Irruptions of crossbills *Loxia* spp. in northern Europe – patterns and correlations with seed production by key and non-key conifers

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Irruptions by boreal seed-eating and frugivorous birds are assumed to be driven by the production of seeds and fruits, crops of which are highly variable between years. Using data from Sweden, we tested whether irruptions of Common Crossbills *Loxia curvirostra* were correlated with low Norway Spruce *Picea abies* seed production in the same year as the irruption and/or high seed production in the year prior to an irruption. Similar tests were made for Parrot Crossbill *Loxia pytyopsittacus* irruptions in relation to Scots Pine *Pinus sylvestris* seed production. In northern Europe, these conifers represent the key food species of the two crossbill species, respectively. Despite differing times that seeds take to mature and asynchronous seed production between the two conifer species, including a 3-year cycle for Norway Spruce, the two crossbill species often irrupted in the same year as one another. Analyses showed that irruptions into Britain and other parts of western Europe by both crossbill species were correlated with low seed production by Norway Spruce in Sweden. Low seed production by Scots Pine had a marginally non-significant additive effect on both crossbill species. In a second set of analyses, the best-fitting model was one in which low seed production by both conifers in a given year and high seed production in the previous year were each correlated with large numbers of irrupting Common and Parrot Crossbills. The models indicate that the incidental co-occurrence of low seed production of Norway Spruce and Scots Pine in a given year, after a year of high seed production, may result in an irruption. The seed production of Norway Spruce and Scots Pine in Sweden was correlated with production by the same species in Finland, indicating widespread synchrony of cropping across northern Europe.

Keywords: cone-crops, Falsterbo, Finland, seed production, Sweden.

Irruptions of boreal, frugivorous and seed-eating birds have fascinated ornithologists for decades (Lack 1954, Svärdson 1957, Newton 1972, 2010, 2023, Alerstam 1990). It is generally assumed that these movements are related to the reliance that each bird species has on a particular food, the availability of which varies synchronously over a wide area. One hypothesis for synchrony in fruiting is that peaks in production swamp the ability of frugivorous and seed-eating birds to exploit the bonanza fully, thereby allowing some seeds a chance to germinate (Kelly 1994). Years of good

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crops are then usually followed by one or more years with poor crops, a situation that is likely to cause irruptions.

In northern Europe, Redpolls *Acanthis flammea* rely on birch *Betula* spp. seeds, Thick-billed Nutcrackers *Nucifraga caryocatactes* on Hazel *Corylus avellana* nuts, Bullfinches *Pyrrhula pyrrhula* and Waxwings *Bombycilla garrulus* on Rowan *Sorbus aucuparia* fruits, and crossbills *Loxia* spp. on conifer seeds (Lack 1954, Newton 1972, 2010, 2023, Alerstam 1990, Fox *et al.* 2009). Different bird species may irrupt together because of synchronous seeding by different food plants (Bock & Lepthien 1976, Koenig 2001), but others show no synchrony (Lack 1954).

The hypothesis for the cause of irruptions revolves around the relationship of the food supply relative to bird density (Lack 1954, Newton 1970, 2023, Bock & Lepthien 1976, Widrlechner & Dragula 1984). Birds are assumed to irrupt when food supply is low relative to bird density and this could be driven by either high bird productivity or low food supply, or the two could become entrained if years of low seed/fruit production tend to follow years of high seed/fruit production.

The species of crossbill in the boreal forests of continental northern Europe are the Common Crossbill *Loxia curvirostra*, Parrot Crossbill *Loxia pytyopsittacus* and Two-barred Crossbill *Loxia leucoptera* (Cramp & Perrins 1994). In our study, the Two-barred Crossbill is not considered because it is rare in Fennoscandia, as its main breeding range lies further east. Of the two species considered, the larger-billed Parrot Crossbill feeds mainly on seeds of Scots Pine *Pinus sylvestris* cones, whereas the smaller-billed Common Crossbill extracts seeds from the cones of Norway Spruce *Picea abies* in northern Europe, though large-billed subspecies of Common Crossbill that reside in the Mediterranean region forage on Aleppo Pine *Pinus halepensis*, Mountain Pine *Pinus uncinata*, Black Pine *Pinus nigra* and sometimes Scots Pine (Lack 1944, Newton 1972, 2023, Senar *et al.* 1993, Cramp & Perrins 1994, Summers & Kalejta-Summers 2003). These differences in diet are consistent with the idea that different crossbill taxa are adapted to 'key' conifer species, although they may also take seeds from other conifers, including non-native species (Benkman 1993, Marquiss & Rae 2002, Summers 2018).

Given the strong associations that Common and Parrot Crossbills have with Norway Spruce and Scots Pine, respectively, the irruptions of each crossbill species are believed to be related to seed production by the associated conifer species (Lack 1954, Cramp & Perrins 1994). Features of the life cycle of the two conifers play an important role in our understanding of irruptions of the two crossbill species. The production of Norway Spruce seed is highly variable, leading to years with seed abundance (mast years) and other years with little or no seed production (Hagner 1965, Broome *et al.* 2007). The spatial synchrony in seeding by Norway Spruce can be countrywide (> 600 km) in Britain, where the species has been introduced as a commercial crop (Broome *et al.* 2007), and across 1000 km in Finland (Zamorano *et al.* 2018). Large variability in seeding by Norway Spruce is consistent with the larger number of Common Crossbill irruptions than Parrot Crossbill irruptions (see below) (Newton 1972). Ringing recoveries and a study of stable isotopes indicate that irruptions of Common Crossbills into western Europe originate from different locations across Europe and western Asia in different years (Newton 2006, Marquiss *et al.* 2008).

