

LONG TERM STUDY

Large-scale importance of bark beetle outbreaks for standing deadwood and woodpeckers

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Funding information

WSL Internal Innovative Project; Swiss Ornithological Institute Sempach

Handling Editor: Catherine Parr

Abstract

1. Resource pulses associated with forest disturbances can significantly influence biological communities, with interacting and sometimes lagged effects on species numbers. Among the most common disturbances in temperate forests are bark beetle outbreaks, which represent a resource pulse and initiate additional resource pulses of other insects and of deadwood. Moreover, bark beetle outbreaks are often followed by changes in habitat conditions due to canopy cover loss or salvage logging that can have contrasting effects on co-occurring forest species. However, the effects of this multi-resource pulse on forest species have rarely been quantified simultaneously.
2. Here, we investigated if and to what extent changes in woodpecker population density were related to resource pulses, specifically spruce bark beetle and standing dead wood of Norway spruce. We used data from long-term monitoring projects collected across Switzerland from 1984 to 2020 to build a network model that estimated relationships among species and resources.
3. We built a semi-mechanistic model that included structured equations of parameters of interest. The equations modelled Norway spruce standing deadwood volume, bark beetle density and density of three woodpecker species as a function of their interactions, as well as climatic, environmental and management variables. The model allowed both same-year and 1-year lagged effects.
4. We found weak relationships between bark beetle outbreaks and woodpecker densities, and strong positive relationships between deadwood amount and woodpecker densities. In turn, standing deadwood was strongly linked to bark beetle outbreaks, highlighting the indirect role of bark beetles in promoting woodpecker populations by means of providing deadwood for foraging and nesting. Salvage logging, that is, the removal of trees infested by bark beetles, had only minor effects on bark beetles.

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5. Bark beetle outbreaks contributed to the generation of deadwood that ensured the continuity of its associated ecosystem functions, which benefited woodpeckers and, potentially, forest biodiversity as a whole. Large-scale consequences of these multi-resource pulses were reflected by species populations over longer time periods than the pulses.

KEYWORDS

Bayesian model, disturbance, forest inventory, *Ips typographus*, long-term monitoring, network model, *Picoides*, resource pulse, woodpecker

1 | INTRODUCTION

Resource pulses quickly increase resource availability and are among the most influential ecosystem processes, affecting biological communities potentially over long periods (several years) and large geographical areas. Resource pulses usually elicit responses in species in different ways, depending on the amount and type of the resource released in space and time (Crook et al., 2020; Holt, 2008; Jentsch & White, 2019). The pulse frequency can affect species over short or long periods of time, with species' responses modulated by their behaviour and life history traits. In particular, a numerical response, such as an increase in population density, is commonly observed over short periods, whereas a functional response, such as an increase in reproductive output, takes more time to occur (Yang et al., 2010). Sometimes, resource pulses are linked with natural disturbances, such as insect outbreaks, and result in spatiotemporal changes of habitat structure and composition (Jentsch & White, 2019). However, if and how changes in resources and habitat interact to elicit different responses in species has rarely been quantified.

Bark beetles are one of the most common disturbances in northern hemisphere forests, and their outbreaks represent intermittent resource pulses for their predators (Anderegg et al., 2015; Hicke et al., 2016; Wermelinger, 2004). Furthermore, bark beetle outbreaks result in extensive tree mortality, which generates a resource pulse of standing deadwood. Although deadwood can last for years in forests, its suitability as resource for different species depends on specific decay stages (Rajala et al., 2011) that are reached later than the initial pulse of bark beetles. Thus, bark beetle outbreaks trigger a series of ecological processes influencing forest structure and biological communities over variable time spans (Franklin et al., 1987; Müller et al., 2008; Thorn et al., 2020).

Among the species greatly affected by these pulses, woodpeckers are a special case as their populations can respond to both pulses in bark beetles and related standing deadwood (Koplin, 1972; Saab et al., 2019; Tingley et al., 2020). Woodpecker populations may respond directly to the increase in bark beetles with short-term changes (within a few years) in abundance or occurrence (Edworthy et al., 2011; Kelly et al., 2019), and indirectly due to the longer-lasting increased availability of nesting and feeding substrates (i.e. standing dead and dying trees) (Hastings et al., 2007; Robles &

Martin, 2014; Thorn et al., 2020; Trzcinski et al., 2022). Therefore, bark beetle outbreaks represent an excellent model for examining the importance of concurring resource pulses on animal populations over time.

The complex network of biotic interactions linked with bark beetle multi-resource pulses can also be subject to human influences (Bollmann et al., 2020). In managed forests, the potential benefits of bark beetle outbreaks for animal populations are often not realised because of salvage and sanitation logging (Basile et al., 2023; Müller et al., 2019; Thorn et al., 2018; Wermelinger et al., 2017). Salvage logging is practised to make use of timber damaged by bark beetles or other disturbances such as wind-throws before decomposition begins, while sanitation logging is practised to mitigate bark beetle outbreaks.

Here, we investigated if and to what extent the population density of woodpeckers is related to the multi-resource pulses of prey (i.e. spruce bark beetles) and deadwood (i.e. Norway spruce *Picea abies*). Specifically, we addressed the following three hypotheses by means of a hierarchical semi-mechanistic network model (Figure 1) that identified direct and indirect relationships between woodpecker populations and bark beetle outbreaks:

1. *Bark beetle pulse hypothesis*: Bark beetle outbreaks may have short-term direct effects on woodpecker populations as a result of increased prey density, which may promote woodpecker populations locally (Bonnot et al., 2009; Edworthy et al., 2011; Saab et al., 2019). Thus, we expected woodpecker population density to increase with bark beetle density (i.e. bark beetle outbreaks). In the following years, we expected lagged positive effects as beetle-killed trees are colonised by other saproxylic insects that develop in later successive stages of deadwood decomposition (Thorn et al., 2020). Hence, the increase in prey abundance may have prolonged benefits for woodpeckers.
2. *Standing deadwood pulse hypothesis*: Standing deadwood promotes woodpecker populations by providing feeding and nesting substrates (Angelstam & Mikusiński, 1994; Bütler et al., 2013). Although these effects are well documented, salvage logging can limit the benefits of resource pulses to woodpeckers (Basile et al., 2023). Thus, we expected woodpecker population density to increase with increasing volume of spruce standing deadwood in the longer term, due to the long-term provisioning of

