

Temporal dynamics of a commensal network of cavity-nesting vertebrates: increased diversity during an insect outbreak

KRISTINA L. COCKLE^{1,2,4} AND KATHY MARTIN^{1,3}

¹Centre for Applied Conservation Research, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada

²School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, Louisiana 70803 USA

³Environment Canada, 5421 Robertson Road, RRI, Delta, British Columbia V4K 3N2 Canada

Abstract. Network analysis offers insight into the structure and function of ecological communities, but little is known about how empirical networks change over time during perturbations. “Nest webs” are commensal networks that link secondary cavity-nesting vertebrates (e.g., bluebirds, ducks, and squirrels, which depend on tree cavities for nesting) with the excavators (e.g., woodpeckers) that produce cavities. In central British Columbia, Canada, Northern Flicker (*Colaptes auratus*) is considered a keystone excavator, providing most cavities for secondary cavity-nesters. However, roles of species in the network, and overall network architecture, are expected to vary with population fluctuations. Many excavator species increased in abundance in association with a pulse of food (adult and larval beetles) during an outbreak of mountain pine beetle (*Dendroctonus ponderosae*), which peaked in 2003–2004. We studied nest-web dynamics from 1998 to 2011 to determine how network architecture changed during this resource pulse.

Cavity availability increased at the onset of the beetle outbreak and peaked in 2005. During and after the outbreak, secondary cavity-nesters increased their use of cavities made by five species of beetle-eating excavators, and decreased their use of flicker cavities. We found low link turnover, with 74% of links conserved from year to year. Nevertheless, the network increased in evenness and diversity of interactions, and declined slightly in nestedness and niche overlap. These patterns remained evident seven years after the beetle outbreak, suggesting a legacy effect.

In contrast to previous snapshot studies of nest webs, our dynamic approach reveals how the role of each cavity producer, and thus quantitative network architecture, can vary over time. The increase in interaction diversity with the beetle outbreak adds to growing evidence that insect outbreaks can increase components of biodiversity in forest ecosystems at various temporal scales. The observed changes in (quantitative) network architecture contrast with the relatively stable (qualitative) architecture of empirical mutualistic networks that have been studied to date. However, they are consistent with recent theory on the importance of population fluctuations in driving network architecture. Our results support the view that models should allow for the possibility of rewiring (species switching partners) to avoid overestimation of secondary extinction risk.

Key words: cavity-nesting vertebrates; insect outbreak; interaction diversity; mountain pine beetle; nest web; network architecture; network dynamics; resource pulse; William’s Lake, British Columbia, Canada.

INTRODUCTION

In ecological communities, interspecific interactions can be studied as networks that may be antagonistic (e.g., predator–prey or host–parasitoid webs), mutualistic (e.g., seed–disperser and plant–pollinator webs), or commensal (e.g., host–epiphyte webs). A network approach can offer important insights into how communities are structured and how they will respond to perturbations. Most interspecific networks are described as snapshots from a single field season, or by combining several years into one network, as a static system (e.g.,

Carvalho et al. 2008, Ramos-Jiliberto et al. 2009, Sáyago et al. 2013). Using computer simulations with these static empirical networks (and model networks), ecologists have shown that removing species or changing resource inputs could lead to cascading secondary extinctions and changes in network architecture, suggesting important consequences of network perturbation for community structure and ecosystem function (Thébault et al. 2007, Ramos-Jiliberto et al. 2009, Poccock et al. 2012). However, it has also been recognized that the structure of interspecific networks depends on species abundances (Vázquez et al. 2007, Fontaine et al. 2008). Some theoretical studies have allowed consumer species to switch partners when resources change in abundance, and their results suggest that consumer plasticity and

Manuscript received 27 June 2014; accepted 10 September 2014. Corresponding Editor: F. S. Dobson.

⁴ E-mail: kristinacockle@gmail.com

adaptive foraging can confer robustness (reduce the number of secondary extinctions) in interspecific networks (Kondoh 2003, Ramos-Jiliberto et al. 2012). Recently, Wells et al. (2014) showed that temporal fluctuations in species abundances have a strong impact on the architecture of model networks, especially when these fluctuations are heterogeneous (i.e., some species increase in abundance and others decline).

Several recent field studies have examined how mutualistic (plant–pollinator and ant–plant) and antagonistic (trophic) networks changed over the course of 2–20 years. Under relatively stable environmental conditions, mutualistic networks exhibited high turnover in links (which species interact with one another) but little change in overall architecture (Alarcón et al. 2008, Olesen et al. 2008, 2011, Petanidou et al. 2008, Burkle and Irwin 2009, Dupont et al. 2009, Díaz-Castelazo et al. 2013). Likewise, in a partial food web of vertebrate predators and their prey, interannual variation in rainfall was related to link turnover but not to variation in overall network structure (Arim and Jaksic 2005). In contrast, after 120 years of anthropogenic disturbance (climate warming and conversion of natural ecosystems to agriculture), Burkle et al. (2013) documented a loss of redundancy of plant–pollinator network structure, weakened interaction strengths, and nonrandom extirpations of 50% of bee species.

Large natural environmental perturbations, such as resource pulses from insect outbreaks, are also recognized as important drivers of community structure and function, and often occur in long-term cycles predicted to affect the topology and architecture of interspecific networks (Ostfeld and Keesing 2000). An outbreak of spruce budworm (*Choristoneura fumiferana*) was associated with increased diversity and complexity of a parasitoid food web (Eveleigh et al. 2007). To our knowledge, however, no long-term empirical studies have examined the dynamics of a vertebrate network over the course of a major resource pulse.

Networks of cavity-nesting vertebrates

Although most studies of interspecific networks have focused on mutualistic and antagonistic interactions, commensal networks are also widespread in nature (e.g., Sáyago et al. 2013). One type of commensal network, a “nest web”, links the species of animals that nest in tree cavities, which account for about 10% of all bird species, as well as many mammals, amphibians, reptiles, and insects (Newton 1998, Martin and Eadie 1999, Gibbons and Lindenmayer 2002, Cockle et al. 2011). Some cavity-nesters create their own cavities (excavators, e.g., woodpeckers), but most species are secondary cavity-nesters, who rely on existing cavities created by excavators or natural decay processes (Martin et al. 2004). Abundance and diversity of secondary cavity-nesters may often be limited by the availability and diversity of tree cavities (Newton 1998, Martin and Eadie 1999, Remm et al. 2008, Aitken and Martin 2012),

which in turn depend critically on the abundance and behavior of excavators (Daily et al. 1993, Cockle et al. 2011). Most excavators make at least one new cavity every year for nesting or roosting, and their old cavities remain available for secondary cavity-nesters for up to two decades (Cockle et al. 2011, Edworthy et al. 2012, Edworthy and Martin 2013). Each secondary cavity-nester species selects cavities with slightly different characteristics (e.g., size, height, location), matching the traits and characteristics of cavities produced by a particular subset of excavators (Aitken and Martin 2004, Martin et al. 2004). Links in a nest web represent flow of cavities from cavity producers to a succession of secondary cavity-nesters, and nest webs have been used to identify key excavators that maintain cavity supply and support communities of cavity-nesting birds and mammals (Martin et al. 2004, Blanc and Walters 2008).

