

# The interacting effects of forestry and climate change on the demography of a group-living bird population

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## Abstract

Anthropogenic degradation of natural habitats is a global driver of wildlife population declines. Local population responses to such environmental perturbations are generally well understood, but in socially structured populations, interactions between environmental and social factors may influence population responses. Thus, understanding

how habitat degradation affects the dynamics of these populations requires simultaneous consideration of social and environmental mechanisms underlying demographic responses. Here we investigated the effect of habitat degradation through commercial forestry on spatiotemporal dynamics of a group-living bird, the Siberian jay, *Perisoreus infaustus*, in boreal forests of northern Sweden. We assessed the interacting effects of forestry, climate and population density on stage-specific, seasonal life-history rates and population dynamics, using long-term, individual-based demographic data from 70 territories in natural and managed forests. Stage-specific survival and reproductive rates, and consequently population growth, were lower in managed forests than in natural forests. Population growth was most sensitive to breeder survival and was more sensitive to early dispersing juveniles than those delaying dispersal. Forestry decreased population growth in managed forests by reducing reproductive success and breeder survival. Increased snow depth improved winter survival, and warmer spring temperatures enhanced reproductive success, particularly in natural forests. Population growth was stable in natural forests but it was declining in managed forests, and this difference accelerated under forecasted climate scenarios. Thus, climatic change could exacerbate the rate of forestry-induced population decline through reduced snow cover in our study species, and in other species with similar life-history characteristics and habitat requirements.

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## Keywords

Climate change

Forestry

Demography

Elasticity analysis

Multi-state mark-recapture

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We show how two anthropogenic drivers of environmental concern affect population dynamics in temperate forests and the implications of heterogeneous responses of individuals of differing social rank.

### Electronic supplementary material

The online version of this article (<https://doi.org/10.1007/s00442-018-4100-z>) contains supplementary material, which is available to authorized users.

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## Introduction

Habitat degradation increases the extinction risk for natural populations, reduces biodiversity, and diminishes resilience of ecosystems to further environmental change (Jiguet et al. 2007; Opdam and Wascher 2004). To mitigate the effect of habitat degradation on natural populations, we need to understand the demographic mechanisms underlying population responses. Changes in food availability, predation rates, and loss of breeding sites have been identified as common causes of population declines through habitat degradation (Gilroy et al. 2008; Peterson et al. 2014; Warkentin et al. 2004). However, the mechanisms underlying degradation effects are far less clear in social species (Donati et al. 2011; Eggers and Low 2014; Li et al. 2013), where individuals live in groups and differ in their social status and consequent access to resources. Depending on the interactions between social and environmental factors, social structure can either mediate the negative effects of habitat degradation (Clarke et al. 2002; Donati et al. 2011) or have an exacerbating effect (Coker et al. 2013). Therefore, determining the vulnerability of a socially structured population to habitat degradation requires explicit investigation of these intertwined factors.

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Boreal forests represent the world's largest terrestrial biome and are globally the most modified forest ecosystem (Linder and Östlund 1998). Intensive forestry has severely degraded this ecosystem by altering tree

stand structure and reducing biodiversity (Imbeau et al. 2001). As a consequence, many species have suffered population declines in this ecosystem (Esseen et al. 1997; Imbeau et al. 2001). A number of resident mammals (e.g. reindeer *Rangifer tarandus*, brown bear *Ursus arctos*) and birds (e.g. willow tit *Parus montanus*, Siberian tit *P.cinctus*) inhabiting boreal forests have complex social systems (Ekman and Askenmo 1984; Espmark 1964; Steyaert et al. 2013; Wiktander et al. 2000). Although social structure in these species is well studied, it remains unclear how social factors interact with environmental degradation and specifically, how individuals of different social status respond to degradation and the population level consequences of this response heterogeneity.

In northern Europe, climate models predict an increase in mean temperature and more frequent snowmelts (Räisänen 2016; Barring et al. 2017). A growing literature exists on the ecological implications of climate change, but its interaction with habitat degradation is rarely considered. While habitat degradation and climate change have been shown to dampen each other's effect in some cases (Warren et al. 2001), climate change will mostly exacerbate the negative effects of habitat degradation (Mac Nally et al. 2009; Mantyka-pringle et al. 2012). Thus, it is important to consider future climate scenarios alongside interactions with other environmental factors, to understand how climate change will modulate the effect of forestry on population persistence (Griffiths et al. 2015).

We used 15 years of mark-recapture data from a study of Siberian jays, *Perisoreus infaustus*, in northern Sweden to investigate the effect of forestry management on a socially structured species. This highly social species lives in stable groups that inhabit year-round territories and occurs throughout the northern Palearctic. Groups are centred around a breeding pair and can include up to five non-breeders, which are either retained offspring that delay dispersal and remain in the natal territory for up to 4 years, or unrelated immigrants that mostly immigrate as juveniles (Ekman and Griesser 2016). While forests in northern areas of the study site are unmanaged, the southern area is heavily managed. Forestry involves predominantly clear cutting and thinning (Griesser and Lagerberg

2012); while clear cutting produces even-aged patches, thinning leads to a less dense habitat, making nests more visible to visual predators such as other corvids, which is the main cause of nest failure and predation in Siberian jays (Ekman and Griesser 2016).

During the period of this study (2000–2014), mean winter snow depth (October–March; inter-annual range = 0.17–0.68 m) and average spring temperature (April–May; range = 0.26–5.59 °C) varied considerably, and these fluctuations are expected to increase due to climate change. A predicted increase in mean annual temperature of 2.3 °C is expected over the next 20–50 years (Bärring et al. 2017), with an associated reduction in snow cover of up to 29% (Räisänen 2016). We may expect that these effects of forestry and climate change potentially interact to exacerbate their effects on demographic rates. Therefore, it is important to assess the interacting effects of environmental factors on population dynamics, and how this can be mediated by social mechanisms.

We first examined the interacting effects of forestry, climatic factors and population density on stage-specific vital rates (i.e. survival, transition, and recruitment), using a multi-state model with seasonal life-history stages. Using these vital rate estimates, we parameterised a periodic, stage-structured matrix model, accounting for social structure, and investigated the demographic consequences of forestry using a retrospective perturbation analysis. As a result, we identified the key life-history processes through which forestry affected population dynamics the most. Finally, we investigated how future climate change and forestry could interact to influence population persistence.

## Materials and methods

### Study site and species

We used 15 years of data from a long-term study on Siberian jays, located near Arvidsjaur, northern Sweden (65°40' N, 19°10' E). In total, 4341 sightings from 1166 individuals were recorded during the study period. Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are the

common tree species at the study site, where the latter is selectively removed in commercially exploited forests. The southern area of the study site is heavily managed, involving thinning, harvesting, and re-planting in 80–120 year cycles (Griesser and Lagerberg 2012; Griesser et al. 2007). Forests in the northern area of the study site have not been managed for at least 200 years, and thus, are structurally more diverse and contain trees of all age classes.