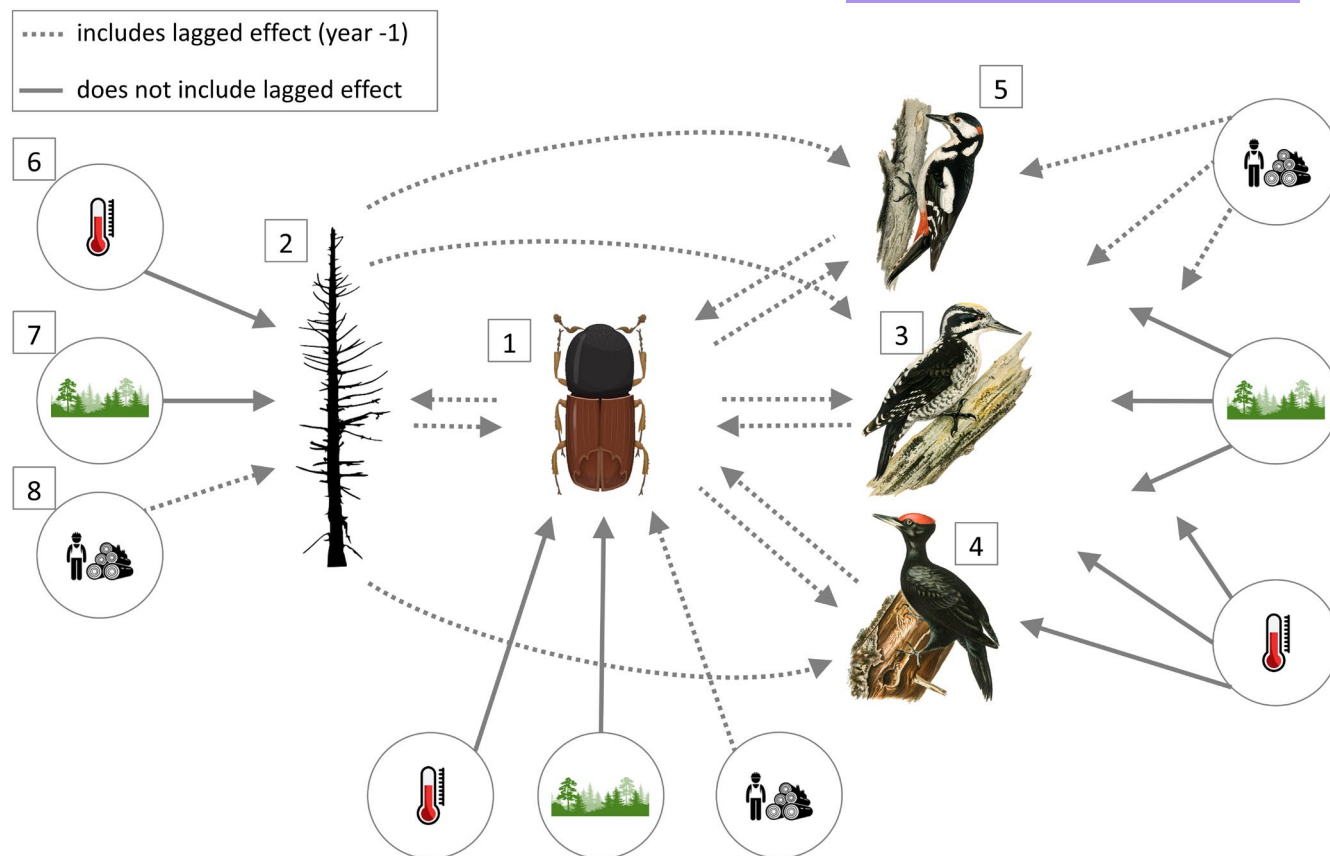


FIGURE 1 Concept of the spruce-bark beetle-woodpeckers interaction network. The network includes five parameters of interest: (1) spruce bark beetle density, (2) Norway spruce standing deadwood volume, and (3, 4, 5) woodpecker densities, including three-toed woodpecker, black woodpecker and great spotted woodpecker, respectively. Each parameter of interest is modelled as a function of the other parameters according to the hypothesised paths which are shown by the arrows. Arrows from (1) to (2–5) represent the effects of bark beetle density on spruce standing deadwood and woodpeckers. Arrows from (2–5) to (1) represent the effects of spruce standing deadwood and woodpeckers on bark beetles. Further variables influencing the network are (6) climatic variables, (7) environmental variables and (8) management variables. For the list of variables, see Table 1. Some relationships include both same-year and one-year lagged effect.

resources. We also expected woodpecker population density to decrease with the removal of deadwood due to salvage and sanitation logging. Aside from effects on woodpecker populations, we also expected a lagged effect of spruce standing deadwood on bark beetle density as bark beetles tend to spread from previous infestation spots to the surroundings, thereby creating new infestations and additional standing deadwood (Kautz et al., 2011; Lausch et al., 2011; Stadelmann, Bugmann, Meier, et al., 2013).

3. *Interaction hypothesis*: Bark beetle outbreaks generate pulses in spruce standing deadwood (Wermelinger, 2004), thus connecting the two resource pulses. Although we assumed positive relationships in the previous hypothesis, standing deadwood volume and bark beetle density may interact to generate non-linear responses in woodpecker population densities. For instance, the benefits for woodpeckers may be halted at high bark beetle density, where environmental changes related to outbreaks (e.g. canopy cover loss) and woodpecker territoriality (i.e. the finite number of territories that can fit in a given area) prevent further increases in density (Zielewska-Büttner et al., 2018).

To test our hypotheses, we built a network with data on spruce standing deadwood, bark beetle populations and woodpecker populations from Swiss nationwide datasets spanning multiple decades. We assessed the relationship between bark beetles and woodpeckers, and the correlation of their temporal dynamics.

2 | MATERIALS AND METHODS

2.1 | Study area

Our data covered the entire territory of Switzerland and spanned up to 37 years (1984–2020 for bark beetles and 1999–2020 for woodpeckers, see below for details). The Swiss Forest Protection Service divides Switzerland into management units, following a hierarchy that encompasses cantons and districts, where it conducts annual surveys of bark beetle infestations (see Supporting Information for the further details on the study area and bark beetle dynamics). The administrative boundaries of multiple districts, as well as the number of districts, changed over the years

TABLE 1 Summary of model parameters and variables used to build the spruce–bark beetle–woodpecker network.

Response variables (N)	Endogenous variables		Exogenous variables		
	Random	Spatiotemporal	Climate and environment	Species**	Management
DW (1480)	Regions=40 levels	Spatial CAR [†]	T_{mean}	$DW^j \leftarrow BB^{j-1}$	Z (volume of
BB (1480)	Years=37 levels*	Non-parametric CRP [‡]	T_{min}	$DW^j \leftarrow BB^j$	infested wood
BW, GSW, TTW (880×3)		Temporal correlation with previous year	T_{max}	$BW^j \leftarrow BB^{j-1}$	removed)
		Spatiotemporal interaction [§]	Rhires	$BW^j \leftarrow BB^j$	G (volume of
			Srel	$BW^j \leftarrow DW^{j-1}$	infested wood left
			Forest type	$BW^j \leftarrow DW^j$	in the forest)
			Spruce occurrence [¶]	$BB^j \leftarrow DW^{j-1}$	N (number of
			Stand age	$BB^j \leftarrow DW^j$	infestation spots)
			Elevation	$BB^j \leftarrow BW^{j-1}$	
			LDW [#]	$BB^j \leftarrow BW^j$	

Note: Variables shown in table columns are independent of table rows. j and $j - 1$ refer to year; $\leftarrow$ points at the response variable. See Table S1 for other abbreviations. Each response variable is modelled using a different set of endogenous and exogenous variables.

Abbreviations: BB, bark beetle density; BW, black woodpecker density; CAR, Gaussian conditional autoregressive process; CRP, Chinese restaurant process; DW, spruce standing deadwood volume; GSW, great spotted woodpecker density; TTW, three-toed woodpecker density.