A nest-web approach in temperate British Columbia, Canada, revealed that nearly all species of secondary cavity-nesters most often used cavities produced by a single excavator, the Northern Flicker (*Colaptes auratus*), which was inferred to be a keystone species for the maintenance of the cavity-nesting community (Martin et al. 2004). However, flickers are relatively weak excavators, and recent work has revealed that their cavities do not persist as long as those of stronger excavators (Edworthy et al. 2012). Furthermore, at least one species of secondary cavity-nester, the Tree Swallow (*Tachycineta bicolor*), experiences lower reproductive output in flicker cavities compared to cavities made by smaller-bodied, stronger excavators (Robles and Martin 2013). Like most studies of interspecific networks, all previous nest-web studies have used a static or snapshot approach. We became interested in a dynamic approach when we observed changes over time in the abundance of several excavators and secondary cavity-nesters, many of which were likely associated with an outbreak of mountain pine beetle (*Dendroctonus ponderosae*; Martin et al. 2006, Drever et al. 2009, Norris and Martin 2010).

Mountain pine beetle outbreaks occur periodically in western Canada, on cycles of about 30–40 years (Alfaro et al. 2010). The recent outbreak killed almost 100% of mature lodgepole pines (*Pinus contorta* var. *latifolia*), accounting for about 40% of trees in the study area. However, the increase in standing dead trees did not result in an increase in nest sites, because cavity-nesters rarely use pines for nesting in this area, and throughout the beetle outbreak they continued to choose trembling aspen (*Populus tremuloides*) for over 95% of nesting attempts (Blanc and Martin 2012, Norris and Martin 2012).

Temporal changes in abundance of cavity producers and users

Populations of most excavator species increased as the beetle outbreak progressed. Adult beetles and their larvae provide an important source of food for Downy

TABLE 1. Trends in abundance of excavator species, availability of their cavities, and use of their cavities by secondary cavity-nesting birds and mammals over a 14-year period, during an outbreak of mountain pine beetle (*Dendroctonus ponderosae*) near William's Lake, British Columbia, Canada.

Excavator species	Abundance		Availability of cavities		Use of cavities by secondary cavity-nesters	
	Change	Peak year	Change	Peak year	Change	Peak year
Excavators that do not usually consume beetles						
Northern Flicker	×2		×1.3	2005	×0.5	
Red-naped Sapsucker	×1.2		×2.5		×2	
Beetle-eating excavators						
Hairy Woodpecker	×3.5		×5		×4	
Pileated Woodpecker	×2		×3		×4	
Red-breasted Nuthatch	×2	2003–2004	×5	2004–2005	×12	2005
Downy Woodpecker	×4	2005	×8	2005–2009	×10	2005–2007
American Three-toed Woodpecker	×2	2004	×8	2006–2007	×25	2006

Notes: Values of change below 1 indicate a decline, where change refers to relative change since the starting year, 1998. Abundance indicates change in standardized point-count detections of woodpeckers 1998–2009 (values predicted by linear regression models; Edworthy et al. 2011) and nuthatches 1998–2006 (Norris and Martin 2010). Peak year is only specified for species which experienced a definable peak; cells left blank indicate species that experienced a steady upward or downward trend over the study period. Availability of cavities is also shown in Fig. 3. Use of cavities by secondary cavity-nesters measures change in number of cavities used by secondary cavity-nesters 1998–2011 (values predicted by generalized linear models), from Fig. 4.

Woodpeckers (*Picoides pubescens*), Hairy Woodpeckers (*Picoides villosus*), American Three-toed Woodpeckers (*Picoides dorsalis*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-breasted Nuthatches (*Sitta canadensis*), all of which increased in the study area as measured by both point-count abundance and nest density (Table 1; Norris and Martin 2010, 2012, Edworthy et al. 2011). Northern Flickers (the species that initially provided most cavities) and Red-naped Sapsuckers (*Sphyrapicus nuchalis*) also increased somewhat over the study period, although it is unlikely that they experienced a strong food pulse from the beetle outbreak (Table 1; Edworthy et al. 2011).

Abundance was monitored for four species of secondary cavity-nesters over the study period. Mountain Chickadees (*Poecile gambeli*), which eat beetles, doubled in abundance during the outbreak, responding to increases in the availability of food and of cavities excavated by the increased densities of Red-breasted Nuthatch and Downy Woodpecker (Norris and Martin 2012). Introduced European Starlings (*Sturnus vulgaris*), which do not eat beetles, were initially the most common secondary cavity-nester, but they declined over time (Martin et al. 2004, Koch et al. 2012). Mountain Bluebirds (*Sialia currucoides*) and Tree Swallows, which are subordinate to starlings and do not eat beetles, increased (Aitken and Martin 2008, Koch et al. 2012).

Here, we use network analysis to examine changes in the identity of interactions and the architecture of the cavity-nesting community of 26 bird and mammal species over a 14-year period encompassing the beginning, peak, and end of an outbreak of mountain pine beetle. Because the study was conducted under changing ecological conditions, including previously documented changes in the abundance of several excavator and secondary cavity-nester species, we expected network architecture to change significantly over time (in

contrast to previous studies, conducted under relatively stable conditions, in which network architecture was found to be relatively static; Alarcón et al. 2008, Olesen et al. 2008, 2011, Petanidou et al. 2008, Burkle and Irwin 2009, Dupont et al. 2009, Díaz-Castelazo et al. 2013).

MATERIALS AND METHODS

Study area

We studied population and nesting ecology of cavity-nesting birds and mammals from 1998 to 2011 in mature and logged warm and dry interior Douglas-fir forest (Meidinger and Pojar 1991) near William's Lake, British Columbia, Canada (51°52' N, 122°21' W). Nests were located in mixed deciduous/coniferous forest patches surrounded by grasslands, as well as in dry coniferous forest with deciduous riparian zones. The forest is dominated by lodgepole pine (41% of stems), Douglas-fir (*Pseudotsuga menziesii*; 29%), trembling aspen (15%), and hybrid white spruce (*Picea glauca engelmannii*; 15%), but 95% of cavity nests are located in aspen (Martin et al. 2004).

An outbreak of mountain pine beetle began in the study area around 1998 and peaked in 2003 and 2004 (Fig. 1; Drever et al. 2009). Beetles lay eggs under the bark of live lodgepole pines in late summer; larvae reach their maximum size the following spring, then emerge from the trees as adults in late summer (Reid 1962). They provided an important year-round source of food for many species of insectivorous excavators and secondary cavity-nesters (Martin et al. 2006).

Small parts of the study area were also affected by selective logging (1998–2002, 2004, and 2010), which removed only pine and/or hybrid spruce, leaving behind most aspen and Douglas-fir, so that the supply of nest-trees experienced little change (Edworthy and Martin 2013). Finally, spot fires occurred on small parts of the study area after the breeding season in 2010, when dead

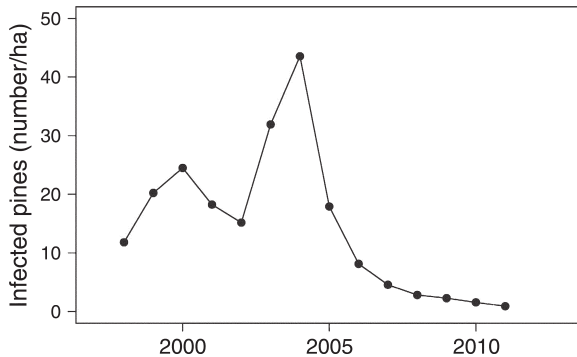


FIG. 1. Number of live lodgepole pines (*Pinus contorta*) infected by mountain pine beetle (*Dendroctonus ponderosae*) in the study area near William's Lake, British Columbia, Canada, representing the availability of beetle adults and larvae as food for avian excavators from 1998 to 2011. The initial drop in number of infected pines in 2001 and 2002 reflects harvest of infected trees in parts of our study area and not a drop in beetle populations over the wider region. The drop in number of infected pines after 2004 reflects a regional decline in beetle populations that resulted in reduced availability of food for avian excavators. However, cavities are a multi-annual resource that remain available for more than a decade, on average, after being excavated (Edworthy et al. 2012).

pinus had accumulated after the beetle outbreak (Edworthy and Martin 2013).