By contrast, seed production by Scots Pine is less variable than that of Norway Spruce and some cones are produced every year (Hagner 1965, Summers & Proctor 2005, Broome *et al.* 2007). Spatial synchrony can be as large as that of Norway Spruce, varying from 200 km within Britain (Broome *et al.* 2007) to 2500 km within boreal forests (Koenig & Knops 1998). With a less variable food supply, the Parrot Crossbill is less prone to irruptions (Newton 1972, Cramp & Perrins 1994). Moreover, with a smaller breeding range than that of Common Crossbills, the origin of their irruptions is restricted to Fennoscandia and western Russia (Cramp & Perrins 1994).

The time taken to form seeds is a further difference between Norway Spruce and Scots Pine. It takes 1 year, spread across two calendar years, for Norway Spruce cones to develop and shed seed (in spring of the second calendar year), but 2 years across three calendar years for Scots Pine cones to do the same (Fletcher 1992). Therefore, the two conifers are usually out of phase in their seed production (Svärdson 1957, Hagner 1965, Broome *et al.* 2007), even though cone bud initiation may be triggered by the same environmental cue, such as sunlight or warmth (Kosiński & Giertych 1982, Kelly & Sork 2002). On this basis, one would not

expect irruptions of Common Crossbills and Parrot Crossbills to coincide.

Given the hypothesis that Common Crossbill irruptions are related to Norway Spruce cropping and Parrot Crossbill irruptions to Scots Pine cropping (Lack 1954, Cramp & Perrins 1994), our study examined time-series data on seed production and crossbill irruptions in northern Europe. Specifically, we tested the hypothesis that irruptions of Common and Parrot Crossbills are correlated with years of low seed production by Norway Spruce and Scots Pine, respectively, or/ and with years with large seed production by Norway Spruce and Scots Pine in the year prior to an irruption, respectively. We also re-examined the observation that the Common and Parrot Crossbills often irrupt in the same years as one another by extending the period of data to over two centuries (Newton 1972, 2006).

METHODS

Sources of data

Years of crossbill irruptions into regions south of the boreal zone – into Britain and other parts of western Europe – were taken from Newton (1972) for the period 1800–1965, and updated for 1966–2008. These data were acquired from searches through ornithological journals and, in Britain, from county avifaunas, county bird reports and bird observatory reports. All the irruptions recorded in Britain from the early 20th century were subsequently also recorded in other western European countries south of the boreal zone, and the same is likely to have held for earlier ones. In the account below, the irruptions are recorded as occurring in Britain, even though (at least from the early 20th century) they also extended to other west European countries.

Annual counts of crossbills were also obtained from the official migration counts at Falsterbo Bird Observatory (55.4°N, 12.8°E), at the southern tip of Sweden, from 1973 to 2018 (Fig. S1). There are no large conifer forests nearby, indicating that these birds were on passage. The two species were distinguished from their flight-calls, and on bill and head size when birds were close (N. Kjellén pers. comm.). The counts were made from the same point between 1 August and 20 November each year by one to two observers operating from dawn until 14:00 h local time. The starting date of

1 August can miss much of the season for Common Crossbill movements, which can begin as early as late June, and are well underway through July (Newton 1972).

Indices of seed production (cone counts) for Norway Spruce and Scots Pine were obtained in five regions aligned north to south in Sweden during 1910–1953 from Hagner (1965). These referred to summer counts of second-summer cones of Scots Pines and first-summer cones of Norway Spruce, thereby representing the food supply for crossbills for the autumn and early winter of the current calendar year through to the late winter and spring of the following calendar year, when the seeds are shed. Thus, 'seed production' in this paper refers to the seeds available to crossbills in the calendar year before the seeds are shed from cones. Mean values of crop sizes from five regions were taken as a countrywide Swedish index. Extending this run of data, additional annual national data from 1954 to 2020 for the estimated number of Norway Spruce and Scots Pine cones were obtained from cone-counting by the Swedish National Forest Inventory (Fridman *et al.* 2014) (Fig. S2).

Data on seed production (seeds per m^2) in Finland were obtained from 1960 to 2000 for Norway Spruces at Heinola (67.8°N, 34.5°E), Kittilä (75.5°N, 33.8°E), Kuorevesi (68.8°N, 33.9°E), Rovaniemi (73.6°N, 34.9°E) and Siilinjärvi (69.9°N, 35.4°E). Similar data were obtained from 1960 to 2004 for Scots Pines at Eckerö (67.0°N, 30.9°E), Kittilä, Kuorevesi, Rovaniemi, Punkaharju (68.6°N, 36.2°E) and Vippula (68.9°N, 33.7°E). Means were taken of all sites for each year for both conifer species. The data on seed production refer to the calendar year after the year that cone counts were made in Sweden. To match the Finnish data with the Swedish data and the year in which crossbills irrupt, the Finnish seed data were aligned to the previous calendar year (Fig. S3).