All individuals in the study population were ringed with 2–3 colour rings for individual recognition (Griesser et al. 2012). Groups form around a single, monogamous breeding pair, including 1–5 non-breeders, which occupy a stable territory (Ekman and Griesser 2016). Most non-breeders queue until a breeding position becomes available in a nearby territory, which can occur at any time throughout the year (Ekman and Griesser 2016). Breeders are socially dominant over non-breeders, and thus their status can be reliably observed through social and reproductive behaviour (Griesser et al. 2015). Around one-third of juveniles remain with their parents (hereon referred to as retained juveniles), benefitting from access to food and nepotistic anti-predator protection (Griesser et al. 2006). Groups also include immigrant non-breeders, mostly immigrating as juveniles during their first summer of life (hereafter referred to as dispersed juveniles). Retained juveniles can have in some years a higher first winter survival than dispersed juveniles (Griesser et al. 2006) and can therefore afford to queue longer for breeding openings in high quality territories, resulting in higher lifetime reproductive success (Ekman and Griesser 2016).

The principal predators of Siberian jays are accipiter hawks (Griesser 2013), which are visual hunters, and consequently predation rates are higher in managed, more open forests. Similarly, nests are under higher predation risk in these habitats as nest predators (mainly other corvids) locate them more easily (Eggers et al. 2006). Pairs breeding in territories with higher predation risk preferably nest in dense patches with colder microclimate, paying a thermoregulatory cost of predator avoidance (Eggers et al. 2006).

## Data collection

Each year, territories were visited repeatedly in March, prior to the onset of breeding, and in September, after the dispersal of juveniles. Nests were located in April with the help of radio tags and all nestlings were ringed in May. Non-ringed individuals that immigrated into the study population were aged based on the shape of their outermost tail feather. In groups where the nest was not located, the breeding success was assessed based on the presence of retained juveniles. Kinship of unringed individuals was reliably determined by observing the social interactions between group members: breeders are very tolerant with retained juveniles and share a feeder, while they displace dispersed non-breeders from the feeder (Griesser et al. 2015). Jays are sexually monomorphic and thus sex of all individuals was determined with molecular methods (Griffiths et al. 1998). Estimates of recruitment were based on the presence of retained juveniles in autumn, which gives robust estimates of reproductive success since the majority of successful breeding attempts result in retained juveniles (Griesser et al. 2014).

## Environmental factors

We used climatological and habitat data to investigate the influence of environmental factors on the demography of Siberian jays. Daily temperature and snow depth data were obtained from the Swedish Institute of Hydrology and Meteorology using three observation stations closest to the study site (Arvidsjaur: 10 km,  $N = 5110$  days; Glommersträsk: 50 km,  $N = 158$  days; Älvsbyn: 83 km,  $N = 69$  days). We calculated mean winter snow depth (December–March) and average temperature during the breeding season (April–May). The same climatological values were used for the whole study area since elevation differed less than 100 m and intra-territory variation in snow depth was greater than inter-territory variation. An earlier study showed that high spring temperatures are associated with higher breeding success (Eggers et al. 2005). Winters with high snowfall may reduce the predation pressure on Siberian jays since goshawks can more easily target more profitable prey, such as hares (*L. timidus*) and grouses (*T. bonasia*) (Widén 1987). Snow depth and spring temperature

were included in models of vital rates as continuous variables, describing average annual values for the whole study site. We measured the proportion of forests that have not been managed for at least 50 years on each territory directly in the field or from aerial images (see Griesser and Nystrand 2009 for details), and included it as a territory-specific continuous covariate. To account for the segregation of the study site into two management types, we included forest type (natural vs. managed) as a bivariate covariate in the analyses. Population density was measured in relation to prevailing social structure (i.e. mean group size per forest type at each census) and was included as a continuous covariate as it may influence vital rates. There was no evidence of collinearity between explanatory variables since all Pearson's correlation coefficients were well below 1 (all  $< 0.16$ ).