Field methods

Mountain pine beetle density.—To sample infection rate by mountain pine beetle, we established 491 permanent 0.04-ha circular plots in 100×100 m grids starting at grassland or wetland edges and extending 500 m into the forest, or at least 100 m apart (in smaller groves where it was not possible to establish a grid). Each summer, we revisited most of the plots (the exact number of plots surveyed each year varied from 381 to 453) to check all live lodgepole pines >12.5 cm diameter at breast height for signs of bark-boring insects (pitch tubes or outflows of dried resin on the outer bark, and/or ~ 2 mm diameter entry holes in the bark; Henigman et al. 2001). We assumed that trees with evidence of beetle infection contained live beetle larvae and/or emerging adult beetles, and represented a food source for bark insectivores for one year beginning the previous summer when eggs were laid. The density of beetle-infected pines was calculated for each year by dividing the number of live infected pines by the total area surveyed.

Nesting vertebrates.—We found active nests of avian excavators and secondary cavity-nesting birds and mammals each spring, on and around grids surveyed for mountain pine beetle, by observing the behavior of adults (excavating, carrying food, entering or exiting cavities) or hearing begging calls of young. We inspected cavities with a ladder, mirror, and a flashlight or camera mounted on a 15-m pole, and considered the cavities to support active nests if they contained eggs or young. For

each nest, we identified the excavator species that produced the cavity, based on observations of excavation (including field work in the same area from 1995–1998), and occasionally from the size and shape of the cavity (Martin et al. 2004). We revisited cavities each year to determine whether they remained available (i.e., tree remained standing with cavity intact) and whether they were used by secondary cavity-nesters (Martin et al. 2004, Edworthy et al. 2012, Robles and Martin 2013). Excavators occasionally renovated old cavities, for example by enlarging the entrance, making the cavities available to larger species of secondary cavity-nesters; we counted these as new cavities produced by the renovator species. We found as many nests as we could each year (i.e., sample was not limited to a certain number of nests). However, we could not determine the species of excavator for some cavities that were first recorded being used by secondary cavity-nesters, and these nests are excluded from the present study. Other nests may have gone undetected, especially if they were depredated on during laying or early in incubation. Search effort (about 6–7 observer hours per 15 ha per week) and sample size (number of interactions) were similar each year beginning in 1998 (Appendix A: Table A1).

Statistical analyses

We used R version 3.0.2 for all statistical analyses (R Core Team 2013). To examine changes in network architecture over time, we first used the bipartite package (Dormann et al. 2009) to generate qualitative and quantitative networks linking cavity producers (i.e., excavator species and natural decay that created cavities) with the secondary cavity-nesting species that used cavities, for each year from 1998 to 2011. In both cases (qualitative and quantitative), the 14 input matrices (one for each year) were comprised of secondary cavity-nesters (upper level, in columns) and cavity producers (lower level, in rows). For each of the 14 qualitative networks, each cell contained a 1 if the interaction occurred that year (i.e., the secondary cavity-nesting species used a cavity generated by that cavity producer) or a 0 if the interaction did not occur that year. For each of the 14 quantitative networks, each cell contained the number of interactions between each species pair that year. Nests were assigned to the year in which the secondary cavity-nester used the cavity. Cavities were generally produced in a previous year, but occasionally they were produced earlier in the same year.

To determine the extent of qualitative changes in the network over time, we calculated the proportion of cavity producers, secondary cavity-nesters, and links that were present in all 14 years, as well as the proportion present one year that were also present the following year. Additionally, we calculated pairwise network dissimilarity (or β -diversity) of interactions between each year and the following year. We used the

betalink package (Poisot et al. 2012) to partition the dissimilarity between each pair of whole networks (β_{WN}) into differences arising from species turnover (β_{ST}) and differences arising from species that occurred in both networks but switched interaction partners (β_{OS}). Thus

$$\beta_{WN} = \beta_{ST} + \beta_{OS}.$$

As our measure of β -diversity, we used the default β_W , which ranges from 0 (sets are perfectly overlapping) to 1 (perfectly nonoverlapping; Whittaker 1960, Poisot et al. 2012). Dissimilarity arising from species turnover, β_{ST} , ranges from 0 (all differences between the two networks are explained by shared species interacting differently) to β_{WN} (all differences between the two networks are explained by species turnover; Poisot et al. 2012).

To understand changes in interaction frequency over time, we used the `glm` command in R to fit simple and quadratic generalized linear models with Poisson error structure and a log-link function, to test for a relationship between year (predictor variable) and the number of nests of secondary cavity-nesters in cavities produced by each of the seven most common excavators and natural decay (response variables). Because of the small number of replicates ($n = 14$ networks), we did not introduce other explanatory variables into the models; however, using the cumulative number of beetle-attacked trees as the predictor variable, instead of year, provided qualitatively similar results. Poisson models were appropriate because our response variables were counts and were not overdispersed; negative binomial models did not improve fit (log-likelihood ratio tests, all $P > 0.05$). To determine how well each model fit the data, we calculated the log-likelihood R^2 analog (pseudo- R^2) where

$$R^2 = 1 - \frac{LL_{\text{model}}}{LL_{\text{null}}}$$

and LL_{model} and LL_{null} are the log-likelihoods of the full model and intercept-only model, respectively. Quadratic terms were retained when significant at $\alpha = 0.05$.

To quantify structure at the network level, we used the bipartite package to calculate two qualitative and four quantitative metrics for each annual network. Qualitative metrics were species richness (total number of species in the network, including natural decay as one “species”) and number of links (number of unique interactions in the network; i.e., the number of 1s in the qualitative matrix). Quantitative metrics were interaction diversity (Shannon’s diversity), interaction evenness (Shannon’s evenness using the log of the product of matrix dimensions as denominator), and nestedness (weighted-interaction nestedness estimator, or WINE, a measure of the extent to which the interactions of specialists are a subset of the interactions of generalists) for the whole network, as well as niche overlap (Horn’s index; Horn 1966) of secondary cavity-nesters. WINE is a nestedness measure for quantitative networks that takes into account the intensity of links or link strength (Galeano et al. 2008).

To quantify temporal change in the architecture of the network, we fitted general linear models with linear and quadratic terms (retained when significant at $\alpha = 0.05$) to test for a relationship between year (predictor variable) and the response variables (1) species richness, (2) number of links, (3) interaction diversity, (4) network evenness, (5) nestedness, and (6) niche overlap ($n = 14$ years). For each model, we used the `lmtest` package to perform a Breusch-Godfrey test for first- and second-order autocorrelation in the data; we found none ($P > 0.05$ for all models).