*Twenty-two levels were considered for the woodpecker sub-models.

[†]NIMBLE Development Team (2021); Rue and Held (2005).

[‡]de Valpine et al. (2017); Escobar and West (1995).

[§]Lawson (2020).

^{||}Waser and Ginzler (2021). Used to model BW and GSW.

[¶]Wüest et al. (2020a). Used to model DW, BB and TTW.

[#]Used to model BB and all woodpeckers.

**The first and last four interactions are included in separate models. The two in the middle are included in both models. Only BW is mentioned but interactions are the same for GSW and TTW.

making an accurate spatial assignment of the data challenging. To account for this, we divided Switzerland into 40 regions of variable size (Figure S1), corresponding to current administrative borders and aggregated the data by region and calendar year for our analyses. The mean forest area of these regions was 248 km² (±232 SD).

2.2 | Model implementation

We built a semi-mechanistic model that included structured equations of parameters of interest and allowed interactions among them (Grace et al., 2012; Joseph et al., 2016; Kéry & Royle, 2021). The model network included Norway spruce standing deadwood volume, bark beetle density and woodpecker density as parameters of interest, as well as a set of additional climatic, environmental and management variables. The hypothesised relationships are shown in Figure 1. The network allowed both same-year and one-year lagged effects; the occurrence of lagged effects was suggested in previous research on bark beetles in the same area (Stadelmann, Bugmann, Wermelinger, et al., 2013). Thus, we structured five equations as Bayesian linear mixed-effects models (Knorr-Held, 2000; Napier et al., 2019) with a set of predictor variables describing the endogenous and exogenous variability in the response (de Valpine et al., 2017; Lawson, 2020). We describe below all model variables and provide further details in the Supporting Information.

2.2.1 | Parameters of interest

Our first parameter of interest was Norway spruce standing deadwood, which is the main host tree for *Ips typographus* bark beetles (Wermelinger, 2004). Deadwood data were extracted from the Swiss National Forest Inventory (NFI), which consisted of inventory campaigns carried out since 1983 on a total of 2910 permanent plots (500m²) (Abegg et al., 2020, 2023) (Figure S4). Spruce bark beetle data were collected by the Swiss Forest Protection Service by means of annual surveys with pheromone traps at 834 forest districts since 1984 (Figure S4). The data consisted of sums of annual beetle counts per region, divided by the number of traps deployed each year in the region to obtain bark beetle (BB) density. We selected for our analysis the black woodpecker *Dryocopus martius* (BW), the great spotted woodpecker *Dendrocopos major* (GSW) and the three-toed woodpecker *Picoides tridactylus* (TTW), according to their traits and their potential use of bark beetles and spruce standing deadwood as resources. The TTW is a spruce/conifer specialist, whose diet can be dominated by bark beetle adults and larvae (Fayt, 1999; Pecachek & Křištín, 2004). The TTW prefers to forage on and nest in live and dead spruce trees (Czeszczewik & Stański, 2024; Pakkala et al., 2018; Versluijs et al., 2020). The TTW does not occur in the Central Plateau and most of the Jura Mountains, despite the occurrence of planted Norway spruce and bark beetle outbreaks. On the other hand, BW and GSW occur across all of Switzerland and are less specialised on conifers. The BW use of conifer forest is mostly linked to the abundance of their

main food, carpenter ants, which are often abundant in young forest stands (Bocca et al., 2007; Rolstad et al., 1998). It nests preferentially in large beech trees (De Rosa et al., 2016; Puverel et al., 2019; Zahner et al., 2012) but can switch to conifers in conifer-dominated forests (Zawadzki, 2023). The GSW forages on various tree species year-round in search of arthropods and mainly on spruce and other conifer species in winter to extract seeds from cones (Dylewski et al., 2017; Stański et al., 2023). The GSW is a generalist in the choice of the nest tree species, usually preferring broadleaf trees (Ćiković, 2014; Kosiński & Winiecki, 2004; Pasinelli, 2007). However, it can select spruce forests as breeding habitat, especially when rich in snags, and can rarely use spruce as nest tree (Hebda et al., 2017; Löhmus et al., 2010; Rolstad et al., 1995). Since 1999, woodpecker data are collected annually within the framework of the common breeding bird monitoring programme led by the Swiss Ornithological Institute (Knaus et al., 2021). The data are collected using territory mapping repeated three times per year (twice above the treeline) during the breeding season at 267 one-km² squares (Figure S4). Data are then collated to return the number of territories per species and square, after a post-hoc data revision to fix potential sampling biases (see Supporting Information for further details). The data included in the model were aggregated for each of the 40 regions. A total of 20,051 territories were counted in the period 1999–2020: 16,762 (83.6%) for GSW, 2996 (14.9%) for BW and 293 (1.5%) for TTW.

2.2.2 | Predictor variables

Our set of predictor variables described the (1) biotic interactions, (2) the climatic and environmental conditions and (3) the management via salvage logging (Table S1).

Biotic interactions were modelled by adding latent parameters of interest in the equations (Basile et al., 2021; Kéry & Royle, 2021). We assumed that this statistical interaction was a proxy of a real-world biotic interaction and considered same-year and 1-year lagged interactions. Following our hypothesised network paths (Figure 1), we considered two models describing the effects of bark beetles on standing deadwood and woodpeckers (Model 1) and, vice versa, the effects of standing deadwood and woodpeckers on bark beetles (Model 2). The effects of woodpeckers on bark beetles were modelled including both single species and summed densities (BW + GSW + TTW).

The second set of variables described the climatic and environmental conditions. The effect of climate was included as temperature, precipitation and sunshine duration (source: MeteoSwiss). The forest landscape was described using forest type (conifer/broadleaf) and Norway spruce occurrence (Waser & Ginzler, 2021; Wüest et al., 2020a). The model also included the mean age of forest stands and the volume of lying deadwood, both derived from the NFI. The last environmental variable considered was elevation, extracted from the swissALTI3D model (source: swisstopo).

The last set of variables described management via salvage logging. Three variables were included in the model: the volume of

infested wood removed; the volume of infested wood left in the forest; and the number of groups of 10 or more infested trees (labelled as bark beetle infestation spots).

2.3 | Model specification

According to our research hypotheses, we evaluated the network's paths to assess whether woodpecker density responds positively to bark beetle densities and to spruce standing deadwood volume, and to quantify the influence of salvage logging on all parameters.

We built the null model (see Supporting Information for the null model parameterization) with a random error level for each region and year, a spatial variability term that accounted for correlation among neighbouring regions, a temporal variability term that accounted for year-to-year dependence in the estimates and a spatiotemporal interaction term that accounted for clustering of parameters of interest in space and time (Table 1).

