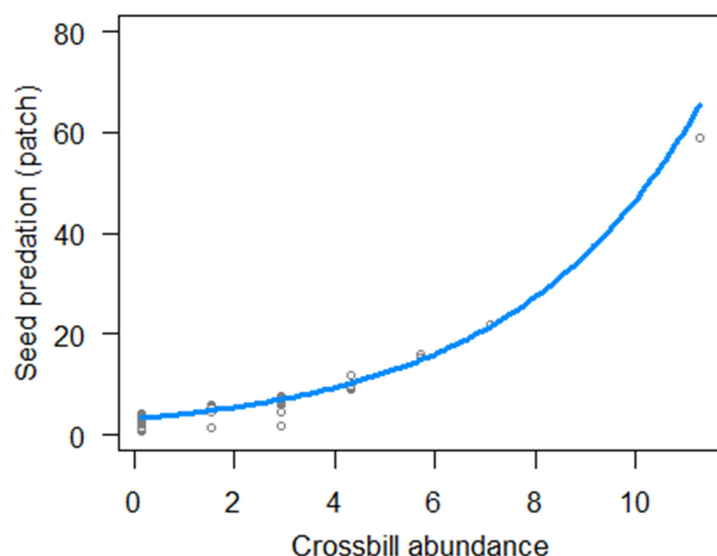
The best hierarchical distance model did not include forest structural variables (fPCs) in the abundance or detection part of the model. This model estimated a total of 105 crossbills on the total area sampled by the 81 point counts in late winter (range = 0.2-11.3 crossbills per point count), corresponding to an average density (\pm SE) of 78.1 ± 12.5 individuals km^{-2} .

Mixed models indicated that crossbill abundance was positively correlated with seed predation in forest patches (Fig. 3; estimate \pm SE: 0.531 ± 0.190 , $Z = 2.8$, $P = 0.005$), as well as with seed predation of individual trees within the patches (0.655 ± 0.261 , $Z = 2.5$, $P = 0.012$).

Discussion

Our interpretation of the results is that crossbills preferentially forage in pine stands that are more open and have more cones, and within these patches forage almost only on trees producing many small, thin-scaled cones. Preferences by crossbills for foraging in more open forests, more productive trees, and on small, thin-scaled cones have been found previously and repeatedly (Mezquida and Benkman 2014, Benkman and Mezquida 2015). Below we discuss our results in relation to previous work, address potential explanations for the nonlinear relationship between crossbill abundance and seed predation, and conclude by discussing implications of our results to forest management.

372



373

374 Figure 3. Relationship between crossbill abundance and seed predation (number of cones
 375 foraged on) by crossbills in Scots pine patches, as estimated by generalized linear mixed
 376 models. Trend line and partial residuals fitted to data from 81 patches in the Valsáin forest.

377

378 *Preference for more open forests*

379 A preference by crossbills for more open forests has been found previously (Summers and
 380 Proctor 1999, Summers et al. 2010, Mezquida and Benkman 2014). One explanation is that
 381 crossbills avoid closed forests because tree squirrels occur disproportionately in closed forests
 382 (Summers and Proctor 1999, Mezquida and Benkman 2014) and their harvesting of cones
 383 reduces the availability of cones to crossbills (exploitative competition). This is consistent
 384 with the negative effect of European red squirrels on the use of mountain pine (*P. uncinata*)
 385 cones by crossbills in the Pyrenees (Mezquida and Benkman 2014) and with the seemingly
 386 large competitive effect of American red squirrels (*Tamiasciurus hudsonicus*) on the
 387 abundance of common crossbills in forests of Rocky Mountain lodgepole pine (*P. contorta*
 388 *latifolia*) (Benkman 1999, Siepielski and Benkman 2005). Although cone depletion by tree

squirrels can have a negative effect on crossbills, the scarcity of European red squirrels in our study indicates that crossbills prefer to forage in more open forests regardless of the occurrence of tree squirrels.

A second explanation relates to crossbills preferentially foraging on trees with more cones (Holimon et al. 1998, Mezquida and Benkman 2014, Behl and Benkman 2018), and the preference for more open forests arises because more open-grown trees produce more cones than do trees in closed forests. Consistent with this explanation, we found that seed predation by crossbills increased with the number of cones produced at both the patch and tree levels. And although our data do not show directly that open-grown trees produced more cones, cone production and tree DBH were positively correlated ($r = 0.53$, $P < 0.001$) and the number of cones increased relative to the amount of pine canopy as canopy closure decreased, both of which indicate open-grown (and larger) trees produce more cones. Thus, our results are consistent with crossbills preferring to forage in open forests because of greater per tree cone production.