RESULTS

Our complete network of cavity producers (excavators and decay) and secondary cavity-users comprised 1610 nesting attempts of 18 species of secondary cavity-nesting birds and mammals over 14 years (1998 to 2011) in cavities produced by nine types of cavity producers (eight species of avian excavators and natural decay; Fig. 2; Appendix A: Table A1, Appendix B, Appendix C: Fig. C1).

Temporal change in cavity availability and use

The total number of available cavities peaked in 2005 and then leveled off (Fig. 3a). There was an initial modest increase in the availability of cavities excavated by Northern Flickers, and then a slight decline after 2005 (Fig. 3b). Cavities excavated by Red-naped Sapsuckers, Pileated Woodpeckers, and Hairy Woodpeckers increased over the study period by a factor of two, three, or five, respectively (Fig. 3). Cavities excavated by Red-breasted Nuthatches increased by a factor of five and peaked in 2005–2006, whereas cavities excavated by Downy Woodpeckers and American Three-toed Woodpeckers increased by a factor of eight and peaked in 2005–2009 and 2006, respectively.

Use of cavities created by Northern Flickers and natural decay processes declined by one-half and one-third, respectively, while use of cavities created by Red-naped Sapsuckers, Pileated Woodpeckers, and Hairy Woodpeckers doubled, tripled, and quadrupled, respectively (Fig. 4). Use of cavities created by Red-breasted Nuthatches, Downy Woodpeckers, and American Three-toed Woodpeckers peaked in 2005 and 2006, one and two years after the peak of the beetle outbreak (Fig. 4).

Temporal change in the network

Six of the nine (67%) cavity producers, six of the 18 (33%) secondary cavity-nesters, and eight of the 59 (14%) links from the complete qualitative interaction network (recorded at least once over the 14 years of the study), were present in all 14 annual qualitative networks (i.e., not missing in any year). On average, $96\% \pm 1.71\%$ (mean \pm SE) of cavity producers, $83\% \pm 1.87\%$ of secondary cavity-nesters, and $74\% \pm 1.93\%$ of links recorded one year were also recorded the following year. Dissimilarity of interactions (β_{WN}) from one year

to the next ranged from 0.18 to 0.39 (mean \pm SE = 0.27 \pm 0.071). About 73% of the interaction dissimilarity was explained by turnover in the links among shared species ($\beta_{OS} = 0.19 \pm 0.052$), and the remainder (27%) was explained by species turnover ($\beta_{ST} = 0.072 \pm 0.019$).

The number of species (general linear model slope coefficient (b_{year}) = 0.052 \pm 0.069, $t = 0.76$, $P = 0.46$; Fig. 5a) and links ($b_{\text{year}} = 0.224 \pm 0.155$, $t = 1.45$, $P = 0.17$; Fig. 5b) in the network remained relatively constant, but quantitative measures of interaction diversity ($b_{\text{year}} = 0.032 \pm 0.010$, $t = 3.36$, $P = 0.0057$; Fig. 5c) and evenness ($b_{\text{year}} = 0.0061 \pm 0.0016$, $t = 3.85$, $P = 0.0023$; Fig. 5d) increased over time. All 14 networks were significantly nested ($P < 0.05$), but nestedness varied between 0.23 and 0.66, with a marginally significant downward trend over time ($b_{\text{year}} = -0.015 \pm 0.0083$, $t = -1.79$, $P = 0.099$; Fig. 5e). Niche overlap also exhibited a marginally significant decrease over time ($b_{\text{year}} = -0.011 \pm 0.0053$, $t = -2.08$, $P = 0.060$; Fig. 5f).

DISCUSSION

Over our 14-year study in central British Columbia, the network of cavity-nesting vertebrates experienced modest changes in the identity of interactions (i.e., link turnover: changes in which pairs of species interacted at least once in a given year) and significant changes in overall architecture. We observed decreased use of flicker cavities, increased use of cavities made by beetle-eating excavators and Red-naped Sapsuckers, increased interaction diversity, and increased evenness. Nestedness and niche overlap declined somewhat, and we observed strong fluctuations in nestedness over time, which have not been observed in other network studies. Although network metrics can be sensitive to sampling effort, number of species, and number of interactions (Dormann et al. 2009, Trøjelsgaard and Olesen 2013), these parameters remained relatively constant over time in our study, and we believe the observed changes in network metrics have a biological explanation, related to the simultaneous outbreak of mountain pine beetle, decline of European Starlings, and increase in Red-naped Sapsuckers.

Interactions with beetle-eating excavators increased in frequency shortly after these excavators and their cavities increased in abundance in our study area (Table 1). Furthermore, the increases in cavity use were of similar or larger magnitude than the increases in excavator abundance, as would be expected if secondary cavity-nesters were responding to a pulse of cavities provided by these excavators and available for several years thereafter (Table 1). Mountain Chickadees switched from cavities excavated by sapsuckers to cavities excavated by Downy

Woodpeckers and Red-breasted Nuthatches (Fig. 2; Norris et al. 2013). Tree Swallows switched from cavities excavated by flickers to cavities excavated by sapsuckers and Hairy Woodpeckers, where they experienced increased reproductive output (Fig. 2; Robles and Martin 2013). In contrast, the reproductive output of Mountain Bluebirds was independent of cavity producer (Robles and Martin 2013) and bluebirds continued to use a high proportion of flicker cavities throughout the study period (Fig. 2). Part of the decline in use of flicker cavities can be explained by the regional decline of European Starlings, one of the principal users of flicker cavities. Although it is difficult to disentangle the influence of the beetle outbreak from starling declines and other concurrent temporal processes, our results are consistent with other evidence that insect outbreaks can contribute positively to forest biodiversity, including interaction diversity, over the short and long term (Eveleigh et al. 2007, Drever et al. 2009).