The parameters of interest were log-scaled (a minimal quantity of 0.001, was added to scale 0 values), and modelled assuming a normal distribution:

$$Y_{ij} \sim \text{Normal}(Y_{ij}, \sigma^Y) \quad (1)$$

where y represents the value of a parameter of interest (one of DW, BB, BW, GSW or TTW) observed at region i in year j , that follows a normal distribution with latent mean Y_{ij} and standard deviation σ . The latent response variable Y was modelled as follows:

$$Y_{ij} = \beta_0 + \theta_{ij} + E_{ij} \quad (2)$$

$$Y_{ij} = \beta_0 + rs_i + rt_j + s_i + t_j + st_{ij} + E_{ij} \quad (3)$$

where β_0 indicates the intercept of the model, θ represents the endogenous variability and E represents exogenous variability. θ was further partitioned into region and year random levels, rs and rt , plus the spatial and temporal variability s and t and the spatiotemporal interaction term st .

2.4 | Model selection

We included predictor variables in each equation according to our hypothesised paths to obtain the above-mentioned Model 1 and Model 2 (Table 1; Figure 1). We applied a variable selection procedure to characterise the exogenous variability, using predictor variables scaled and centred to 0. We selected variables in both models by retaining only those with equal-tailed credible intervals not overlapping 0 for >90% of the posterior distribution ($f > 0.9$). Models 1 and 2 were then compared to the null model (including only endogenous variables) via mean squared error (MSE) and the Bayesian R^2 (see Supporting Information for model diagnostics). The MSE was calculated from a 10-fold cross-validation and measured the difference between observed and predicted values, with

lower MSE indicating better predictive performance (de Valpine et al., 2021). The Bayesian R^2 ranges from 0 to 1 and measures the expected proportion of variance explained by the model when making predictions based on new data, including the full posterior prediction uncertainty (Gelman et al., 2019).

2.5 | Model assessment

We assumed uninformative prior distributions for all parameters of interest and variables. The models were built using R v. 4.1 (R Core Team, 2021) and the package 'nimble' (de Valpine et al., 2021), and posterior distributions were sampled with the default MCMC algorithm. The MCMC ran one chain of 220,000 samples, with the first 20,000 discarded. The Metropolis–Hastings sampler implemented by the package 'nimble' does not require multiple chains; thus, chain convergence was assessed by visualising the posterior distribution of the samples of any given parameter and by calculating the Geweke Z-scores (Geweke, 1992; Ponisio et al., 2020). To assess the presence of potential missing paths in the network, which may result in a poor fit, we evaluated residual correlations among parameters of interest (Grace et al., 2012; Joseph et al., 2016).

2.6 | Model inference

Model 1 differed from Model 2 regarding the inclusion of an indirect path from bark beetle density to woodpecker density via standing deadwood. Hence, we used model 1 to estimate the total effect of bark beetles on woodpeckers, including both direct and indirect effects, using a generalised additive mixed-effect model (GAMM) built with the R package 'mgcv' (Wood, 2018). The GAMM can estimate the effect of a variable by using flexible smooth functions with shape determined by the data and not restricted to a specific form (Hastie & Tibshirani, 1990). The degrees of freedom of the smooth represent loosely the number of parameters used to fit the function (Fewster et al., 2000). Higher degrees of freedom allow non-linear trends and can be specified to reflect hypothesised relationships (Zuur et al., 2009). We modelled the relationship between the density of woodpeckers and bark beetles by allowing 22 degrees of freedom to approximate the time period (years) of the data. We included the year as a random effect. We assessed the convergence of the smooth using the function 'gam.check'. The resulting diagnostic was significant for black woodpecker ($k\text{-index}=0.92$, $p=0.01$) and the residuals indicated a good fit (Figure S9). The higher predictive power of the smooth was also indicated by the adjusted $R^2=0.5$. The diagnostic for the three-toed woodpecker was acceptable ($k\text{-index}=1.04$, $p=0.81$), but the residuals were not ideal (Figure S9) and the adjusted- $R^2=0.09$ indicated lower predictive power. Finally, we assessed for how many years bark beetle density and spruce standing deadwood volume correlated with woodpecker densities. We used multivariate rolling window correlation coefficients to assess changes in correlations of woodpecker densities with bark

beetle density and spruce standing deadwood volume across all years. We used the estimated parameters of interest from Model 1 and measured Pearson correlations ($r>0.7$) with corrected p values for multiple observations and time windows using the R package 'RoWinMulCor' (Polanco-Martínez, 2020).

3 | RESULTS

The two models describing the network of relationships between bark beetle, spruce standing deadwood and three species of woodpeckers indicated several significant relationships (Figure 2) and a high explanatory power (see Supporting Information for model diagnostics).

3.1 | Bark beetle pulse hypothesis

The densities (number of territories per region) of black woodpecker (BW) and three-toed woodpecker (TTW) were related to bark beetle (BB) density pulses (Figure 2a), whereas the density of great spotted woodpecker (GSW) was not. We found a positive relationship between the densities of BW and BB in the same year (Model 1, 0.06 ± 0.03 SD, $CI_{90\%}=0.007\text{--}0.1$; Figure 3a; Figure S2). In contrast, the densities of both BW and TTW were negatively related to BB from the previous year (Model 1, -0.08 ± 0.04 SD, $CI_{90\%}=-0.14$ to -0.02 , Figure 3b; Table S2; Model 1, -0.09 ± 0.03 SD, $CI_{90\%}=-0.14$ to -0.03 , Figure 3c; Table S2). The density of BW was also positively related to forest type (Model 1, 0.69 ± 0.25 SD, $CI_{90\%}=0.28\text{--}1.12$) and negatively to the volume of lying deadwood (Model 1, -0.16 ± 0.08 SD, $CI_{90\%}=-0.3$ to -0.02). Contrary to our expectation, BB was positively related to BW density in the previous year (Model 2, 0.45 ± 0.21 SD, $CI_{90\%}=0.1\text{--}0.81$; Table S3).

3.2 | Standing deadwood pulse hypothesis

The densities of BW, GSW and TTW were influenced by the pulses of spruce standing deadwood volume (Figure 2). In particular, the density of the BW showed a positive relationship with spruce standing deadwood both in the previous (Model 1, 0.47 ± 0.14 SD, $CI_{90\%}=0.24\text{--}0.71$; Figure 4a; Table S2) and in the same year (Model 2, 0.5 ± 0.17 SD, $CI_{90\%}=0.22\text{--}0.77$; Table S3). Similarly, TTW showed a positive relationship with spruce standing deadwood in the previous (Model 2, 0.37 ± 0.2 SD, $CI_{90\%}=0.06\text{--}0.67$; Table S3) and in the same year (Model 1, 0.6 ± 0.19 SD, $CI_{90\%}=0.18\text{--}0.89$; Figure 4b; Table S2). In contrast, the density of GSW was negatively related to spruce standing deadwood volume in the same year (Model 2, -0.21 ± 0.12 SD, $CI_{90\%}=-0.39$ to -0.02 ; Table S3).