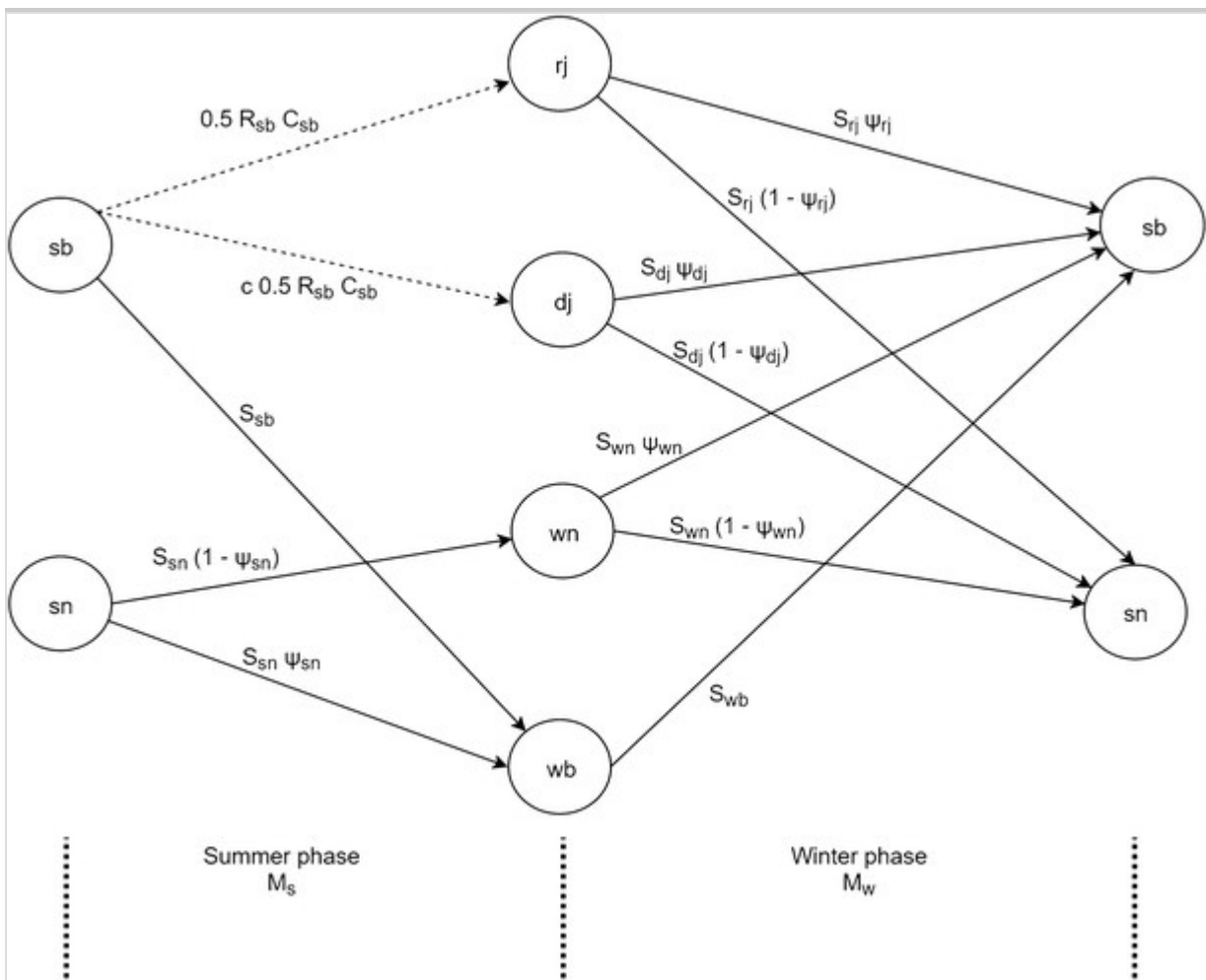
## Vital rates

In socially structured populations, vital rates can vary substantially among different life-history stages (Calhoun 1952; Ozgul et al. 2014). We developed a periodic life cycle, with a summer and a winter season including six life-history stages based on the social status: retained juvenile (rj), dispersed juvenile (dj), summer non-breeder (sn), winter non-breeder (wn), summer breeder (sb), and winter breeder (wb) (Fig. 1). Summer (March–August) includes the reproductive period and juvenile dispersal, while winter (September–February) is the non-reproductive period with little dispersal. Because the fate of summer juveniles was confounded by permanent emigration, we considered only recruitment into the winter juvenile stages (rj and dj). Our life cycle included the following stage-specific vital rates: apparent survival rates ( $S_{rj,dj,sn,wn,sb,wb}$ ), transition rates (probability of transitioning to a breeding stage;  $\Psi_{rj,dj,sn,wn}$ ), reproductive rate (probability of recruiting into retained juvenile stage,  $R_{sb}$ ), and recruitment (per capita number of offspring recruited into retained juvenile stage,  $C_{sb}$ ).

### Fig. 1



Siberian jay life cycle.  $S_x$  is the probability of an individual in stage  $x$  surviving until the next census, and  $\Psi_x$  is the probability of an individual in stage  $x$  transitioning to a breeder stage in the next census. The reproductive rate,  $R_{sb}$ , is the probability of a nest producing at least one offspring that survives and remains in their natal territory to the next census.  $C_{sb}$  is the per capita recruitment, describing the number of offspring per nest that survive until the next census and remain in their natal territory as a retained juvenile. Dispersed juvenile recruitment is estimated based on the retained juvenile recruitment, multiplied by a constant  $c$  (see main text for details). Abbreviations for life-history stages correspond to: retained juvenile (rj), dispersed juvenile (dj), summer non-breeder (sn), winter non-breeder (wn), summer breeder (sb) and winter breeder (wb)



We modelled survival,  $S$  and transition rates  $\Psi$ , while taking into account stage-specific recapture rates ( $p_{sn,wn,wb}$ ), using a multi-state mark-recapture model (Brownie et al. 1993; Hestbeck et al. 1991; Williams et al. 2002) implemented using the RMark interface (Laake 2013) for Program MARK (White and Burnham 1999). Multi-state models are commonly adopted to account for individual heterogeneity in demographic rates resulting from social status (Cayuela et al. 2014; Townsend and Anderson 2007); however, seasonality in social status has rarely been incorporated. Transition rates were dependent on survival in the starting stage, since this was a post-breeding census.  $S$ ,  $p$  and  $\Psi$  were initially modelled as a function of sex, however, this term did not improve the model fit for any of the demographic rates and thus the data were pooled for both sexes. The recapture rates for juveniles were fixed to zero since they cannot be recaptured in these stages. These vital rates were analysed using data from both sexes, assuming no difference between the sexes. The goodness of fit of a global model was assessed using Program RELEASE (Burnham 1987).

Recruitment was only possible during the summer stage, and thus, only summer breeders could contribute to the next generation. Reproductive success was assessed by two parameters; the reproductive rate ( $R_{sb}$ ), describing the proportion of summer breeding pairs that successfully recruited at least one retained juvenile and number of retained juveniles per breeding pair ( $C_{sb}$ ). We considered only retained juveniles since dispersed juveniles had already dispersed prior to the September census, and thus could not be observed. Previous work has shown that per every retained juvenile, there were two dispersed juveniles and these dispersers were subject to further 20% dispersal mortality (Griesser et al. 2014). Dispersed juvenile recruitment was therefore estimated based on the retained juvenile recruitment, by multiplying retained juvenile recruitment by a constant  $c$ , which is equal to  $2 \times 0.8$ . Recruitment was further multiplied by 0.5 since our stage-structured model is asexual and there was no evidence of bias in juvenile sex ratios. Thus, recruitment was modelled as  $0.5R_{sb}C_{sb}$  for retained juveniles and  $c0.5R_{sb}C_{sb}$  for dispersed juveniles.

Reproductive rates ( $R_{sb}$ ) and recruitment ( $C_{sb}$ ) for summer breeders were estimated using generalized linear mixed models (GLMMs) implemented in the R package ‘lme4’ (Bates et al. 2014).  $R_{sb}$  was fitted as a binomially distributed response variable with a logit link function and  $C_{sb}$  as a Poisson distribution with a log link; breeder identity was included as a random effect. Reproductive rates were conditional on survival in the starting stage (i.e. post-breeding census), and recruitment was conditional on reproduction.

Environmental covariates and their interactions were included as linear constraints in the candidate models of  $S$ ,  $p$ ,  $\Psi$ ,  $R$  and  $C$ . A list of biologically relevant model structures was developed for each vital rate. We used Akaike’s information criterion corrected for small sample size ( $AIC_c$ ), for model comparison and for identification of the most parsimonious model from a candidate model set (Burnham and Anderson 1987). Model comparison was based on the differences in  $AIC_c$  values ( $\Delta AIC_c$ ) and the model weights, where  $\Delta AIC_c > 2$  indicates reasonable support for a difference. If two competing models were within  $2 \Delta AIC_c$ , following rules of parsimony, the model with fewer parameters was selected. When the removal of a variable from the model resulted in a  $< 2$  increase in  $AIC_c$ , we considered the variable significant and after selecting the most parsimonious model, the relevance of covariates was confirmed by ensuring the standard error of coefficients did not overlap zero (see supplementary information, S3). Life-history stage and habitat-specific vital rates, and their associated uncertainties were estimated at mean values of environmental covariates. 95% confidence intervals were calculated using the delta method as described in Powell (2007). Survival rates at different snow depths were only estimated for winter stages. All analyses were performed using R 3.3.1 (R Core Team 2016).