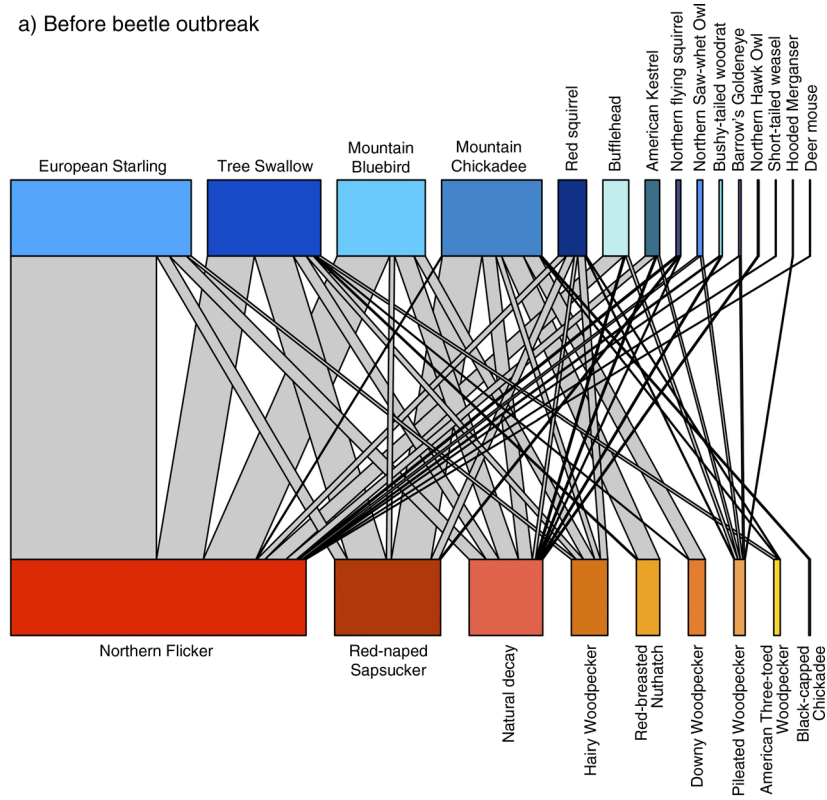
Importantly, the changes in the community were still evident in 2011, seven years after the peak of the beetle outbreak. Availability and use of cavities produced by Red-naped Sapsuckers, Hairy Woodpeckers, and Pileated Woodpeckers continued to increase after the peak of the outbreak, whereas availability and use of cavities produced by Red-breasted Nuthatches, Downy Woodpeckers, and American Three-toed Woodpeckers peaked and declined. These different patterns can be explained partly by the population trends for these excavator species (continuing increase for the former group, but peak and decline for the latter; Table 1) and partly by differences in loss rates of cavities produced by the various excavators. Cavities in our study area remain available for a median >12 years; however, those produced by strong excavators (Pileated Woodpeckers, Red-naped Sapsuckers, and Hairy Woodpeckers) experience about half the annual loss rates compared to those produced by weak excavators (Red-breasted Nuthatches and Downy Woodpeckers) and Northern Flickers (Edworthy et al. 2012).

Our commensal cavity-nester network was characterized by low link turnover (about 74% of links conserved from one year to the next), in direct contrast to mutualistic networks, which, under relatively stable conditions, exhibited high link turnover (about 25% of links conserved from one year to the next; e.g., Olesen et al. 2008, Dupont et al. 2009). Much of the annual link turnover in pollination and ant-plant networks may be driven by strong year-to-year variation in phenology of flowering plants, a phenomenon that does not apply to cavity-nester networks because cavities, once produced,

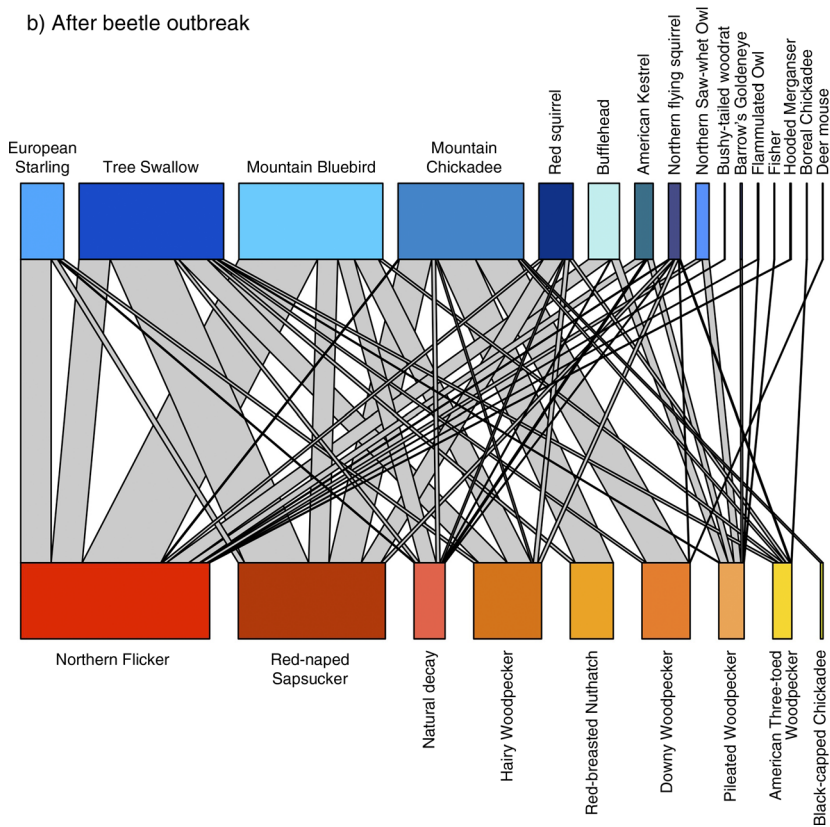
→

Fig. 2. Bipartite networks of cavity-nesting vertebrates (a) before (1998–2003) and (b) after (2004–2011) the peak of the outbreak of mountain pine beetle near William's Lake. Secondary cavity-users (top row of blue and green boxes) are connected by links (gray lines) to the excavators and natural decay (bottom row of red and yellow boxes) that produced their nesting cavities. The width of boxes and lines represents the number of nests in the sample. Each species is a different color. A list of common and scientific names is available in Appendix A.