As expected, BB was positively related to spruce standing deadwood in the previous year (Model 2, 0.76 ± 0.28 SD, $CI_{90\%}=0.31\text{--}1.23$; Table S3). Furthermore, BB was negatively related to the volume of infested wood left standing in the same year (Model 1,

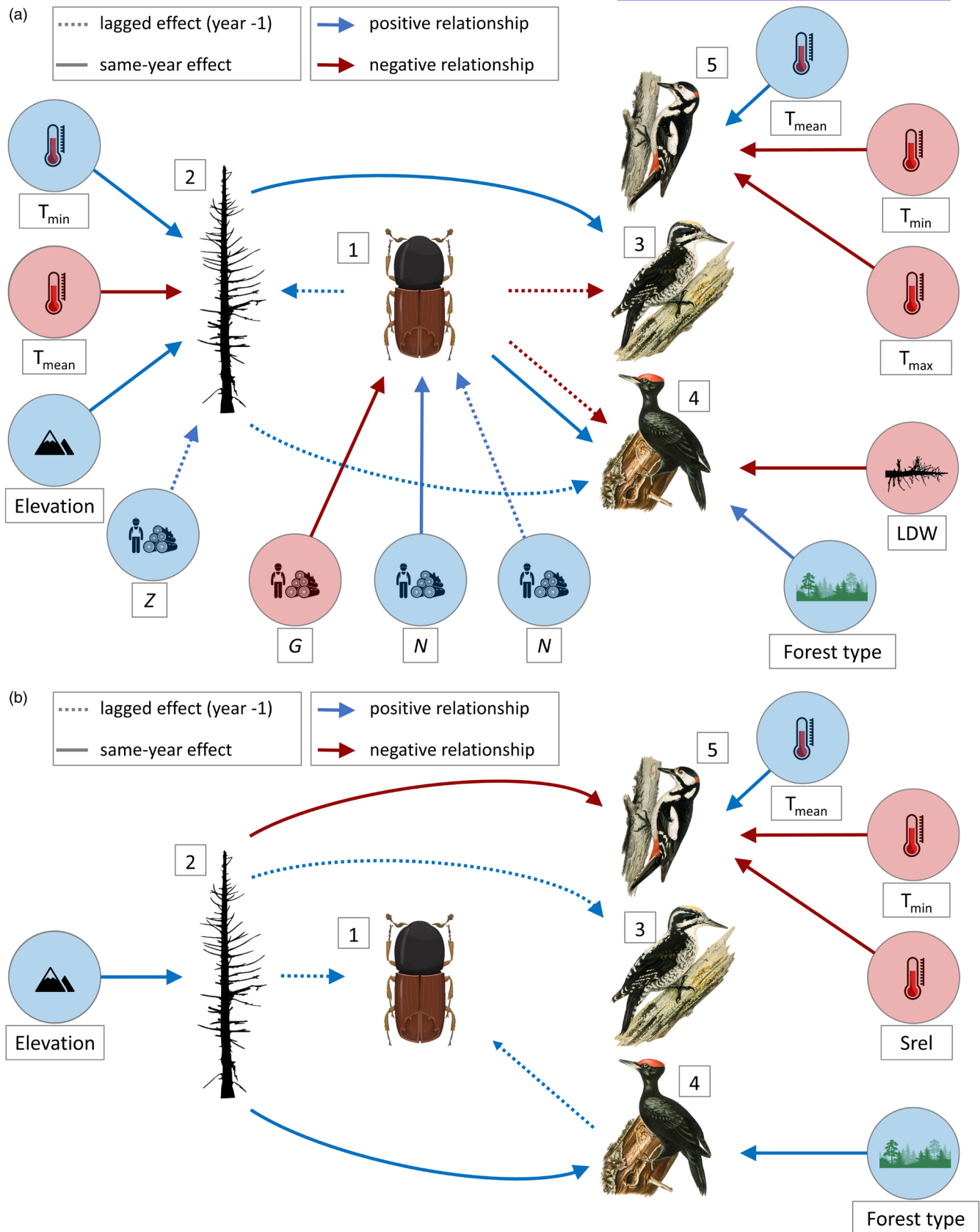


FIGURE 2 Significant network paths found by Models 1 (a) and 2 (b). Model 1 (a) included the effect of bark beetle density on spruce standing deadwood and on woodpecker density. Model 2 (b) included the effects of spruce standing deadwood and woodpecker density on bark beetle density. Arrow colours indicate negative (red) or positive (blue) relationships, arrow type indicates 1-year lagged (dotted) and same-year (continuous) effects. G, volume of infested wood left; N, number of infestation spots; $T_{\max}$, maximum temperature; T_{mean} , mean temperature; $T_{\min}$, minimum temperature; Srel, duration of relative sunshine; Z, volume of infested wood removed.

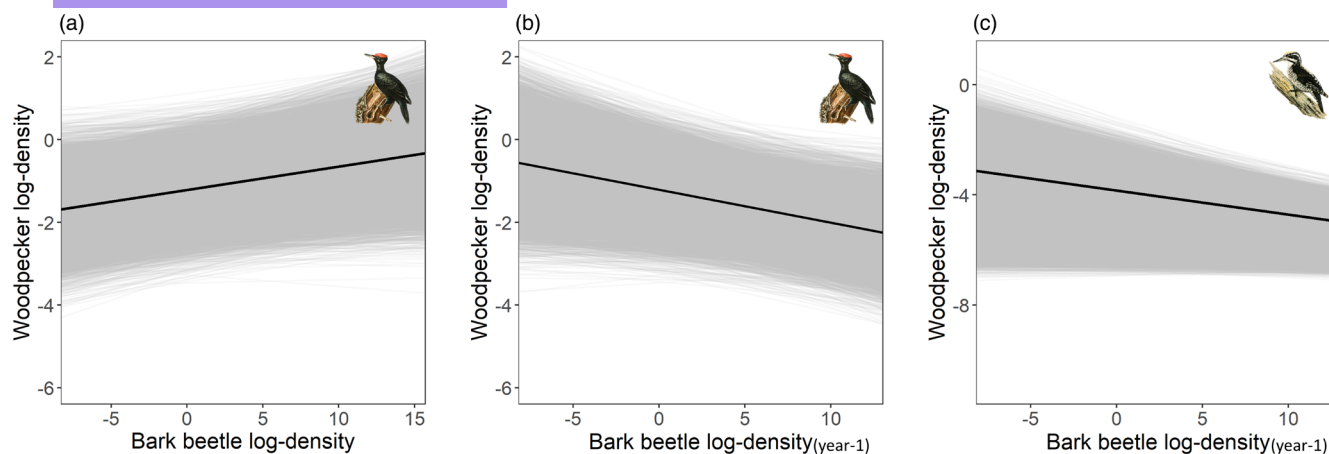


FIGURE 3 Relationships of woodpeckers with bark beetle density. Relationships of (a) black woodpecker with bark beetle density in the same year, and of (b) black woodpecker and (c) three-toed woodpecker density, respectively, with bark beetle density in the previous year (*year-1*) from Model 1. The continuous line indicates the effect when all other variables are set to their mean values, with shaded areas showing the full posterior distribution. The relationships are estimated over 22 years. $N=880$.