Analyses

Comparisons between datasets were limited to those years with matching data. Indices of seed production (cone counts) in Sweden were standardized (setting the mean to 1 and dividing by the standard deviation). This allowed the two datasets (1910–1953 and 1954–2020) to be combined. For the 1910–1953 data, synchrony in seeding between the five regions of Sweden was

examined using Spearman rank correlations. In addition, synchrony between the conifers among regions was examined. Pearson correlation analyses were used to test for relationships between seed production of Norway Spruce and Scots Pine within and between Sweden and Finland. Autocorrelations tested for regular periodicity in seeding.

Years of crossbill irruptions (Newton 1972 and updated) were tested against the national seed production in Sweden using logistic analyses for 1911–2008. Within binomial models (R Core Team 2019), years with irruptions were set at 1 and those without were set at 0, and a logit link function was applied. We tested whether the probability of an irruption was associated with indices of seed production by Norway Spruce and Scots Pine in the current year and the year prior to an irruption. Interactions were also tested.

Counts of Common and Parrot Crossbills at Falsterbo were each compared with seed production of Norway Spruce and Scots Pine in Sweden from 1973 to 2018. Hierarchical generalized additive models (HGAMs) (Pedersen et al. 2019) were applied, with a crossbill count as the response variable, and the corresponding crossbill species, cone indices of each of the conifer species and year as potential explanatory variables. Poisson, Quasi Poisson and negative binomial were tested as possible response distributions. Model selection was based on the lowest Akaike Information Criterion (AIC) value and/or on explanatory power. These regression models allowed for both linear and smooth functions (based on splines) of the covariates to explain variation in crossbill numbers, including two- and three-way interactions between conifer species, crossbill species and years. Interaction terms between lagged conifer indices in the current and previous year were also tested to check for an association between crossbill count and the product of the two covariates; for example, the product of Norway Spruce in the current year and Scots Pine in the previous year, testing for the effect of combined failures of the two crops or a situation where large crops lead to a high density of crossbills followed by a shortfall of food in the following year. The best combination of interaction terms was chosen to optimize model fit. The smooth terms were modelled using thin-plate spline basis functions, except for crossbill species, for which a random effect was used. Terms not deemed to be significant were progressively removed from models and AIC was recalculated to ensure that both parsimony and predictive fit were maintained.

The hierarchical structures of the models allow for varying levels of smoothness to be fitted to each crossbill species and attributed to covariate(s), with each smooth term having potentially different levels of smoothness, depending on the data. Whether they were linear slopes or smooth effects, (approximate) significance and hypothesis tests of zero vs. non-zero were calculated in mgcv (mixed GAM computational vehicle) using methods described in Marra and Wood (2012) and Wood (2013a, 2013b). After applying a range of HGAMs to the data in which the numbers of both crossbill species at Falsterbo were compared with the Swedish seed production of both conifers in a given year and/or the previous year, the best-fitting model was used for inference.

RESULTS

Crossbill irruptions

From 1800 to 2008 (209 years), 81 Common Crossbill irruptions and 36 Parrot Crossbill irruptions were documented for Britain and other parts of western Europe. Although there were fewer Parrot Crossbill irruptions, many occurred in the same years as Common Crossbill irruptions, showing a significant positive association (Table 1).

There was also a significant correlation between the number of Common Crossbills and Parrot

Table 1. The association between irruption years by Common and Parrot Crossbills from 1800 to 2008. Numbers in parentheses are the expected number of years for each irruption type. Yates' corrected $\chi^2 = 29.9$, $P < 0.001$.

	Number of years with a Common Crossbill irruption	Number of years without a Common Crossbill irruption	Total
Number of years with a Parrot Crossbill irruption	29 (14)	7 (22)	36
Number of years without a Parrot Crossbill irruption	52 (67)	121 (106)	173
Total	81	128	209

Crossbills counted each year at Falsterbo (Fig. 1; Fig. S1). The median number of Common Crossbills, 508 (range 0–31 626), was similar to that for Parrot Crossbills, 439 (range 0–4490) (Mann–Whitney $U = 1150.5$, $P = 0.47$).

To check whether both datasets on crossbills (from Britain and Falsterbo) were describing the same pattern of irruptions, the 36 years (1973–2008) that provided data for both locations were compared. For Common Crossbills, which had 10 irruptions in this period, the mean counts of crossbills at Falsterbo in years classified as irruption and non-irruption years in Britain were 5017 and 846, respectively, a difference that is statistically significant (Mann–Whitney $U = 60$, $P = 0.013$). For Parrot Crossbills, which had six irruptions, the mean counts were 1023 and 611, respectively, a difference that was not statistically significant (Mann–Whitney $U = 51$, $P = 0.098$) but followed the same pattern as the Common Crossbills.