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## Population dynamics

To investigate population dynamics in natural and managed forests, we parameterised a periodic, stage-structured, female-based matrix model for

each forest type (Caswell 2001). A periodic, rather than annual, matrix model was used due to the time dependency of life-history stages, since individuals cannot exist in all stages at the same time in the annual cycle. We divided the year into a summer and a winter phase, both of 6 months' duration, containing different, seasonal life-history stages. Summer matrix  $M_s$  projects the population from two summer stages (*sn* and *sb*) to four winter stages (*rj*, *dj*, *wn* and *wb*):

$$\begin{array}{c}
 \begin{array}{cc}
 & \begin{array}{cc}
 sn & sb
 \end{array} \\
 \begin{array}{c}
 rj \\
 dj \\
 wn \\
 wb
 \end{array} & \left[ \begin{array}{cc}
 0 & 0.5R_{sb}C_{sb} \\
 0 & c0.5R_{sb}C_{sb} \\
 S_{sn}(1-\Psi_{sn}) & 0 \\
 S_{sn}\Psi_{sn} & S_{sb}
 \end{array} \right]
 \end{array}
 \end{array}$$

1

Winter matrix  $M_w$  projects four winter stages (*rj*, *dj*, *wn* and *wb*) to two summer stages (*sn* & *sb*):

$$\begin{array}{c}
 \begin{array}{cccc}
 & rj & dj & wn & wb \\
 \begin{array}{c}
 sn \\
 sb
 \end{array} & \left[ \begin{array}{cccc}
 S_{rj}(1-\Psi_{rj}) & S_{dj}(1-\Psi_{dj}) & S_{wn}(1-\Psi_{wn}) & 0 \\
 S_{rj}\Psi_{rj} & S_{dj}\Psi_{dj} & S_{wn}\Psi_{wn} & S_{wb}
 \end{array} \right]
 \end{array}
 \end{array}$$

2

We estimated the asymptotic population growth rate  $\lambda$  as the dominant eigenvalue of the population projection matrix for natural and managed forests. Means and 95% confidence intervals were estimated for  $\lambda$  using a parametric bootstrapping approach (Wisdom et al. 2000).  $\lambda_i$  was estimated from 10,000 replicate population projection matrices using demographic rates sampled from their associated probability distributions. The annual

population projection matrix (see supplementary information, S4) is calculated as

$$A = M_s M_w. \quad 3$$

We used elasticity analysis, a widely used prospective perturbation analysis, to measure the sensitivity of  $\lambda$  to a proportional change in a given vital rate, based on the annual projection matrix (Caswell and Trevisan 1994). Lower-level elasticities for Siberian jay vital rates were calculated analytically as

$$\frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}, \quad 4$$

where  $a_{ij}$  is the matrix element in row  $i$  and column  $j$ , and  $x$  is a lower-level parameter (i.e. vital rate). Using a fixed one-way life table response experiment (LTRE), a commonly used retrospective perturbation analysis (Caswell 1989), we identified the demographic causes of differences in  $\lambda$  between the two forest types. Using natural forests as a reference matrix, the observed difference in  $\lambda$  between natural and managed forests ( $\Delta\lambda$ ) was decomposed into contributions from each vital rate as

$$\Delta\lambda = \lambda_M - \lambda_N \approx \sum_{i,j} (x_M - x_N) \frac{\partial \lambda}{\partial x_N}, \quad 5$$

where subscripts  $N$  and  $M$  indicate the natural and managed forest matrices, respectively.

Regional climate forecasts for northern Sweden predict an increase in annual temperature of 2.3 °C by the period 2035–2065 (Barring et al. 2017) and the consequent decreases in snow cover of 7–29% (Räisänen 2016). With this in mind, we investigated changes in density-independent population growth under different climatic conditions. To calculate  $\lambda$  under different conditions, vital rates were estimated at a range of temperatures and snow depths using the most parsimonious models (Table 1).  $S$ ,  $\Psi$  and

$R$  were modelled at different temperatures, ranging from the mean spring temperature recorded during our study (3.6 °C) to a 1.5 °C increase (5.13 °C). Snow depths ranged from the recorded mean (0.42 m) to a 0.2 m decrease (0.23 m), which are conservative projections, based on the regional climate forecasts (Barring et al. 2017; Räisänen 2016).

**Table 1**

The most parsimonious vital rate models of survival, recapture, transition, reproduction coefficients and associated standard errors (SE)

Vital rate	Best model	Npar
Survival, $S$	~ habitat + stage + snow + density + stage:density	14
Recapture, $p$	~ - 1 + stage + density	5
Transition, $\Psi$	~ - 1 + stage + habitat + snow + habitat:snow	7
Reproduction, $R$	~ habitat + density + temp + habitat:temp + density:temp	6

‘Habitat’ refers to a territory’s classification as managed forest; ‘stage’ to life-history stage; ‘temp’ to mean spring temperature during April/May; and ‘density’ to mean density of the territory over each time step. Life-history stages are: retained juvenile (rj), disperse breeder (sn), winter non-breeder (wn), summer breeder (sb) and winter breeder (w)

Vital rate	Best model	Npar
Recruitment, <i>C</i>	~ 1	1

‘Habitat’ refers to a territory’s classification as managed forest; ‘stage’ to life-history stage; ‘temp’ to mean spring temperature during April/May; and ‘der’ to mean spring territory over each time step. Life-history stage are; retained juvenile (rj), disperse breeder (sn), winter non-breeder (wn), summer breeder (sb) and winter breeder (w)