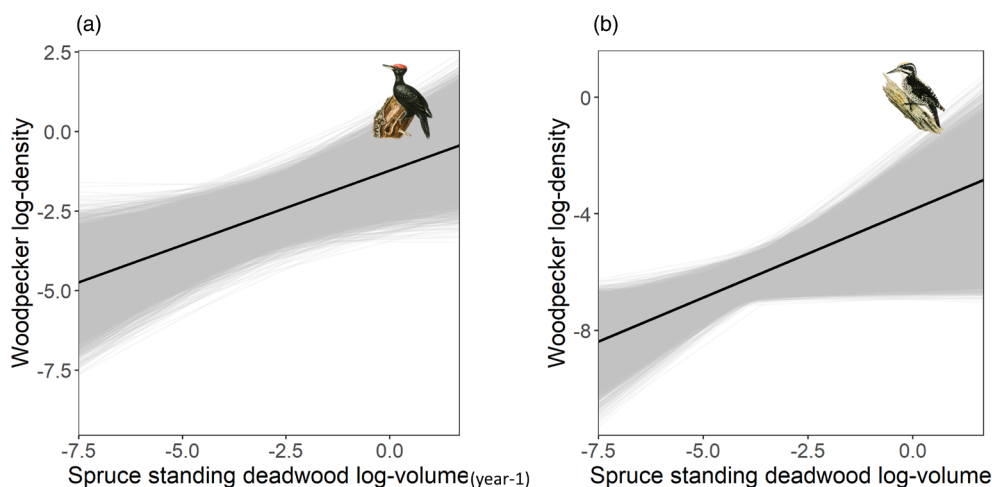


FIGURE 4 Relationships of woodpeckers with spruce standing deadwood. Relationships of (a) black woodpecker and (b) three-toed woodpecker density with spruce standing deadwood volume in the previous year (*year-1*) and in the same year from Model 1. The continuous lines indicate the relationships when all other variables were set to their mean values, with shaded areas showing the full posterior distribution. The relationships are estimated over 22 years. $N=880$.

-0.20 ± 0.11 SD, $CI_{90\%} = -0.38$ to -0.02) and positively related to the number of BB infestation spots both in the previous (Model 1, 0.39 ± 0.13 SD, $CI_{90\%} = 0.18$ – 0.6) and in the same year (Model 1, 0.47 ± 0.14 SD, $CI_{90\%} = 0.24$ – 0.71).

3.3 | Interaction hypothesis

Spruce standing deadwood volume was positively related to the density of BB in the previous year (Model 1, 0.11 ± 0.02 SD, $CI_{90\%} = 0.08$ – 0.15 ; Table S2) and to the volume of infested wood removed in the previous year (model 1, 0.13 ± 0.05 SD, $CI_{90\%} = 0.05$ – 0.22 ; Table S2). Other variables with credible relationships to spruce standing deadwood were elevation (model 1, 1.52 ± 0.24 SD, $CI_{90\%} = 1.14$ – 1.92 ; Table S2; model 2, 1.17 ± 0.22

SD, $CI_{90\%} = 0.8$ – 1.56 ; Table S3), annual mean temperature (model 1, -0.97 ± 0.44 SD, $CI_{90\%} = -1.77$ to -0.29 ; Table S2) and annual minimum temperature (model 1, 1.4 ± 0.5 SD, $CI_{90\%} = 0.64$ – 2.34 ; Table S2). The net relationship of BW with BB, including the indirect effects mediated via interaction with spruce standing deadwood volume, was overall positive (cubic smooth: 21 df, $F=48.6$, $p<0.01$). In particular, the relationship became steeper for high bark beetle densities, above tens of thousands (Figure 5). The net relationship of TTW with BB, instead, was strongly positive only within a particular range of bark beetle densities (cubic smooth: 21 df, $F=4.3$, $p<0.01$). At low bark beetle density (below hundreds of individuals), TTW was not related to BB (Figure 5). At medium density, between hundreds and tens of thousands of bark beetles, TTW increased and then plateaued when BB reached hundreds of thousands.

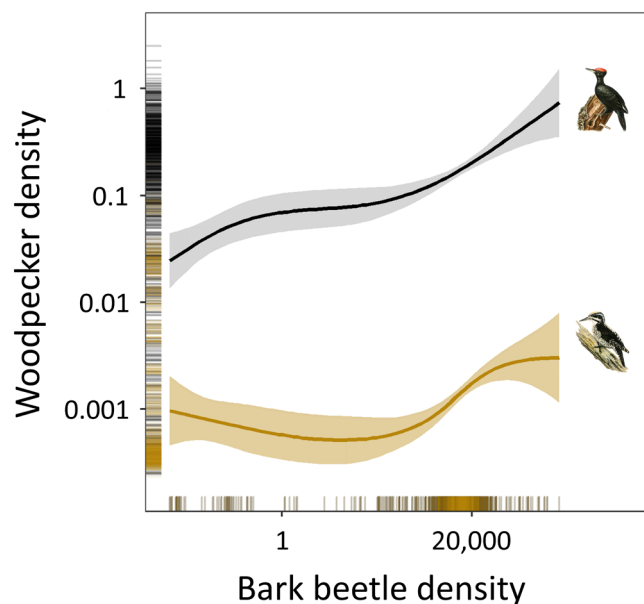


FIGURE 5 Total response of woodpeckers to bark beetle density on log scales. Relationship of black woodpecker (black line) and three-toed woodpecker (orange line) density (number of territories per region) with bark beetle density, with 95% confidence intervals (shading) and individual data points (rugs, $N=880$). The relationships are based on the posterior estimates of Model 1 across 22 years and account for the indirect effects of bark beetle density via spruce standing deadwood.

3.4 | Spatiotemporal network dynamics

The temporal variation of spruce standing deadwood, bark beetle density and woodpecker densities in Switzerland showed marked differences across regions, with some regions having more congruent temporal patterns among parameters of interest than others (Figure S11). In mountain regions, for instance, the pulses of bark beetle density and spruce standing deadwood after the exceptional windstorms in the years 1999–2000 and the summer heat in 2003 coincided with increases in woodpecker densities (Figure 6, panels BE_04, GR_03). In the lowlands, however, we observed a less marked congruence in the spatiotemporal dynamics (Figure 6, panels BS, ZH).

Over the entire country, black woodpecker density was correlated ($r > 0.7$, $p < 0.05$) with bark beetle density and spruce standing deadwood within time windows spanning 9 years after the beginning of the time series in 1999 (Figure S12). For the three-toed woodpecker, instead, correlations were observed over the entire period, stronger within seven years at the beginning of the time series, and slightly decreasing for longer time windows (Figure S13).

4 | DISCUSSION

Woodpecker populations were directly and indirectly related to bark beetle outbreaks. The largest effect on woodpeckers was delivered by the pulse in spruce standing deadwood linked to the pulse of bark

beetles. Our three hypotheses were supported to varying degrees for two of the three woodpecker species.

4.1 | Bark beetle pulse hypothesis

We found the expected positive relationship between black woodpecker density and bark beetle density in the same year. We also unveiled negative relationships between black woodpecker and three-toed woodpecker densities, respectively, and bark beetle density in the previous year. Despite these partly contrasting relationships, we confirmed that pulses of bark beetles have direct effects on woodpecker density, although the effect was not consistent among species (and lacking for great spotted woodpecker). Thus, our results are partly in line with findings from several small-scale studies that documented increases in the abundance of other woodpecker species during or in the aftermath of bark beetle outbreaks (Baldwin, 1968; Bonnot et al., 2009; Bull, 1983; Saab et al., 2019). As woodpeckers are mostly resident species, they may experience temporary population increases in bark beetle-infested forests, as they rely on overwintering bark beetle adults and larvae for survival (Koenig, 1984; Ricklefs, 1980). Despite this, we observed only a weak direct response to bark beetle pulses that did not translate into a large-scale increase of density. Other studies showed that large bark beetle outbreaks can modify the forest conditions so that woodpeckers may actually avoid the heavily infested forests due to negative effects of canopy cover loss, such as increase in predation risk or decrease in forest structural complexity (Kebrel et al., 2022; Zielewska-Büttner et al., 2018). Finally, we did not find evidence that woodpecker populations could affect bark beetle density measurably at the scale of the study.