Seed (cone) production in Sweden

For 1909–1953, there was significant synchrony between neighbouring regions for the indices of seed production for each of the conifers, and particularly for Norway Spruce (Table 2). The degree of synchrony between regions declined with increasing distance between pairs of regions, though all coefficients were positive.
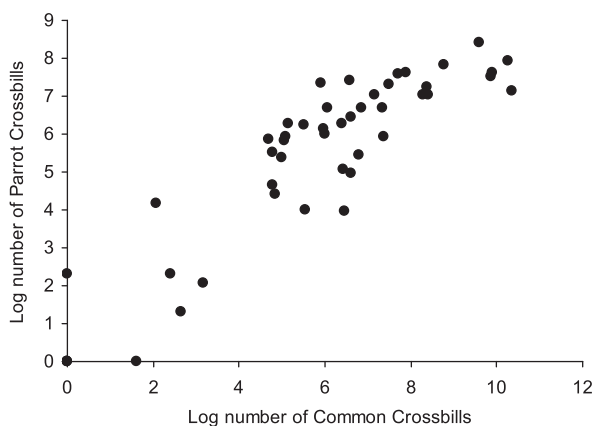

Figure 1. The relationship between the log number (+1) of Parrot Crossbills against log number (+1) of Common Crossbills at Falsterbo, southern Sweden, from 1973 to 2018 ($r = 0.898$, $n = 46$, $P < 0.001$).

There were no significant correlations between Norway Spruce and Scots Pine indices of seed production either nationally ($r = -0.044$, $n = 109$, n.s.) or for any of the five regions (Table 2, Fig. S2).

Auto-correlations for Norway Spruce seed production revealed a significant negative lag at year 1 for three regions (regions 2, 3 and 5) and for the national indices (Fig. 2), showing that years of low seed production tended to follow years of high production. There was also a positive correlation at year 3 in regions 4 and 5, and nationally (Fig. 2), indicating a 3-year cycle in seed production. For Scots Pine, no significant auto-correlations were detected (Fig. 2).

Seed production in Finland

There was no significant correlation between Norway Spruce and Scots Pine in seed production ($r = 0.026$, $n = 41$, n.s.) (Fig. S3). There was a significant increase over time in seed production of Norway Spruce ($r_s = 0.467$, $n = 41$, $P < 0.005$) but no trend for Scots Pine ($r_s = 0.219$, $n = 45$, ns).

Auto-correlation analyses showed a weak effect for a 3-year cycle in Norway Spruce seed production, but there was no evidence for regular cycling in Scots Pine seed production (Fig. 2).

For each of the conifer species, seed production in Finland and Sweden were significantly correlated (Fig. 3).

The relationship between crossbill irruptions and seed production

Years of Common and Parrot Crossbill irruptions were correlated with low seed production of Norway Spruce in Sweden. There were additional marginally non-significant indications that irruptions could be related to low seed production by Scots Pine, but there were no significant non-linear interactions between the two conifers (Table 3), nor were there significant associations with the Norway Spruce and Scots Pine seed crops in the year prior to irruptions, either in association with the current year's seed production or independently.

The final GAM resulted in the predicted crossbill count as below, following backwards elimination of non-significant covariates:

E (crossbill count) = exp (slope (Norway Spruce) + slope (Scots Pine lagged) + slope

Table 2. Spearman correlation coefficients for cone indices comparing different conifers and pairs of five regions of Sweden.

	SP1	SP2	SP3	SP4	SP5	NS1	NS2	NS3	NS4
SP2	**0.79**								
SP3	0.63	**0.73**							
SP4	0.17	0.17	0.29						
SP5	0.14	0.27	0.28	0.51					
NS1	−0.03	0.01	−0.07	−0.06	−0.14				
NS2	0.02	0.09	0.10	0.24	0.08	**0.77**			
NS3	−0.12	−0.10	0.00	0.21	−0.05	0.62	**0.80**		
NS4	−0.07	−0.19	−0.17	0.30	0.02	0.32	0.49	**0.78**	
NS5	−0.30	−0.29	−0.25	0.24	0.01	0.33	0.45	0.70	**0.91**

NS, Norway Spruce; SP, Scots Pine. 1 is the most northerly region and 5 the most southerly. $n = 45$. Those coefficients which indicate strong correlations (above 0.7) are in bold.

(Norway Spruce:Scots Pine lagged) + smooth (Scots Pine) + smooth (Norway Spruce) + smooth (Scots Pine lagged) + smooth (Norway Spruce lagged) + smooth (year) + smooth (crossbill species)), where the crossbill count followed a negative binomial distribution. Slope refers to a linear trend, consisting of a constant multiplicative rate of change, whereas a smooth term is made up of a spline basis function. Models are fitted using the *gam* function in the R package *mgcv*.

In this model, large numbers of crossbills were related to low seed production of both conifers in a given year, plus combined high seed production of both conifers in the previous year (Table 4). Figure 4 shows the relationship between numbers of both species of crossbill passing through Falsterbo and the corresponding seed indices of the given year and previous year. The smooth relationship with the current year suggests that both crossbill species are likely to irrupt at combined lower levels of seed production. The estimate of the negative binomial variance scale parameter θ was 0.59, suggesting greater variance relative to the equivalent Poisson distribution. For the negative binomial, the variance is $\text{Var}(y) = \mu + \frac{\mu^2}{\theta}$, whereas for a Poisson model it is $\text{Var}(y) = \mu$.