a) Before beetle outbreak



b) After beetle outbreak



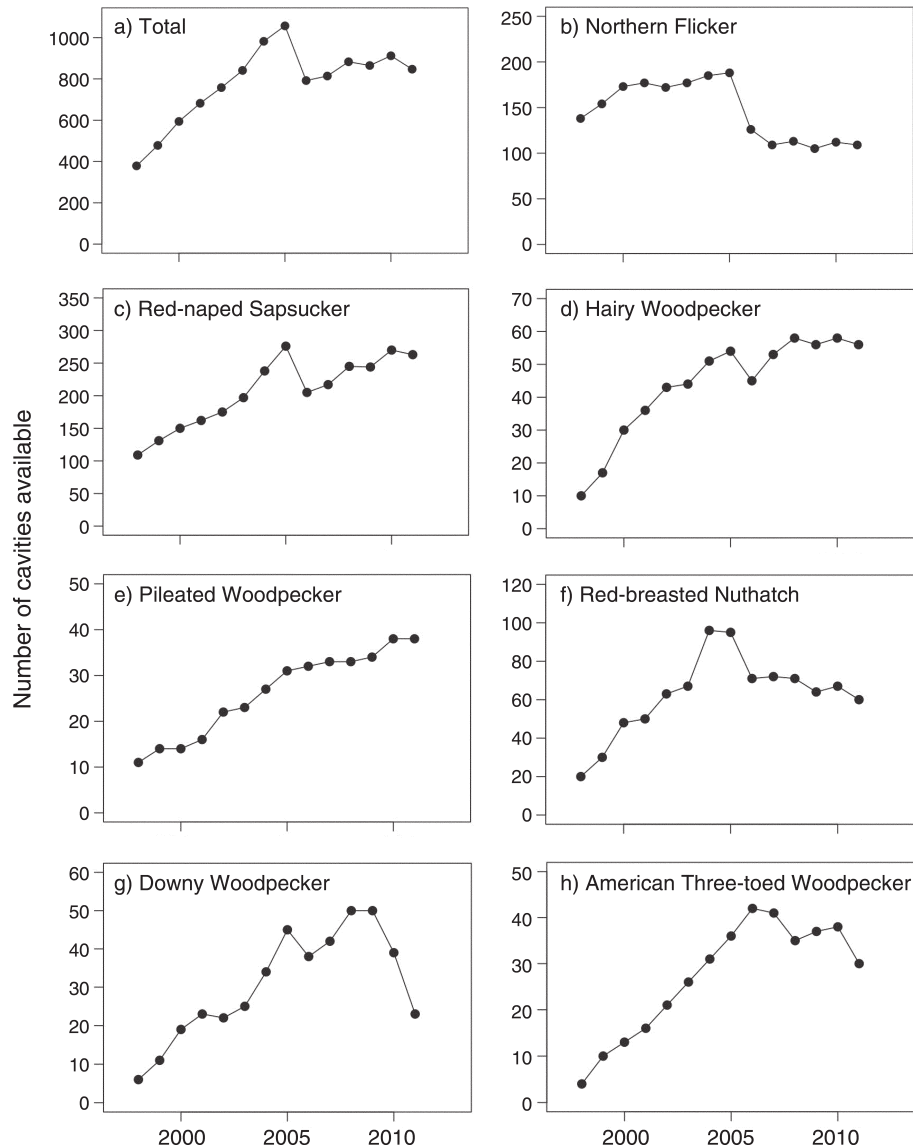


FIG. 3. Number of tree cavities available annually from 1998 to 2011 near William's Lake. (a) Total for all cavities (includes cavities produced by natural decay and Black-capped Chickadees (*Poecile atricapillus*), and cavities for which we could not identify the excavator). (b–h) Cavities made by seven species of avian excavators. These should be considered minimum numbers, because cavities only entered this data set when they were used at least once by an excavator or secondary cavity-nester. Note the different scales on y-axes.

often remain available for one or more decades (Wesołowski 2011, 2012, Edworthy et al. 2012, Edworthy and Martin 2013). Additionally, interannual variation in pollination networks may result from opportunistic foraging by insect pollinators (Alarcón et al. 2008); however, secondary cavity-nesters are unlikely to behave opportunistically, because they invest their entire reproductive effort for the year in just one cavity, the choice of which directly affects their reproductive output (Nilsson 1984, Rendell and Robertson 1989, Wesołowski and Rowiński 2012, Robles and Martin 2013). Secondary cavity-nesters exhibit species-specific nest-site selection for tree, cavity, and site characteristics, which limit them

to interacting with partners (excavators) that have compatible traits, such as body size and foraging habitat (Stauffer and Best 1982, Martin et al. 2004). Trait-matching was recently shown to play an important role in structuring hummingbird–plant pollination webs (Vizenin-Bugoni et al. 2014; Maglianesi et al. 2014), and merits attention in studies of insect–plant pollination networks and vertebrate nest webs. Territoriality and competition among secondary cavity-nesters may also limit the ability of individual secondary cavity-nesters to occupy available high-quality cavities, which could explain why we found low link turnover and only marginally significant declines in nestedness and niche overlap. The changes we observed

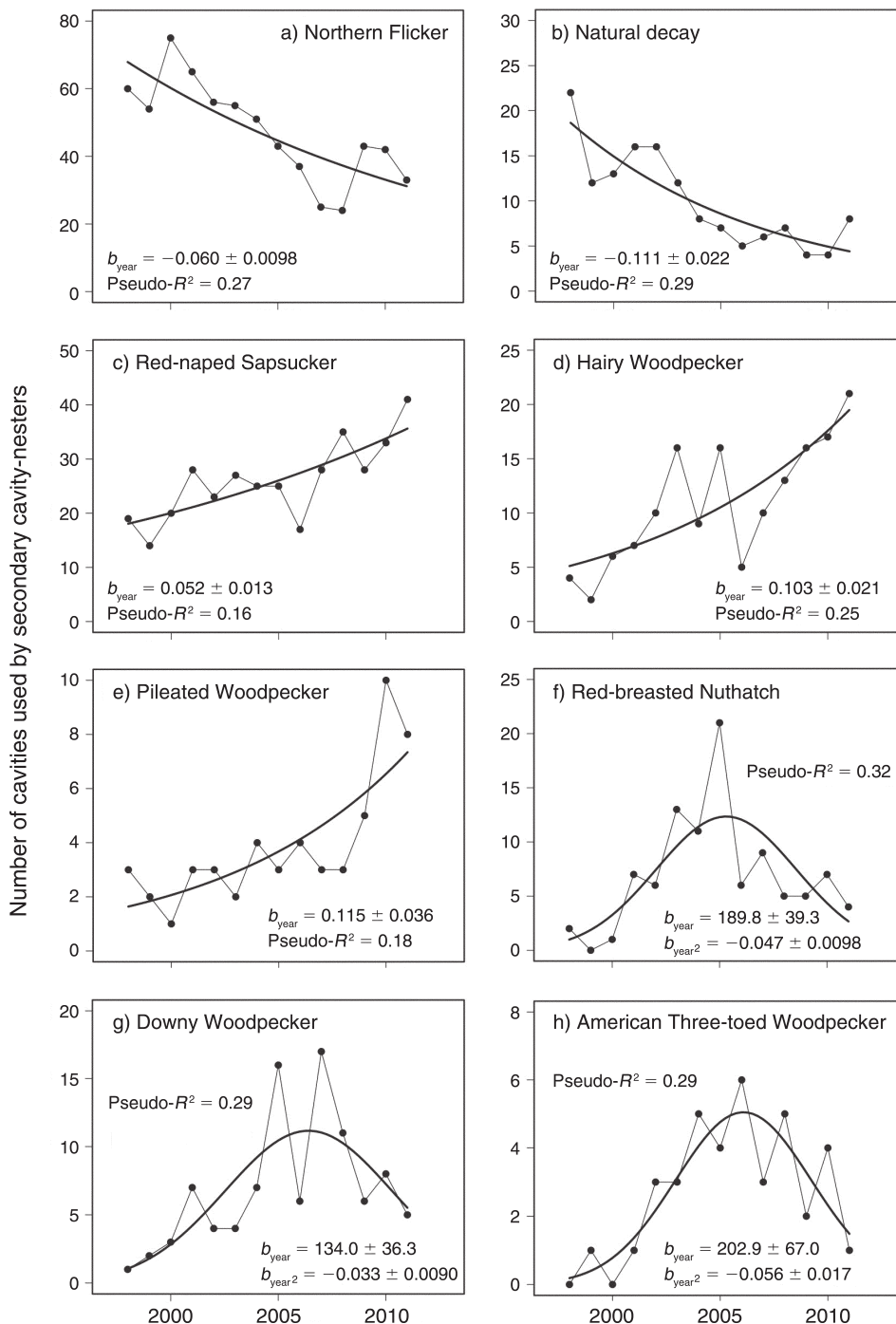


FIG. 4. Number of tree cavities (solid circles) used by secondary cavity-nesting birds and mammals, separated by cavity producer (seven species of avian excavators and natural decay) from 1998 to 2011 near William’s Lake. Fitted lines represent the best-fit linear or quadratic generalized linear models predicting the number of cavities. Values for b_{year} (slope parameter estimates in the models) are presented as mean \pm SE; squared b_{year} values in panels f–h are a quadratic term. Note the different scales on y-axes. Cavities produced by Black-capped Chickadees were excluded because they were used by secondary cavity-nesters only six times.

in network architecture (increases in evenness and diversity of interactions, slight declines in nestedness and niche overlap) are consistent with the idea that an overall increase in availability of cavities, produced by a wider variety of excavators during the beetle outbreak,

increased the opportunities for secondary cavity-nesters to interact with formerly uncommon partners.