4.2 | Standing deadwood pulse hypothesis

Our findings showed that the availability of spruce standing deadwood promotes woodpecker populations, for two out of the three species studied. Rather than a response to the pulse of bark beetles, we observed a strong increase of woodpecker density with the pulse of deadwood. This stronger response is likely driven by the increase of deadwood-inhabiting insects and other invertebrates that gradually change with decay stages over time (Parisi et al., 2018; Saint-Germain et al., 2007). Recently disturbed forests are recognised as key sites for birds due to the sequence of insect colonisations on damaged, dying and dead trees (Czeszczewik et al., 2013; Thorn et al., 2020; Versluis et al., 2022). In addition, dead and decaying trees improve nesting opportunities for woodpeckers (Gutzat & Dormann, 2018). Even after accounting for the effect of salvage logging, the beneficial effects provided by spruce standing deadwood persisted at the large spatiotemporal scale of the study. At smaller spatial scales, post-disturbance removal of deadwood can have detrimental effects on woodpecker populations probably due to the combined effects of prey

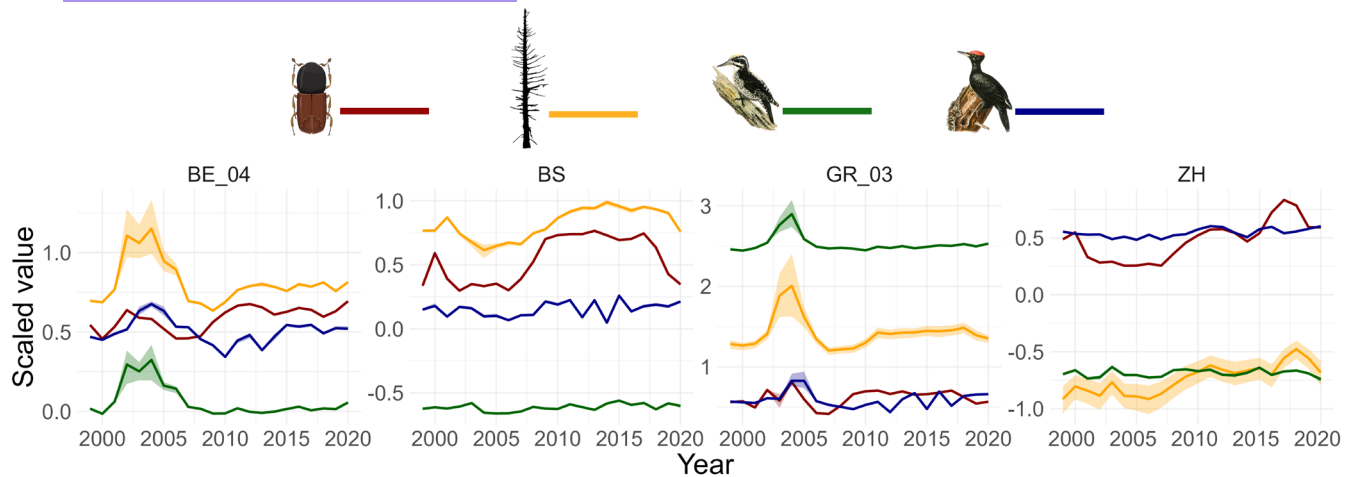


FIGURE 6 Estimated temporal patterns of the spruce standing deadwood–bark beetle–woodpeckers network. Annual variation in bark beetle density (red line), spruce standing deadwood volume (orange line) and density of three-toed woodpecker (green line) and black woodpecker (blue line) in selected regions of Switzerland (temporal trends for all regions are shown in [Figure S11](#)). Region names on top of each panel follow Swiss cantonal abbreviations (BE_04, Berne region 4; BS, Basel city; GR_03, Grisons region 3; ZH, Zurich; note, three-toed woodpecker does not occur in BS and ZH, thus the model provided some estimates oscillating around minimal values). Values on the y-axis are scaled to enhance comparison among parameters. Shading represents 90% credible intervals.

reduction and nest site removal as well as habitat modification (Basile et al., 2023). Thus, we remark that our results do not imply the absence of a negative effect of salvage logging on woodpeckers at local scales. Moreover, the great spotted woodpecker showed negative responses to spruce standing deadwood, probably due to their reliance on spruce cones as an important winter food (Dylewski et al., 2017; Stański et al., 2023).

4.3 | Interaction hypothesis

We expected that the interaction between bark beetle density and spruce standing deadwood would influence woodpeckers in a non-linear way, being positive especially during epidemic phases of infestations, when bark beetle densities peak. Our results confirmed our expectations that bark beetle outbreaks increased spruce standing deadwood and played a major role in promoting woodpecker populations. Our findings also revealed nuances in the responses of the black woodpecker and the three-toed woodpecker to the multi-resource pulses, probably linked to the different use of spruce standing deadwood. The amount of spruce standing deadwood is a key habitat component for the three-toed woodpecker for nesting and feeding (Angelstam & Mikusiński, 1994; Büttler et al., 2004). Therefore, three-toed woodpeckers may concentrate at sites of large infestations and be less affected by minimally disturbed forests. On the other hand, the habitat requirements of the black woodpecker are different, being able to forage extensively on many tree species and to feed on prey like ants, while nesting mainly in live trees (Angelstam & Mikusiński, 1994). The broader ecological requirements of the black woodpecker may result in smoother, more gradual responses to bark beetle outbreaks.

4.4 | Ecosystem implications

The interactions between the environment and resource pulses affect the probability and magnitude of future pulses as a function of time since the last event and their spatial legacy (Hanle et al., 2020; Johnstone et al., 2016). In our case, deadwood creation at a given location precluded the creation of new deadwood in the short term, generating space- and time-dependent population responses. Large-scale consequences of resource pulses were reflected by population parameters of species over longer time periods than the pulses. Positive and negative effects of resource pulses were simultaneous, and functional traits modulated how species exploited changes in resource availability. The most evident example from our study was the consequence of the massive cyclone Lothar in 1999 that caused forest damage across large areas of Switzerland. The combined effects of new deadwood and bark beetle outbreaks following the cyclone were reflected by woodpecker population parameters many years after tree death and salvage operations. Such long-lasting effects are probably caused by the fact that the main pulsed resource, that is, deadwood, has been actively removed from European forests for decades, creating artificial scarcity and consequent strong responses by woodpeckers.