DISCUSSION

The positive correlation between the irruptions of Common and Parrot Crossbills, as observed by Newton (1972), is supported statistically. In addition, counts at Falsterbo confirmed that numbers of both species can fluctuate together, despite being associated with different key conifers that have different life cycles and show no general synchrony in their seed production, either in Sweden or Finland. For the years in which we had data on irruptions in Britain and counts in Falsterbo, a significant positive correlation emerged for the Common Crossbill. For Parrot Crossbills, which had fewer irruptions, there was no significant correlation but a similar pattern. Numbers of the two crossbill species counted at Falsterbo were similar to one another, although this could be an artefact of the start date of counting, which will have missed the early part of Common Crossbill irruptions (Newton 1972). The reason why the two crossbills irrupt at different dates within a year is unclear.

The variation in seeding followed patterns that have been described previously: greater year-to-year variation in the seeding of Norway Spruce than of Scots Pine, with peaks in cone production every few years (Hagner 1965, Broome *et al.* 2007). Reinikainen (1937) noted that Norway Spruce has peaks in seeding every 3–5 years in Finland, while Newton (1972) listed 2-year seeding for the Alps, 3–4 years in the southern boreal region and 5 years in the north. Broome *et al.* (2007) recorded a 4-year pattern in the UK. Our study noted that for the Norway Spruce, seed production followed a 3-year cycle, suggesting some intrinsic governing factor, rather than an extrinsic factor such as the weather (Zamorano *et al.* 2018). Although there was no evidence of cycling by Scots Pines in this study, there is some evidence for a 3-year cycle in Scotland (Summers 2011). However, there was no indication of regular cycling in the irruptions of crossbills.

The tendency for Norway Spruce to have a poor seed (cone) crop following a large crop has
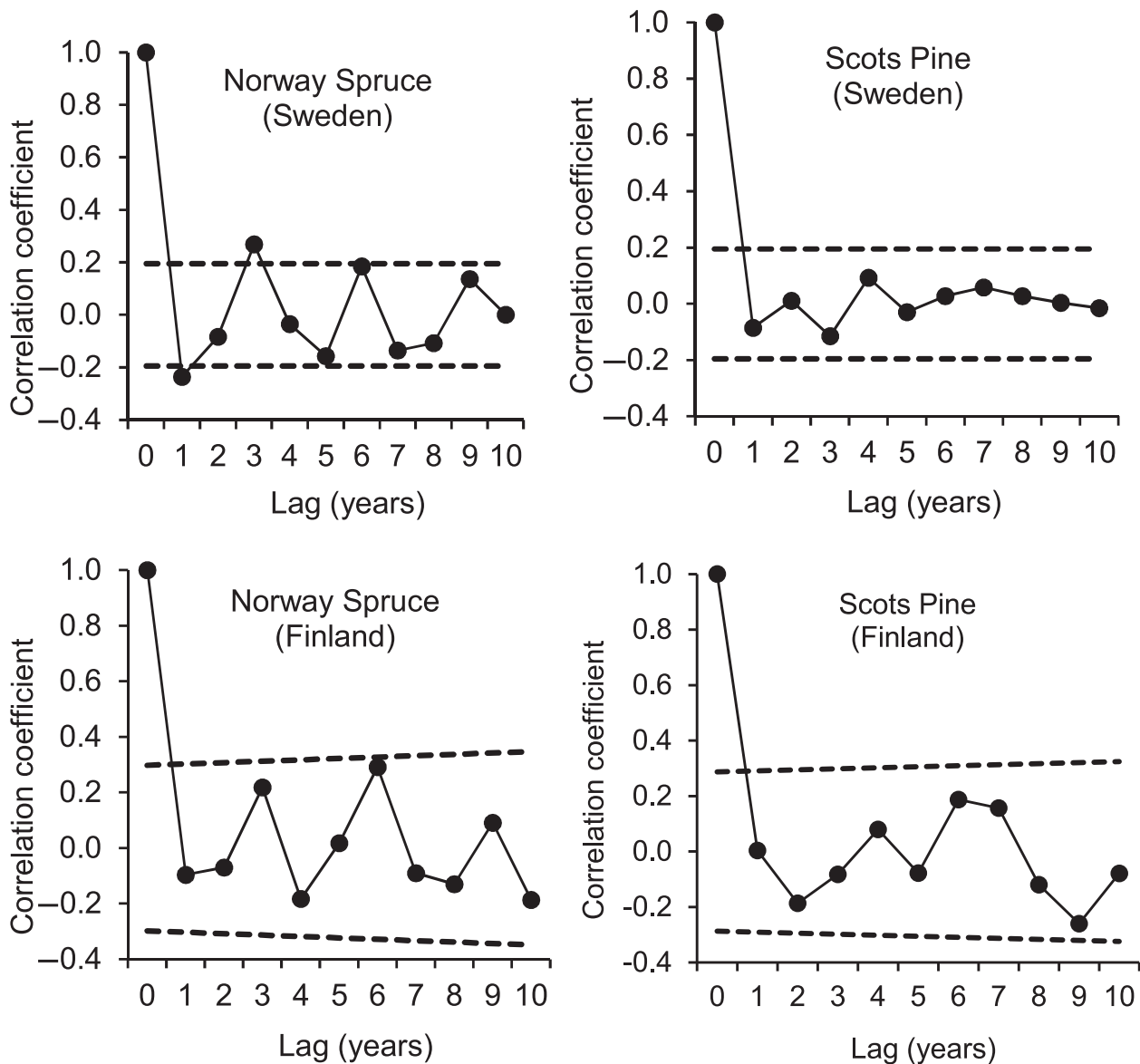
Figure 2. Auto-correlation coefficients at different time lags for national indices for Norway Spruce and Scots Pine cone (seed) production in Sweden from 1910 to 2020, and seed indices for Finland from 1960 to 2000 for Norway Spruce and 1960 to 2004 for Scots Pine. The dashed lines show the critical values where $P = 0.05$.