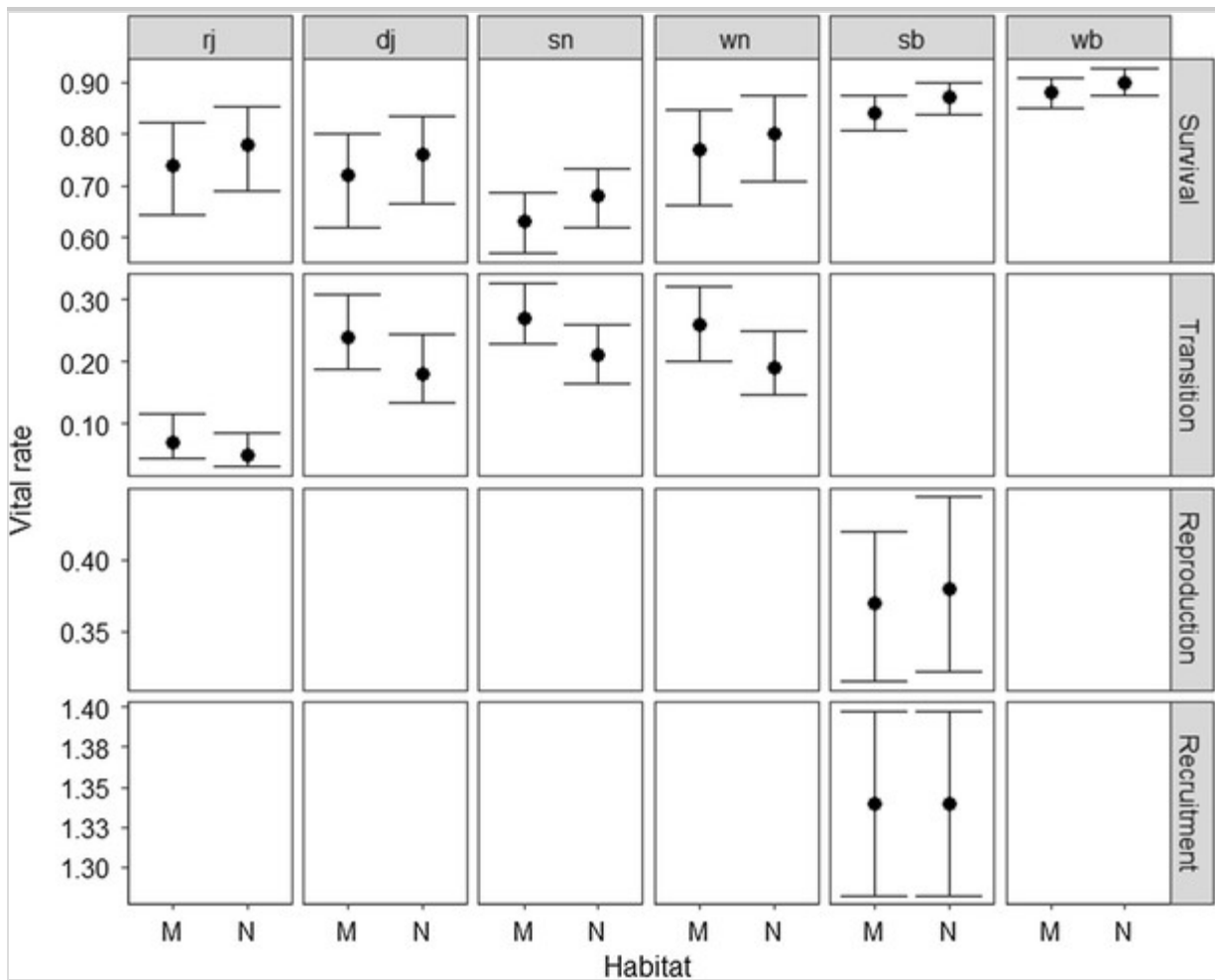
## Results

### Climate and forestry effects on life-history rates

The most parsimonious models, with regression coefficients and associated standard errors, for each vital rate are shown in Table 1. Vital rates varied among life-history stages (Fig. 2): breeders had the highest and the least variable survival rates (mean  $\pm$  standard error) compared to other life-history stages, and their survival was higher in winter (natural:  $0.90 \pm 0.02$ , managed:  $0.88 \pm 0.02$ ) than in summer (natural:  $0.87 \pm 0.02$ , managed:  $0.84 \pm 0.02$ ). Survival of retained juveniles (natural:  $0.78 \pm 0.06$ , managed:  $0.74 \pm 0.1$ ) was higher than dispersed juveniles (natural:  $0.76 \pm 0.07$ , managed:  $0.72 \pm 0.09$ ), although confidence intervals overlapped. Non-breeders also had lower survival in summer (natural:  $0.68 \pm 0.05$ , managed:  $0.63 \pm 0.06$ ) than in winter (natural:  $0.80 \pm 0.07$ , managed:  $0.77 \pm 0.08$ ).

#### Fig. 2

Survival (row 1), transition (row 2), reproductive (row 3) and recruitment rates (row 4) in managed (M) and natural (N) forest



The most parsimonious model of seasonal survival rates included additive effects of mean winter snow depth, forest type and population density (Table 1). Survival rates increased with snow depth for all life-history stages and were higher in natural forests. Population density interacted with life history stage where larger group sizes negatively influenced summer non-breeder survival, but was beneficial for all other stages (Table 1).

Recapture rates were high for breeder stage both during summer ( $0.99 \pm 0.01$ ) and winter ( $0.98 \pm 0.01$ ). Summer non-breeders ( $0.76 \pm 0.04$ ) were more likely to be recaptured than winter non-breeders ( $0.52 \pm 0.08$ ).

Transition rates from non-breeder to breeder were about 3.5 times higher for dispersed juveniles (natural:  $0.18 \pm 0.05$ , managed:  $0.24 \pm 0.05$ ) than