By following an empirical interspecific network during a major perturbation, our study reveals the changing roles of individual species. Whereas a static nest web

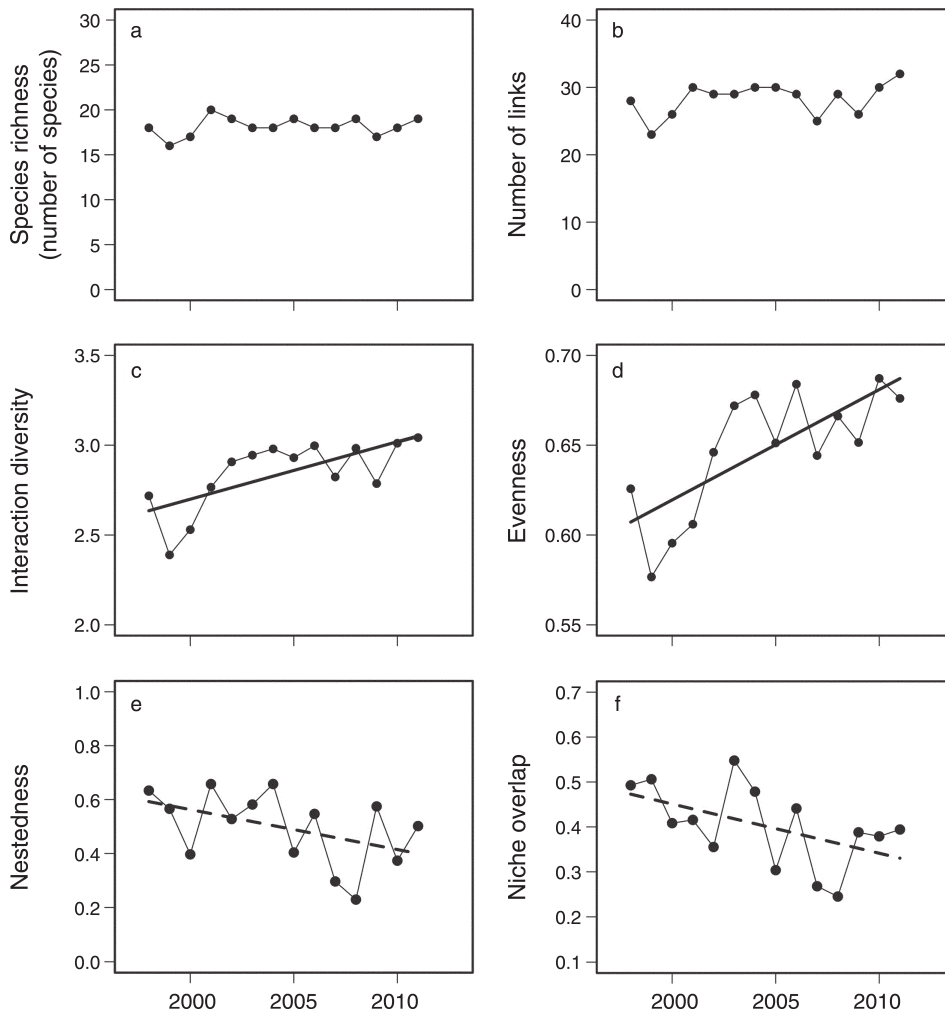


FIG. 5. (a) Species richness, (b) number of links, (c) Shannon's diversity of interactions, (d) Shannon's evenness of interactions, (e) nestedness (weighted-interaction nestedness estimator; WINE), and (f) Horn's index of niche overlap (Horn 1966) for secondary cavity-nesters, in a network of cavity-nesting birds and mammals over a 14-year period that included an outbreak of mountain pine beetle. Shannon's evenness ranges from 0 (all interactions occur between a single pair of species) to 1 (equal partitioning of interactions among all species in the network). WINE ranges from 0 (random distribution) to 1 (maximal nestedness). Horn's index ranges from 0 (no niche overlap; i.e., each species of secondary cavity-nester interacts with an exclusive partner or suite of partners among the cavity producers) to 1 (complete niche overlap; i.e., proportional use of cavities made by each producer is constant over all species of secondary cavity-nesters). Predicted values from simple linear regression are shown as solid lines for indices with significant patterns ($P < 0.05$ for slope parameter), and as dashed lines for indices with marginally significant trends ($0.05 < P < 0.1$).

suggested that the northern flicker was a keystone species whose persistence would maintain populations of most cavity-nesting vertebrates (Martin et al. 2004), a dynamic approach revealed that under some ecological conditions (such as when stronger excavators increase during and after a bark beetle outbreak), flickers become much less important as cavity providers. Our result that network architecture changed over time is consistent with the predictions of network theory that incorporates population fluctuations (Wells et al. 2014). It supports the idea that theoretical studies should account for the fundamental niche of each species and the possibility of rewiring in the network, to avoid overestimating the risk of secondary extinctions (Kondoh 2003, Staniczenko et

al. 2010). In studying the structure and function of interspecific networks, ecologists should recognize that patterns conferring stability (e.g., high vs. low nestedness) may vary among antagonistic, mutualistic, and commensal networks (Thébault and Fontaine 2010, Sáyago et al. 2013), and also that these architectural patterns can vary naturally over time.

ACKNOWLEDGMENTS

We thank numerous field assistants and graduate students who contributed to data collection. For comments on the analyses and manuscript, we thank Amanda Edworthy, Diego Vázquez, Konstans Wells, Mark Drever, Andrea Norris, Karen Wiebe, Lori Blanc, Karl Mokross, Hugo Robles, Peter Arcese, the ESPCA São Paulo School on Ecological Networks,

anonymous referees, and members of the K. Martin lab. The research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC Special Strategic Grant to K. Martin), Environment Canada, Sustainable Forest Management Network, and Forest Renewal BC. K. L. Cockle was supported during the research by post-doctoral fellowships from CONICET and NSERC.