From 2001 to 2020, bark beetle outbreaks led to the infestation of more than 13 million m³ of timber in Switzerland (Stroheker et al., 2021). Weak effects of salvage logging on bark beetle numbers have been reported already in the past for Switzerland (Stadelmann, Bugmann, Meier, et al., 2013) and are contrasted by the well-documented negative effects on forest biodiversity (Basile et al., 2023; Thorn et al., 2018). To this end, we showed that the volume of infested wood left standing was negatively related to bark beetle density. Most likely, the intensity of management interventions was not proportional to the intensity of the outbreaks, that is, during smaller outbreaks, a greater proportion of infested wood was

left standing, whereas during large outbreaks less is left in proportion to the infested wood. Accordingly, spruce standing deadwood was positively related to the amount of infested wood removed in the previous year, suggesting that years with large outbreaks and, consequently, large volumes of wood removed, are followed by increases in standing deadwood, due to protracted infestation and tree mortality. Thus, the practice of salvage logging should not be considered the only option but rather assisted by biodiversity-oriented bark beetle management practices (Hlásny et al., 2021; Zarges et al., 2023). In this way, outbreaks of bark beetles and other forest insects could be managed as a nature-based solution for increasing deadwood in European forests and avoiding the loss of species that contribute to rare ecosystem functions, like cavity provision, and to more diverse forest communities (Basile, 2022; Mikusiński et al., 2001). Therefore, the provision of resources and benefits for woodpeckers and other species created by the legacy of bark beetle outbreaks should gain more relevance in management plans and forest policies.

AUTHOR CONTRIBUTIONS

Conceptualization: Marco Basile, Eckehard G. Brockerhoff and Gilberto Pasinelli. **Methodology:** Marco Basile, Eckehard G. Brockerhoff, Gilberto Pasinelli, Sophie Stroheker, Thomas Sattler and Meinrad Abegg. **Investigation:** Marco Basile. **Visualization:** Marco Basile. **Supervision:** Eckehard G. Brockerhoff and Gilberto Pasinelli. **Writing—original draft:** Marco Basile, Gilberto Pasinelli and Eckehard G. Brockerhoff. **Writing—review and editing:** Marco Basile, Gilberto Pasinelli, Eckehard G. Brockerhoff, Kurt Bollmann, Martin M. Gossner and Thomas Sattler.

ACKNOWLEDGEMENTS

We are grateful to Bernard Volet for helping with the woodpecker data extraction, to Marc Kéry for suggestions with the modelling approach and to Nicolas Strebel for commenting on an earlier draft of the manuscript. Meteorological data were obtained from the Swiss Federal Office of Meteorology and Climatology MeteoSwiss. Woodpecker illustration by the von Wright brothers (1838). Pictures in graphical abstract by Marco Basile (three-toed woodpecker pair) and Matteo Ceruti (forest, Adobe Stock | 522193605). Open access publishing facilitated by Schweizerische Vogelwarte, as part of the Wiley - Schweizerische Vogelwarte agreement via the Consortium Of Swiss Academic Libraries.

FUNDING INFORMATION

This project was funded by a WSL Internal Innovative Project grant and by the Swiss Ornithological Institute Sempach.

CONFLICT OF INTEREST STATEMENT

Authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The dataset with woodpecker counts is available at <https://doi.org/10.17632/y24fj5gn64.1> (Basile, 2025). Count data were kindly

provided by the Swiss Ornithological Institute. Further information can be requested by contacting the corresponding author or data@vogelwarte.ch (code for query: #####.count, with ##### = year, for example, 2000.count = count data for year 2000). Other data supporting this research is owned by third parties and is available on request from the respective data owners following these instructions: (1) Standing deadwood volume, forest stand age and volume of lying deadwood (code for query: INVNR, CLNR, BANR, RPSTZ, D13, VMRD, BART, IPOPTOT, IPOPTOT1, IPOPSTE, IPOPLIE, X, Y, TOSPECHT, SBILDGR1, SBILDGR2, ANZJAHRDEAD/ZPKDEAD, ANZJAHRPOP, RINGE, BALTER, BALTERMETHO) are available from the Swiss National Forest Inventory by contacting the Swiss Federal Research Institute WSL, Scientific Service NFI, fabrizio.cioldi@wsl.ch. A written agreement is signed for each data provision, stipulating in particular the permitted use of the data, the identification of the data in publications and the type of cooperation. Data reference: Abegg et al. (2023). <https://doi.org/10.21258/1769925>. (2) Spruce bark beetle (*Ips typographus*) data, trap deployment data, bark beetle infestation data, volumes of infested spruce wood removed and left (code for query, with ## = year, for example, k84 = beetle data for year 1984: k##, f##, ne##, z##, g##) are available from the Swiss Forest Protection Service by contacting the Swiss Federal Research Institute WSL, Swiss Forest Protection, waldschutz@wsl.ch. More information at <https://borke.nkaefer.wsl.ch/de/kaeferholzmengen.html>. (3) Daily temperature, precipitation and sunshine duration (code for query: TabsD, TminD, TmaxD, RhiresD, SrelD) are available from MeteoSwiss by contacting the Federal Office of Meteorology and Climatology, kud@meteoschweiz.ch. A written agreement is signed for each data provision, stipulating in particular the permitted use of the data, the identification of the data in publications and the type of cooperation. General terms and conditions are at <https://www.meteoswiss.admin.ch/services-and-publications/service/weather-and-climate-products/data-from-land-based-stations.html>. (4) Elevation data (swissALTI3D model, resolution 0.5, coordinate system LV95): <https://www.swisstopo.admin.ch/en/geodata/height/alti3d.html>. (5) [envidat.ch](https://doi.org/10.16904/envidat.148): Wüest et al. (2020b) <https://doi.org/10.16904/envidat.148>; Waser and Ginzler (2021) <https://doi.org/10.16904/100001.7>. The model code is available with the following DOI: <https://doi.org/10.6084/m9.figshare.23717910>.

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SUPPORTING INFORMATION

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

Figure S1. Division of Switzerland into 40 regions.

Figure S2. Bark beetle trap catches.

Figure S3. Volume of sanitary felling.

Figure S4. Distribution of the data points.

Figure S5. Volume of spruce standing deadwood.

Figure S6. Bark beetle density.

Figure S7. Woodpecker density.

Figure S8. Residuals of the generalised linear model used to infer the volume of infested wood left standing before year 2000.

Figure S9. Generalised additive mixed model diagnostic plots.

Figure S10. Predicted and observed values of the parameters of interest.

Figure S11. Temporal patterns of the spruce standing deadwood-bark beetle-woodpeckers network for the 40 study regions.

Figure S12. Multivariate temporal correlation of spruce standing

deadwood volume and bark beetle density with black woodpecker density.

Figure S13. Multivariate temporal correlation of spruce standing deadwood volume and bark beetle density with three-toed woodpecker density.

Table S1. List of the variables used in the network models.

Table S2. Posterior estimates of model 1.

Table S3. Posterior estimates of model 2.

How to cite this article: Basile, M., Pasinelli, G., Stroheker, S., Abegg, M., Bollmann, K., Gossner, M. M., Sattler, T., & Bockerhoff, E. G. (2025). Large-scale importance of bark beetle outbreaks for standing deadwood and woodpeckers. *Journal of Animal Ecology*, 00, 1–15. <https://doi.org/10.1111/1365-2656.70096>