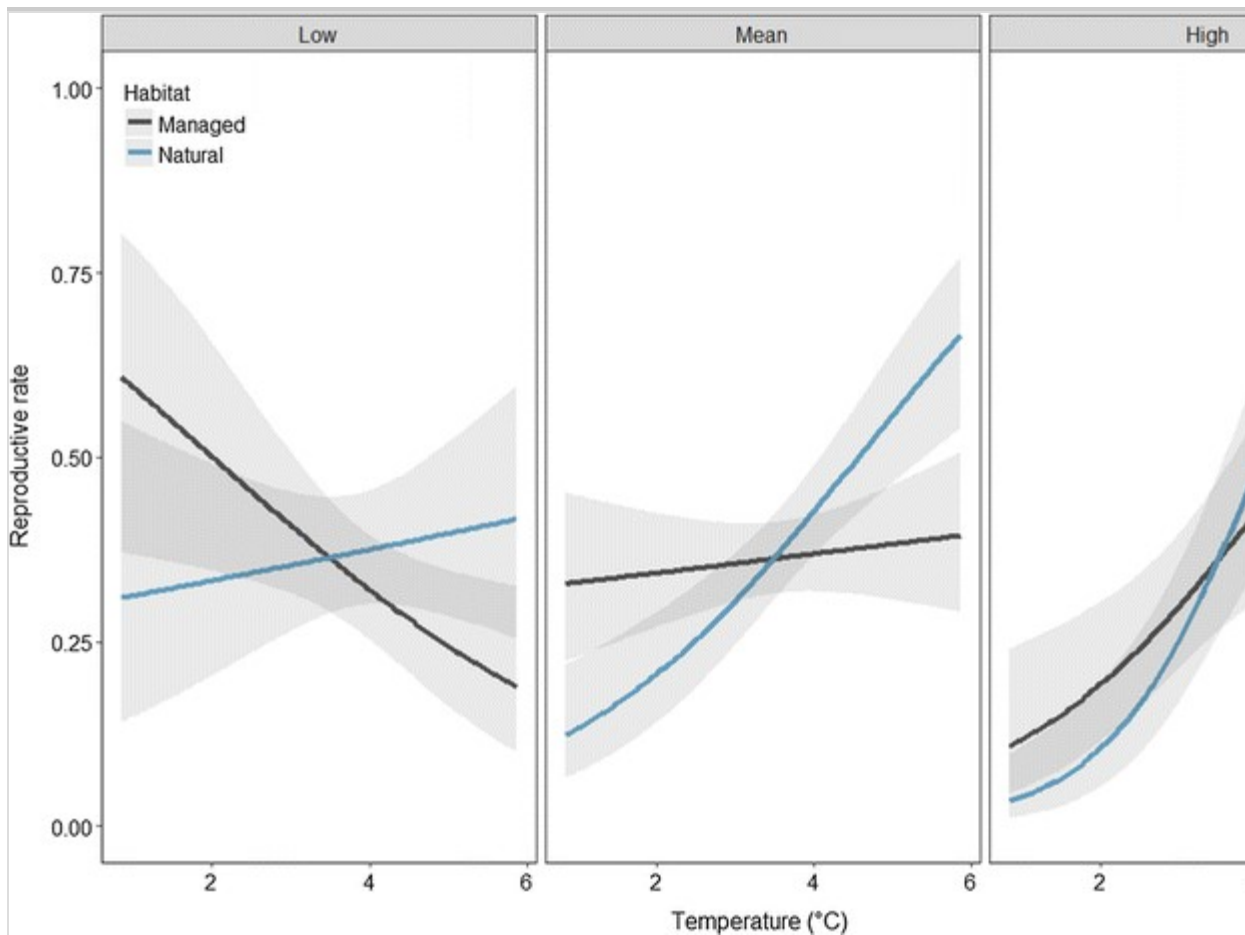


for retained juveniles (natural:  $0.05 \pm 0.02$ , managed:  $0.07 \pm 0.03$ ) and were higher in managed forests than in natural forests. In years with greater snow depth, transition rates from non-breeder to breeder were lower as a density-dependent consequence of higher breeder survival in the previous time step. Transition rates were higher in summer (natural:  $0.21 \pm 0.05$ , managed:  $0.28 \pm 0.05$ ) than in winter (natural:  $0.19 \pm 0.05$ , managed:  $0.26 \pm 0.05$ ); however, confidence intervals overlapped.

Reproductive rate ( $R_{sb}$ ) ranged from  $0.08 \pm 0.04$  to  $0.84 \pm 0.10$  among years. The most parsimonious model included additive effects of spring temperature, population density, forest type, and interaction effects of forest type and temperature, as well as population density and temperature (Table 1). Reproductive rate was higher in years with warmer mean spring temperature, particularly in natural forests, except at low population density (Fig. 3). At high population densities and during cold springs, reproductive rates were low. Conversely, the highest reproductive rates were recorded when population density and temperature were simultaneously high (Fig. 3, panel 3).

### **Fig. 3**

Model predictions of reproductive rate at the recorded range of spring temperatures. The panels from left to right correspond to lowest, mean and highest recorded population density. The blue line corresponds to predictions for natural forest and the black line for managed forest



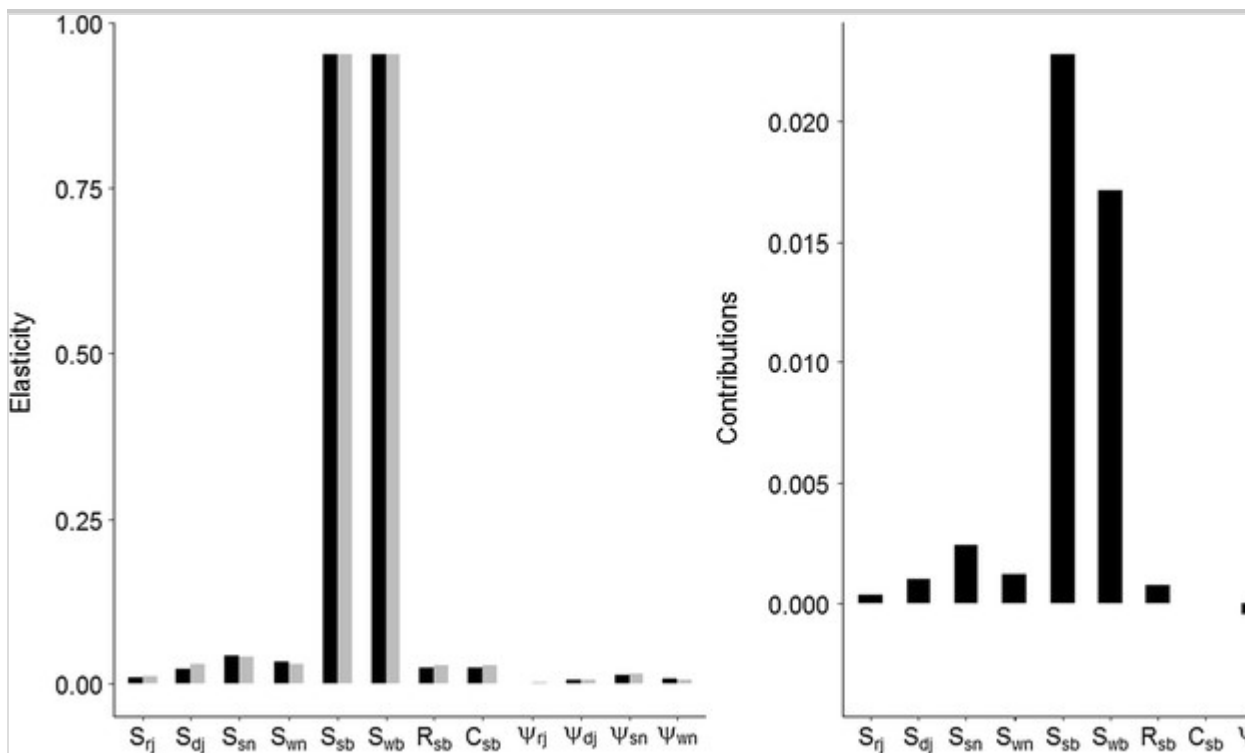
## Climate and forestry effects on population dynamics