LITERATURE CITED

- Aitken, K. E. H., and K. Martin. 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. *Canadian Journal of Forest Research* 34:2099–2109.
- Aitken, K. E. H., and K. Martin. 2008. Resource selection plasticity and community responses to experimental reduction of a critical resource. *Ecology* 89:971–980.
- Aitken, K. E. H., and K. Martin. 2012. Experimental test of nest-site limitation in mature mixed forests of central British Columbia, Canada. *Journal of Wildlife Management* 76:557–565.
- Alarcón, R., N. M. Waser, and J. Ollerton. 2008. Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos* 117:1796–1807.
- Alfaro, R. I., E. Campbell, and B. C. Hawkes. 2010. Historical frequency, intensity and extent of disturbance in British Columbia. Mountain Pine Beetle Working Paper 2009-30. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.
- Arim, M., and F. M. Jaksic. 2005. Productivity and food web structure: association between productivity and link richness among top predators. *Journal of Animal Ecology* 74:31–40.
- Blanc, L. A., and K. Martin. 2012. Identifying suitable woodpecker nest trees using decay selection profiles in trembling aspen (*Populus tremuloides*). *Forest Ecology and Management* 286:192–202.
- Blanc, L. A., and J. R. Walters. 2008. Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. *Ecology* 89:506–514.
- Burkle, L., and R. Irwin. 2009. The importance of interannual variation and bottom-up nitrogen enrichment for plant-pollinator networks. *Oikos* 118:1816–1829.
- Burkle, L. A., J. C. Marlin, and T. Knight. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339:1611–1615.
- Carvalho, L. G., E. R. M. Barbosa, and J. Memmott. 2008. Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *Journal of Applied Ecology* 45:1419–1427.
- Cockle, K. L., K. Martin, and T. Wesołowski. 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment* 9:377–382.
- Daily, G. C., P. R. Ehrlich, and N. M. Haddad. 1993. Double keystone bird in a keystone species complex. *Proceedings of the National Academy of Sciences USA* 90:592–594.
- Díaz-Castelazo, C., I. R. Sánchez-Galván, P. R. Guimarães, Jr., R. L. Galdini Raimundo, and V. Rico-Gray. 2013. Long-term temporal variation in the organization of an ant-plant network. *Annals of Botany* 111:1285–1293.
- Dormann, C. F., J. Fründ, N. Blüthgen, and B. Gruber. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal* 2:7–24.
- Drever, M. C., J. R. Goheen, and K. Martin. 2009. Species-energy theory, pulsed resources, and regulation of richness during a mountain pine beetle outbreak. *Ecology* 90:1095–1105.
- Dupont, Y. L., B. Padrón, J. M. Olesen, and T. Petanidou. 2009. Spatio-temporal variation in the structure of pollination networks. *Oikos* 118:1261–1269.
- Edworthy, A. B., M. C. Drever, and K. Martin. 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. *Forest Ecology and Management* 261:203–210.
- Edworthy, A. B., and K. Martin. 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. *Journal of Wildlife Management* 77:770–776.
- Edworthy, A. B., K. L. Wiebe, and K. Martin. 2012. Survival analysis of a critical resource for cavity-nesting communities: patterns of tree cavity longevity. *Ecological Applications* 22:1733–1742.
- Eveleigh, E. S., et al. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proceedings of the National Academy of Sciences USA* 104:16976–16981.
- Fontaine, C., C. L. Collin, and I. Dajoz. 2008. Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology* 96:1002–1010.
- Galeano, J., J. M. Pastor, and J. M. Iriondo. 2009. Weighted-interaction nestedness estimator (WINE): a new estimator to calculate over frequency matrices. *Environmental Modelling and Software* 24(11):1342–1346.
- Gibbons, P., and D. Lindenmayer. 2002. Tree hollows and wildlife conservation in Australia. CSIRO Publishing, Collingwood, Australia.
- Henigman, J., T. Ebata, E. Allen, J. Westfall, and A. Pollard. 2001. Field guide to forest damage in British Columbia. MOF/CFS Joint Publication Number 17. <http://www.for.gov.bc.ca/hfp/publications/00198/>
- Horn, H. S. 1966. Measurement of “overlap” in comparative ecological studies. *American Naturalist* 100:419–424.
- Koch, A. J., K. Martin, and K. E. H. Aitken. 2012. The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, Canada. *Ibis* 154:590–600.
- Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299:1388–1391.
- Maglianesi, M. A., N. Blüthgen, K. Böhning-Gaese, and M. Schleuning. 2014. Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology* 95:3325–3334.
- Martin, K., K. E. H. Aitken, and K. L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106:5–19.
- Martin, K., and J. M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243–257.
- Martin, K., A. Norris, and M. Drever. 2006. Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: implications for critical habitat management. *B. C. Journal of Ecosystems and Management* 7:10–24.
- Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests Special Report Series No. 6. Victoria, British Columbia, Canada.
- Newton, I. 1998. Population limitation in birds. Academic Press, San Diego, California, USA.
- Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica* 15:167–175.
- Norris, A. R., M. C. Drever, and K. Martin. 2013. Insect outbreaks increase populations and facilitate reproduction in a cavity-dependent songbird, the Mountain Chickadee *Poecile gambeli*. *Ibis* 155:165–176.
- Norris, A. R., and K. Martin. 2010. The perils of plasticity: dual resource pulses increase facilitation but destabilize populations of small-bodied cavity-nesters. *Oikos* 119:1126–1135.

- Norris, A. R., and K. Martin. 2012. Red-breasted Nuthatches (*Sitta canadensis*) increase cavity excavation in response to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. *Ecoscience* 19:308–315.
- Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. *Ecology* 89:1573–1582.
- Olesen, J. M., C. Stefanescu, and A. Traveset. 2011. Strong, long-term temporal dynamics of an ecological network. *PLoS ONE* 6(11):e26455.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters* 11:564–575.
- Pocock, M. J. O., D. M. Evans, and J. Memmott. 2012. The robustness and restoration of a network of ecological networks. *Science* 335:973–977.
- Poisot, T., E. Canard, D. Mouillot, N. Mouquet, and D. Gravel. 2012. The dissimilarity of species interaction networks. *Ecology Letters* 15:1353–1361.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Ramos-Jiliberto, R., A. A. Albornoz, F. S. Valdovinos, C. Smith-Ramírez, M. Arim, J. J. Armesto, and P. A. Marquet. 2009. A network analysis of plant–pollinator interactions in temperate rain forests of Chiloé Island, Chile. *Oecologia* 160: 697–706.
- Ramos-Jiliberto, R., F. S. Valdovinos, P. Moisset de Espanés, and J. D. Flores. 2012. Topological plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology* 81:896–904.
- Reid, R. W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. *Canadian Entomologist* 94:531–538.
- Remm, J., A. Löhmus, and P. Rosenvald. 2008. Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. *Acta Ornithologica* 43:83–91.
- Rendell, W. B., and R. J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *Condor* 91: 875–885.
- Robles, H., and K. Martin. 2013. Resource quantity and quality determine the inter-specific associations between ecosystem engineers and resource users in a cavity-nest web. *PLoS ONE* 8(9):e74694.
- Sáyago, R., M. Lopezaraiza-Mikel, M. Quesada, M. Y. Álvarez-Añorve, A. Cascante-Marín, and J. M. Bastida. 2013. Evaluating factors that predict the structure of a commensalistic epiphyte–phorophyte network. *Proceedings of the Royal Society B* 280:20122821.
- Staniczenko, P. P. A., O. T. Lewis, N. S. Jones, and F. Reed-Tsochas. 2010. Structural dynamics and robustness of food webs. *Ecology Letters* 13:891–899.
- Stauffer, D. F., and L. B. Best. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bulletin* 94:329–337.
- Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856.
- Thébault, E., V. Huber, and M. Loreau. 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163–173.
- Trojelsgaard, K., and J. M. Olesen. 2013. Macroecology of pollination networks. *Global Ecology and Biogeography* 22: 149–162.
- Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–1127.
- Vizentin-Bugoni, J., P. K. Maruyama, and M. Sazima. 2014. Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. *Proceedings of the Royal Society B* 281: 20132397.
- Wells, K., H. Feldhaar, and R. B. O’Hara. 2014. Population fluctuations affect inference in ecological networks of multi-species interactions. *Oikos* 123:589–598.
- Wesołowski, T. 2011. “Lifespan” of woodpecker-made holes in a primeval temperate forest: a thirty year study. *Forest Ecology and Management* 262:1846–1852.
- Wesołowski, T. 2012. “Lifespan” of non-excavated holes in a primeval temperate forest: a thirty year study. *Biological Conservation* 153:118–126.
- Wesołowski, T., and P. Rowiński. 2012. The breeding performance of Blue Tits *Cyanistes caeruleus* in relation to the attributes of natural holes in a primeval forest. *Bird Study* 59:437–448.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1256.1.sm>