previously been noted by Tiren ([1935](#)) and for Scots Pine by Watson *et al.* ([2009](#)). For Norway Spruce, poor cropping may be influenced not only by the low nutrient stores in the trees, but also by insect and rust fungus species that can damage a large part of a seed crop, especially after years with high cone production (Annila [1981](#), Kaitera [2013](#)).

The positive correlation in Sweden and between Sweden and Finland in seeding by Norway

Spruces, and the same pattern occurring separately for Scots Pines, showed that synchrony in seeding within each conifer species was widespread. We obtained no data from Russia to test for correlations with conifers further east, but by predicting cone crops from tree ring data, Koenig and Knops ([1998](#)) suggested that seed crops can be synchronized across 500 km for Norway Spruce and 2500 km for Scots Pines. According to Zamorano *et al.* ([2018](#)), Norway Spruce showed spatial
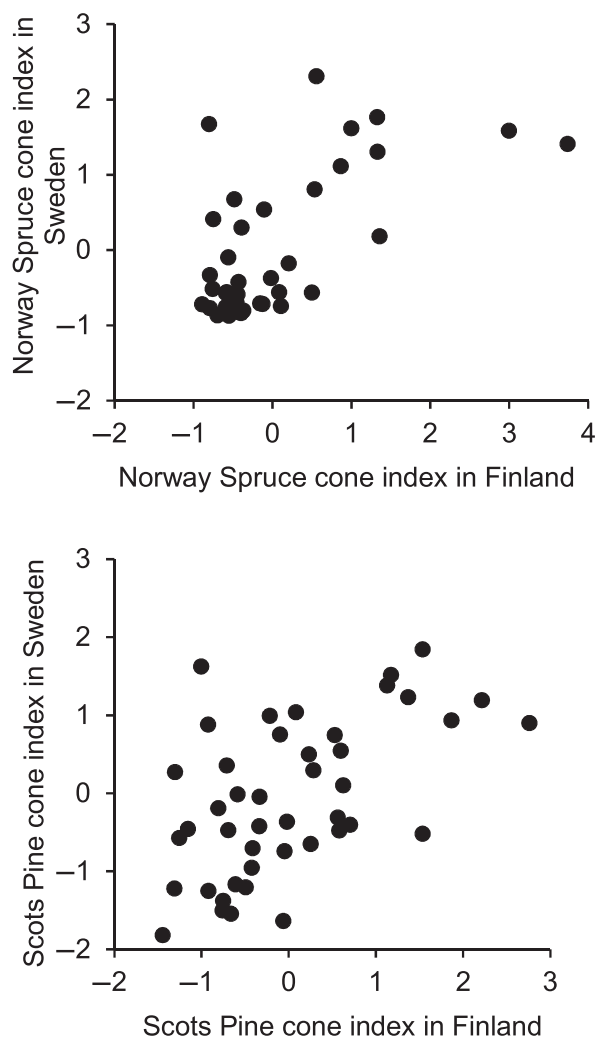
Figure 3. Relationships between standardized indices of seed (cone) production for Norway Spruce (1961–1999) and Scots Pine (1960–2003) in Sweden and Finland in matching years. $r = 0.63$, $n = 39$, $P < 0.001$ for Norway Spruce and $r = 0.51$, $n = 44$, $P < 0.001$ for Scots Pine.

Table 3. Results of logistic regression analyses of crossbill irruptions in relation to standardized cone (seed) indices of abundance in the current year in Sweden from 1911 to 2008.

	df	Estimate (se)	Z (P)
Common Crossbill irruptions			
Intercept	1	−0.962 (0.260)	−3.70 (< 0.0001)
Norway Spruce index	1	−0.813 (0.305)	−2.67 (0.0077)
Scots Pine index	1	−0.450 (0.246)	−1.83 (0.067)
Dispersion parameter* = 1.17			
Parrot Crossbill irruptions			
Intercept	1	−2.142 (0.484)	−4.42 (< 0.0001)
Norway Spruce cone index	1	−1.706 (0.598)	−2.85 (0.0044)
Scots Pine cone index	1	−0.583 (0.305)	−1.91 (0.056)
Dispersion parameter* = 0.86			

*The dispersion parameter would be 1 if there was no under- or overdispersion.