At mean values of climatic factors and population density, the asymptotic population growth rate (with associated 95% credible intervals), was stable (1.00, CI: 0.97, 1.03) in natural forests and declining (0.96, CI: 0.93, 0.98) in managed forests. The elasticity of  $\lambda$  to survival and transition rates increased with life-history stage, but was especially high to the survival of summer and winter breeders (Fig. 4a). Elasticities to survival and reproductive rates were marginally higher in natural forests, whereas transition rates had more influence on  $\lambda$  in managed forests. A retrospective perturbation analysis showed that lower survivals of summer and winter breeders were the main contributors to the lower population growth rate in managed forests (Fig. 4b). With the exception of winter non-breeders, the contribution of survival rates to  $\Delta\lambda$  increased with life-history stage. Recruitment of juveniles ( $C_{sb}$ ) made no contribution to  $\Delta\lambda$

since there was no difference in this vital rate between managed and natural forests. Higher transition rates in managed forests contributed to an increase in  $\lambda$ , as a density dependent consequence of higher breeder mortality resulting in more breeding positions becoming available in managed forests.

**Fig. 4**

Elasticity of  $\lambda$  to vital rates for managed (dark grey) and natural (light grey) forest (left panel) and the contribution of the difference in vital rates to the difference in  $\lambda$  between natural and managed forest (right panel)

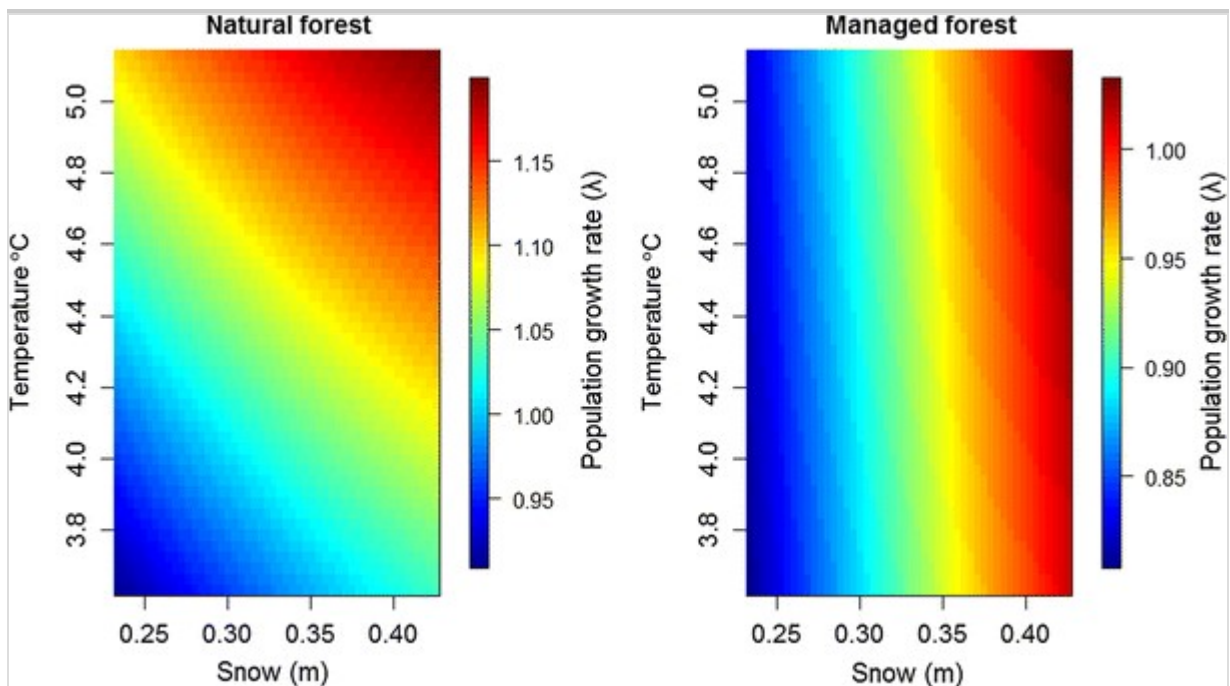


2500 asymptotic population growth rates were generated for natural and managed forests, based on vital rates estimated at mean population density and at a range of spring temperature and snow depth values (Fig. 5).  $\lambda$  decreased with snow depth in both forest types, but the interaction effect of temperature and habitat on reproduction (Table 1) meant that  $\lambda$  only increased with temperature in natural forests. With a 1.5 °C increase in temperature and 0.1 m decrease in mean snow depth,  $\lambda$  was 1.12 for natural forests and 0.94 for managed forests. With a further 0.1 m decrease in

mean snow depth,  $\lambda$  was 1.07 for natural forests and 0.86 for managed forests.

### Fig. 5

Image plot of population growth rates using vital rates predicted at a range of temperatures, from the mean observed spring temperature (April–May) (3.62 °C) to a 1.5 °C increase (5.13 °C), and snow depths, from a two standard deviation decrease in mean winter snow depth (October–March) (0.23 m) to the mean observed snow depth (0.43 m), for natural (left panel) and managed (right panel) forest



## Discussion

Effects of habitat degradation on population persistence remain poorly understood for socially structured populations, where environmental and social factors interact to determine vital rates (Crook 1970). Climate change is expected to have strong impacts on populations in boreal forests, exposing them to the combined effects of habitat degradation and climate change, likely increasing their extinction risk. However, individuals of different social status can react heterogeneously to these changes. Using a

multi-state modelling approach, we linked the demographic effects of forestry and climate to larger-scale population dynamics, while considering the influence of social structure. Our results revealed that forestry negatively affected stage-specific survival, acting predominantly through breeder survival and reproductive rates, and consequently the population growth rate. Moreover, increased snow depth positively affected winter survival, and warmer spring temperatures enhanced reproductive success, particularly in natural forests. Future climate scenarios with less snow cover and warmer spring temperatures are predicted to increase the difference in population growth rates between natural and commercially managed forests. Thus, climate change and further habitat degradation through forestry are likely to exacerbate the rate of population decline, highlighting that forestry can increase the vulnerability of a population to climate change, predominantly acting through the vital rates of breeders.

## Social structure

Social structure is often an integral part of avian life-history and has been shown to modulate environmental effects on vital rates (Garrott et al. 2003; Wiley 1974). In our study, vital rates varied greatly among life-history stages, where breeder survival was consistently high and buffered from environmental variation. There was little difference in the survival of retained and dispersed juveniles, in agreement with a recent study (Griesser et al. 2017a), although retained juveniles may have a higher first winter survival than dispersed juveniles some years (Griesser et al. 2006). However, transition rates to the breeding stage varied greatly, reflecting that dispersed non-breeders move into a breeding position sooner than retained offspring. Breeding positions are not gained competitively, but rather non-breeders wait until a breeder dies or abandons a territory. Given the prolonged parental investment into retained offspring, they can afford to wait longer and often achieve breeding positions in higher quality territories (Ekman and Griesser 2016). The positive effect of population density (i.e., mean group size per forest type at each census) on survival highlights the general benefits of group living, in case of the Siberian jays an increased probability of detecting predators in larger groups (Griesser et

al. 2017a). Interestingly, summer non-breeders had the lowest survival rates and did not benefit from large group sizes, which may reflect an increased rate of permanent dispersal.