A third explanation is that cone size and structure vary with forest stand structure, and that crossbills forage more often in more open forests because of covarying cone traits. Such an explanation can account for the preferential use of open stands of Scots pine in the Scottish Highlands, where cone size decreased with increasing tree DBH and decreasing tree density (Summers and Proctor 1999). However, crossbills preferred open stands even after cones opened and crossbills shifted to preferring longer cones (Summers et al. 2010), implying a preference for open stands regardless of cone size. We detected only weak correlations between either DBH or canopy closure and cone size or length at individual trees within the patch. Thus, the strong increase in forest use as canopy closure decreased (Fig. 1) is unlikely to be related to the weak covariation in cone traits with canopy closure. However, cone size

and structure ultimately influenced which trees were foraged on within the patch (Table 3, Fig. 2).

A fourth explanation for preferential foraging in more open forests is related to crossbills experiencing a reduced risk of predation (Benkman 1987a, Summers and Proctor 1999, Mezquida and Benkman 2014). Key to evading predators is the distance at which a predator is detected, with potential prey less likely to be captured the farther away a predator is detected (Kenward 1978). More open forests should allow crossbills to detect an approaching predator from a greater distance. The sparrowhawk (*Accipiter nisus*), which can be an important predator on crossbills (Petty et al. 1995), uses cover to conceal its approach to ambush prey (Newton and Marquiss 1982). Open forests therefore might help crossbills evade attacks by ambush predators like sparrowhawks. Although we do not have measures of sparrowhawk abundance nor direct observations of attacks, this hypothesis for crossbills using more open forests cannot be excluded. Interestingly, crossbills in Scotland also preferred more open forests for nesting but in this case it was likely related to avoiding nest predators and in particular red squirrels (Summers et al. 2002; see also Summers et al. 2010). Notably, in a study of crossbills nesting in forests without tree squirrels, crossbills did not nest preferentially in more open forests (Latta et al. 2000).

Preference for small, thin-scaled cones

A review of eight studies on common crossbills foraging on the closed cones of five species of pine, including one study on Scots pine, found consistently strong preferences for smaller, thin-scaled cones above all other cone traits (Benkman and Mezquida 2015). Similarly, Summers and Proctor (1999) and Summers et al. (2010) found crossbills preferred to forage on shorter Scots pine cones, and presumably also cones with thinner scales as cone length and scale thickness were positively correlated. However, we detected a weaker correlation

between cone length and scale thickness ($r = 0.19$, $df = 79$, $P = 0.086$), and found that crossbills foraged almost exclusively on the subset of smaller cones with especially thin scales (Fig. 2).

A preference for shorter, thinner scaled cones is consistent with how crossbills extract seeds from closed cones. Once crossbills bite between the scales with their decurved and pointed mandibles, they abduct their lower mandible to the side spreading the scales apart to expose the seeds at the base of the scales (Newton 1972, Benkman 1987b). Because thicker scales require greater forces to spread them apart (Summers and Proctor 1999, assuming scale thickness increased with cone length; $r^2 = 0.80$ in their study), a preference for thin scales reduces the force, effort, and time required to expose seeds so that they can be lifted from between the scales with their tongue. Of particular note is the small subset of cones on which crossbills fed (Fig. 2). This is presumably related to the difficulty the relatively small-billed common crossbill has accessing seeds in closed Scots pine cones (Lack 1944, Marquiss and Rae 1994, Summers et al. 2010). Farther north in Europe, the parrot crossbill (*Leucophaea pytyopsittacus*) evolved massive bills that allow them access to seeds in Scots pine cones year round. However in Spain, there are several months of seed scarcity between when Scots pine has shed its seeds from one year's crop and the new crop of cones have developed sufficiently to support crossbills (see Alonso and Arizaga 2011) thereby preventing the occurrence of a Scots pine specialist like the parrot crossbill (Mezquida et al. 2018).

Seed predation by crossbills in relationship to crossbill abundance

An increase in the level of seed predation by crossbills was expected with increases in the estimated local abundance of crossbills (Fig. 3), but the disproportionately high levels of predation at the highest abundances of crossbills was not. We expected a linear relationship. One explanation for the nonlinear relationship (Fig. 3) is that the crossbills were surveyed in a different cone year than when measures of seed predation were estimated (the cone year after

the crossbill surveys), and that variation in cone production between years was inconsistent among trees or sites. However, this should cause a weaker but not necessarily a nonlinear relationship. A second explanation is related to making estimates of cone predation when cones were closed (late October and early November), while crossbill surveys were conducted after cones began opening (late February to early March). Putative crossbill defenses such as thick scales have their greatest impact on crossbill feeding performance when cones are closed (Benkman 1987b), strongly favoring selective foraging on small, thin-scaled cones. In contrast, differences in cone traits have less of an influence on feeding performance after the cones have begun opening. Consequently, crossbills would have been less restricted to trees with small, thin-scales when the crossbill surveys were conducted (Summers et al. 2010). The result would be an underestimation of crossbill abundance in the most intensively used sites in autumn when cone predation was estimated, such that sites with the highest levels of predation in Figure 3 would effectively move to the left making the line curve. A third alternative is that crossbills are less likely to be detected when foraging (for example, they are less vocal) than during other periods of activity resulting in crossbills being increasingly underestimated with increasing foraging activity. We suspect that the latter two explanations contributed to the nonlinearity of the relationship (Fig. 3). Finally, the predictive nature of crossbill abundance in one cone year of seed predation in the following cone year is consistent with crossbills preferring to forage where canopies are more open and forest structure influencing cone production that is consistent in its relative effects among years.