Table 4. Summary statistics of a negative binomial HGAM fitted to Falsterbo crossbill counts (1973–2018) in relation to seed production of Scots Pine and Norway Spruce in the current year and with lags.

Parameter	Estimate (se)	Z/χ^2	P
Model (crossbill[t] = Norway Spruce[t] × Scots Pine[t]) + (spruce [t−1] × Scots Pine[t−1])			
Scots Pine	0.27 (0.020)	−4.574	<0.0001
Norway Spruce	0.35 (0.044)	8.324	<0.0001
Pine × spruce	0.004 (0.001)	3.095	0.002
Smooth (year)	–	15.351	0.001
Smooth (Scots Pine)	–	30.206	<0.0001
Smooth (Norway Spruce)	–	36.572	<0.0001
Smooth (Scots Pine lag)	–	79.470	<0.0001
Smooth (Norway Spruce lag)	–	12.778	0.003
Smooth (crossbill species)	–	4.556	0.017

Significant fixed and smooth effects are shown. Z-scores are for the fixed effects and chi-square values are for the smooth effects.

synchrony in seed production at scales up to 1000 km. Thus, the correlation in seed production within species, as seen between Sweden and Finland, may extend well into Russia.

Joint irruptions by Common and Parrot Crossbills indicated that they are not independently governed by the seed production of their key conifer (Fig. 4). Both sets of analyses showed an interplay between both crossbill species and both conifer species. Low seed production, especially for Norway Spruce, had an apparent influence on the irruptions of both crossbills (first analysis, Table 3), and the second analysis revealed that counts of

both crossbill species were related to seed production by both conifers in the year of an irruption and the year prior to an irruption. The initial positive correlation between crossbill counts and cone crop size (Fig. 4) may suggest that irruptions are
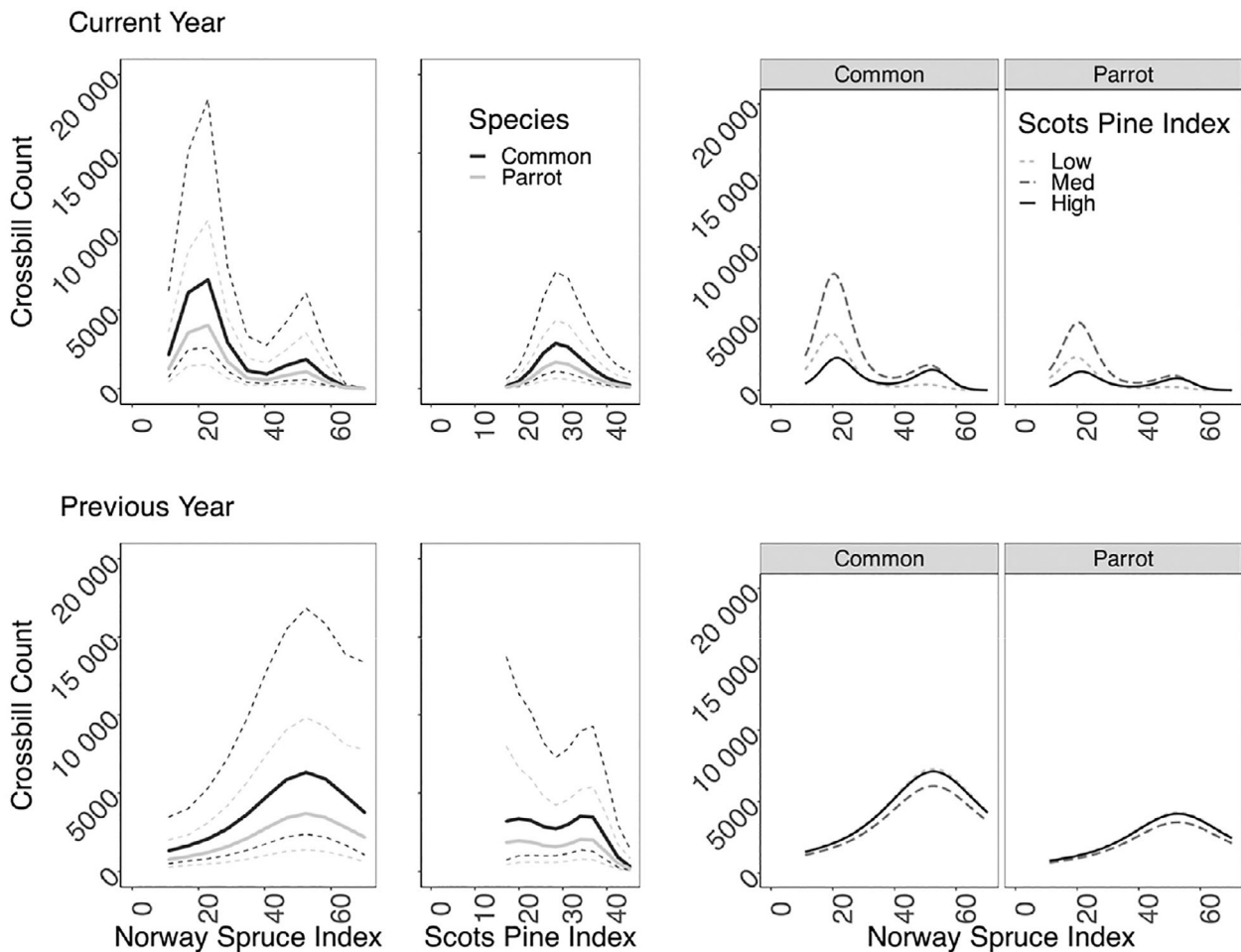
Figure 4. Fitted smooth relationships between crossbill numbers at Falsterbo and Norway Spruce and Scots Pine seed indices in the current (top) and previous (bottom) year, as estimated from the HGAM (Table 4). In each subfigure, the two left-hand plots show the fitted smooth relationships between Common (dark lines) and Parrot Crossbills (light lines) and Norway Spruce and Scots Pine indices, with 95% confidence regions in the corresponding dashed lines. The right-hand two interaction plots show the estimated marginal relationships between crossbill numbers and the Norway Spruce seed index, for the cases where the corresponding Scots Pine seed index was low, medium or high.