## Climate and forestry effects on vital rates

Climate change is expected to cause severe declines in avian diversity, particularly at higher latitudes (Jetz et al. 2014; Jiguet et al. 2007). Accordingly, the majority of life-history rates in this study were influenced by climate. Survival increased with snow depth possibly because alternative prey sources become more vulnerable to predators, reducing predation pressure on Siberian jays (Lui 2010). Reproductive rates increased with temperature (Fig. 3), since warmer springs reduced the cost of breeding in dense vegetation and lead to earlier food availability in spring, causing a shift in the trade-off between the anti-predation benefits and thermoregulatory cost of reproducing in dense patches (Eggers et al. 2006). Furthermore, the benefit of higher temperatures for reproduction was greater at higher population densities, which may reflect that larger groups compete less for resources in warmer springs, resulting in a higher reproductive allocation by breeders.

Habitat degradation is predicted to exacerbate the negative effects of climate change on many avian populations (Jetz et al. 2014). Our results confirm reduced reproduction and higher mortality in managed forests (Griesser et al. 2017a), and show that mortality effects were consistent among life-history stages. Open, managed forests provide less visual protection from nest and adult predators than natural forests. Although larger groups benefitted individuals through increased vigilance against predators, we did not observe any greater benefit of larger group sizes in managed forest. However, reproductive success was not consistently worse in managed forests. The interaction between habitat and temperature suggests that it is beneficial to nest in managed forests in cold springs. While nests in natural forests have a lower nest predation rate, these forests experience a colder microclimate, and snowmelt is delayed after cold spells compared to less dense, managed forests (Eggers et al. 2006). Such microclimatic interactions can alter the predictions of demographic

responses to habitat degradation (Opdam and Wascher 2004). Furthermore, forestry had the reverse effect on transition rates, which were higher in managed forests, since higher breeder mortality increases the availability of breeding positions (Nystrand et al. 2010), resulting in a more rapid progression of individuals through the life cycle. The best models of vital rates did not include proportion of natural forest as an explanatory variable, which is a more detailed measure of the degree of management in a territory. This may be because forest type is a more general indicator of management, encompassing all issues relating to forestry.

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## Climate and forestry effects on population dynamics

Elasticity analysis showed that the breeder stage influences population growth disproportionately more than other life-history stages. Vital rates with a large influence on population growth often display lower variance (Gaillard and Yoccoz 2003; Rotella et al. 2012), as was observed in our study population (Griesser et al. 2017b). In contrast, non-breeders have lower and more variable survival rates, and kinship strongly determines their transition to breeding stage. Dispersed juveniles had a higher probability of becoming breeders than retained juveniles (see above), and therefore this vital rate had a greater influence on population growth at this stage. Furthermore, although model selection did not favour a model where individuals were defined as dispersed or retained throughout the life cycle, a previous study revealed higher lifetime reproductive success of retained offspring (Ekman and Griesser 2016), which could not be incorporated at the population level.

The main effects of forestry on population growth occurred via reduced breeder survival, since this rate has the largest effect on population growth. Per capita recruitment did not vary between forest types. This result may reflect that we used the number of retained offspring as proxy for reproductive success, while forestry could have a stronger effect on dispersing offspring. Higher transition rates in managed forests positively influenced population growth, which compensated for some of the difference in  $\lambda$  resulting from forestry. The effect was greatest at the

summer non-breeding stage, when transitions to breeding status occur most frequently, resulting in a trade-off between survival and reproductive rates, and transition rates. Such trade-offs are central to life-history theory and assume that an increase in certain fitness-related vital rates can be associated with a decrease in others (Stearns 1992). Despite this trade-off, the net effect of forestry on population growth was still negative due to the overriding contribution of summer breeder survival and reproductive rate to the lower growth rate in managed forests.

## Future population projections

Moderate changes in future climate predict increased population growth in natural forests, through enhanced reproductive success, but decreased population growth in managed forests, through reduced snow depth. However, this model is only relevant at average population densities and at stable age structure, and thus, such a rapid increase in  $\lambda$  is unlikely to be realised as natural forest populations quickly reach their carrying capacity.

## Management implications

Commercial forestry has caused declines in many populations inhabiting boreal forests (Thingstad et al. 2003). Our long-term data support a negative trend in the Siberian jay population occupying managed forests. The response heterogeneity amongst life-history stages to forestry management highlights the importance of considering a population's social structure in formulating species-specific management plans. Declining population growth in managed forests reflects the generally reduced reproductive rate and increased breeder mortality. Given that both vital rates are decreased by a less dense forest structure, future management plans need to re-consider the use of thinning practices. Forest management in Finland demonstrates that it is possible to combine commercial forestry with a more diverse forest structure (Mielikäinen and Hynynen 2003). Many boreal species would benefit from increased habitat heterogeneity (Mielikäinen and Hynynen 2003), more similar to that of old forest patches, making Siberian jays an umbrella species to demand more sustainable forestry, and thereby ensuring their future population



persistence. Conservation of remaining natural forests would also be beneficial, since they can act as sources of individuals through dispersal (Nystrand et al. 2010).

Climate change adds further complexity to this system by interacting with the effects of habitat degradation to influence vital rates, and consequently population dynamics. In our model of long-term population dynamics, climate change exacerbated the effect of forestry, putting further emphasis on the impact of forestry on vulnerable populations. In conclusion, we argue that explicit consideration of social structure and interacting environmental factors is necessary to determine a population's vulnerability to habitat degradation and for effective conservation planning. For instance, the greater relative importance of dispersed juveniles for population growth, compared to retained juveniles, indicates the importance of habitat connectivity that facilitates dispersal between territories. This in-depth understanding of the system contributed to identifying conservation measures, specifically in identifying the disproportionate effect of forestry on breeding individuals that would effectively increase growth of Siberian jay populations, and other species with similar ecological requirements, occupying managed boreal forests.

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## Author contribution statement

MG collected the data; KLM and AO analysed the data; KLM wrote the manuscript; AO and MG assisted in writing and revising the manuscript.

## Compliance with ethical standards

*Data accessibility* Data used in this study will be submitted to Dryad.

## Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary material 1 (PDF 345 kb)

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