Implications for forest management and conservation

Although managing forests with regard to crossbill preferences for small, thin-scaled cones is of uncertain general value, managing to maintain a high proportion of mature and open forests that crossbills prefer benefits other bird species as well (Verschuyl et al. 2011). Currently, the

pine forest of Valsain is managed using a rotation period of 120 years, which is longer than in other managed Scots pine forests in the same mountains (e.g., 100 years in the Navafría pine forest; Barbeito et al. 2011). Following a group shelterwood system, regeneration stands are progressively harvested, although some seed trees are retained (10-25 trees ha⁻¹) in the final harvest. Crossbills forage in these progressively more open older stands and forage on cones on the old trees, so that the shelterwood system for natural regeneration coupled with long rotation intervals likely benefits crossbill populations (Benkman 1993a, Behl and Benkman 2018). In particular, longer rotation intervals (1) generate more open old-growth stands, which tend to produce large numbers of seeds, (2) increase the proportion of a tree's lifetime during which it produces seeds because Scots pine only begins to produce cones at 10 or more years of age and the number of cones produced increases thereafter as the tree grows, and (3) increases the likelihood of exceptional seed crops, which are also the most critical for natural regeneration (Smith and Balda 1979, Benkman 1993a).

In addition to increasing rotation age, another potential management action is to increase tree thinning of the more closed middle-aged stands that crossbills avoid. This would accelerate development of a structure similar to old-growth stands with larger trees and larger seed crops (Verkaik and Espelta 2006). Because timber production has declined in importance over the last decades in favor of other management goals such as biodiversity conservation, landscape preservation, and recreation, such a policy would seem more feasible. Moreover, thinning of dense forests reduces the occurrence and spread of high-intensity crown fires and thereby increases the likelihood that a forest stand survives a fire (especially low thinning; Agee and Skinner 2005), decreases drought stress and tree mortality (Navarro-Cerrillo et al. 2019), and generally provides a positive effect on bird communities (Verschuyl et al. 2011).

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Appendix A. Supplementary material

Table A.1. Mean (SE) and range values for tree DBH and cone traits of Scots pines sampled in the Valsaín forest ($n = 81$) and subsamples of trees in the lower ($n = 21$) and upper ($n = 20$) quartile of the distribution of scale thickness (cPC2).

Trait	All trees		Lower quartile		Upper quartile	
	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
DBH (m)	0.43 (0.02)	0.15-0.86	0.44 (0.04)	0.15-0.86	0.44 (0.03)	0.18-0.84
Cone length						
(mm)	40.80 (0.36)	34.26-47.67	40.06 (0.58)	35.40-44.73	41.15 (0.78)	36.26-47.67
Cone width (mm)	22.49 (0.16)	19.45-26.92	21.79 (0.22)	20.35-23.76	22.90 (0.41)	19.45-26.92
Cone mass (g)	4.83 (0.10)	3.14-7.60	4.50 (0.12)	3.54-5.67	4.98 (0.23)	3.14-6.76
Scale thickness						
(mm)	2.68 (0.03)	2.12-3.40	2.33 (0.03)	2.12-2.52	3.07 (0.03)	2.86-3.40
Scale length						
(mm)	16.76 (0.15)	12.99-20.52	16.55 (0.26)	14.17-18.61	16.33 (0.34)	12.99-19.18

699 Table A.2. Principal component loadings from the 11 forest structure variables derived from
700 LiDAR at 81 circular patches (75 m radius) in the Valsaín pine forest. Loadings after varimax
701 rotation for the three extracted components (eigenvalue > 1) are shown.

702

Forest structure	fPC1	fPC2	fPC3
Canopy cover at 5 m	0.84	0.04	-0.54
Canopy cover at 2 m	0.93	0.03	-0.32
Canopy cover at 0.2 m	0.98	0.10	-0.11
Contribution of the tree layer	0.82	0.16	-0.53
Contribution of the regeneration layer	-0.22	-0.02	0.88
Contribution of the shrub layer	-0.17	0.25	0.79
Contribution of the herbaceous layer	-0.93	-0.32	-0.11
Heterogeneity of the canopy height (>5 m)	0.11	0.95	0.11
Heterogeneity of the canopy height (>2 m)	0.07	0.95	0.20
Heterogeneity of the canopy height (>0.2 m)	0.06	0.97	0.10
Maximum canopy height	0.31	0.86	-0.30
Explained variance (%)	38.75	33.40	20.48

703

704