likely to occur prior to the complete failure of a crop. This is supported by the interaction plots that show that the largest irruptions tend to occur when low (but not complete failure of) Norway Spruce seed availability is combined with reasonably low (middle tercile) Scots Pine seed availability. In other words, it is the lack of an alternative seed crop when the seed crop of the key conifer is low that drives irruptions. The second peak in the interaction plots corresponds to very high seed indices of both Norway Spruce and Scots Pine and may suggest that years with very high seed crops attract crossbills to feed on the available crop and to breed successfully.

The fact that irruptions by both crossbill species showed relationships with seed indices in Sweden may seem surprising because irrupting crossbills do not come from just Fennoscandia. There have been ringing recoveries of Common Crossbills from as far as central Russia (Newton 2006), and isotope data from feathers of irruptive birds imply that some irruptions begin even further east (Marquiss *et al.* 2008, 2012). However, if those birds irrupting from regions east of Sweden move west through the boreal forest, they are likely to arrive in Sweden. This is the last country with a substantial amount of conifer forest, so any onward movement into regions further south could be

influenced by the seed crop in Sweden. It is less surprising that Parrot Crossbill irruptions are influenced by the seed crop in Sweden because their breeding range is restricted to Fennoscandia and western Russia (Cramp & Perrins 1994).

Although the two crossbill species are associated with different key conifers as food sources, two factors may account for the correlations we found. First, seed crops for a given conifer fluctuate in synchrony over wide areas, exemplified by the correlation in seeding between Sweden and Finland, and tree ring data (a surrogate for seeding) indicate synchrony over 2500 km for Scots Pine (Koenig & Knops 1998). Secondly, although Parrot Crossbills forage largely on Scots Pine, they also utilize Norway Spruce, Sitka Spruce *Picea sitchensis* and larch *Larix* spp. (Cramp & Perrins 1994, Marquiss & Rae 2002). Similarly, Common Crossbills make use of several species of conifers: Sitka Spruce, Lodgepole Pine *Pinus contorta* (both are North American conifers introduced to Europe for timber cropping), larch and Scots Pine (Marquiss & Rae 2002, Summers *et al.* 2002). They also breed in pure Scots Pine forests when the cones open to release seeds in spring (Haapanen 1966, Summers & Proctor 2005, Summers *et al.* 2010). Therefore, crossbills are flexible in their use of conifers. It would seem that if, having bred successfully in a year when seed production by both conifers is high, and there is low seed production by both conifers in the following year, there is no alternative for the crossbills but to move outside their normal ranges in search of food. Such combinations in seed production by both conifers will occur only by chance, given that seeding is normally asynchronous.

AUTHOR CONTRIBUTIONS

Ron W. Summers: Conceptualization; investigation; data curation; formal analysis; methodology; writing – original draft; writing – review and editing. **Ben T. Swallow:** Data curation; investigation; formal analysis; methodology; writing – original draft; writing – review and editing. **Jonas Fridman:** Data curation; investigation; writing – review and editing. **Tatu Hokkanen:** Data curation; writing – review and editing; investigation. **Ian Newton:** Data curation; investigation; writing – original draft; writing – review and editing. **Stephen T. Buckland:** Formal analysis; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicting interests to declare.

ETHICAL NOTE

None.

CONSENT FOR PUBLICATION

Not applicable.

Data Availability Statement

All data required to run the analysis will be made available by the authors on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Standardized numbers of crossbills at Falsterbo, southern Sweden, from 1973 to 2018.

Figure S2. Standardized values of Norway Spruce and Scots Pine cone (seed) production in Sweden from 1910 to 1953 (Hagner 1965) and 1954 to 2020 (Fridman *et al.* 2014).

Figure S3. Standardized values for Norway Spruce and Scots Pine seed production in Finland from 1960 to 2000 for Norway Spruce and 1960 to 2004 for Scots Pine.