Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak

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Abstract. Species–energy theory provides a framework through which to link two features commonly noted in local communities: episodic production of resources (i.e., resource pulses) and the regulation of local species richness through time. We examined the pathways through which a resource pulse, a large-scale outbreak of mountain pine beetles, was borne out in six foraging guilds comprising a forest bird community in British Columbia, Canada, 1997–2007. We investigated statistical relationships between richness and abundance in each guild to evaluate the prediction that the outbreak should be manifested in species most reliant upon bark beetles (i.e., the bark insectivore guild). We then employed randomization methods to evaluate whether the beetle outbreak obscured evidence for local regulation for the six foraging guilds. Density and richness of bark insectivores increased over the course of the outbreak. More species of bark insectivores were detected for a given number of individuals following the outbreak, consistent with an increase in the number and types of resources. Richness of bark insectivores showed no evidence of regulation. In contrast, densities of most other foraging guilds were not strongly correlated with the habitat changes resulting from the beetle outbreak and displayed only weak evidence of regulation of richness. We suggest that such weak regulation of richness may be a general feature of forest bird communities. Coupled with long-term data, resource pulses provide exceptional opportunities through which to test predictions of species–energy theory.

Key words: Dendroctonus ponderosae; density compensation; foraging guilds; forest birds; more individuals hypothesis; resource pulse; resource specialization hypothesis.

Introduction

Understanding the mechanisms underlying patterns of species richness continues to be a central focus of community ecology. For over 25 years, species–energy theory (Wright 1983) has provided a conceptual basis through which ecologists have linked richness to resource availability. Support for species–energy theory comes primarily from comparisons over space, where richness increases with available energy across local communities, with "local" indicating the area over which individuals of different species come into contact and potentially interact (Turner et al. 1988, Blackburn and Gaston 1996, Currie 2007, Evans et al. 2008). The spatial emphasis of species–energy theory complements studies that focus on richness at a single locality through time, many of which have documented the prevalence of resource pulses (i.e., episodic production followed by ephemeral availability of high levels of resources; Ostfeld and Keesing 2000, Schmidt and Ostfeld 2003, Yang et al. 2008). In addition, long-term studies have identified a second feature common to local communi-

ties: despite considerable variation in composition, local richness often remains relatively constant through time (Collins 2000, Ernest and Brown 2001, Parody et al. 2001, Lekve et al. 2003, Goheen et al. 2005). Such constancy across a broad range of taxa and time spans has led to the notion that local richness may be regulated, in that colonization from the species pool and local extinction are approximately balanced and serve to maintain richness between narrow limits, hereafter the "community regulation hypothesis" (Brown et al. 2001). The community regulation hypothesis requires 1) that the local community comprises an open system with opportunity for compensatory colonizations, and 2) that resource availability must remain relatively constant (Brown et al. 2001). Because local richness should be set largely by local conditions such as resource availability (Wright 1983, Lekve et al. 2003), evaluating this second requirement as it relates to local richness effectively provides a temporal test of the central prediction of species–energy theory, namely, that local richness and available energy should be related positively (Brown 1981, Wright 1983).

Identifying how species richness varies with abundance in response to resource pulses may provide clues toward more explicitly combining species–energy theory
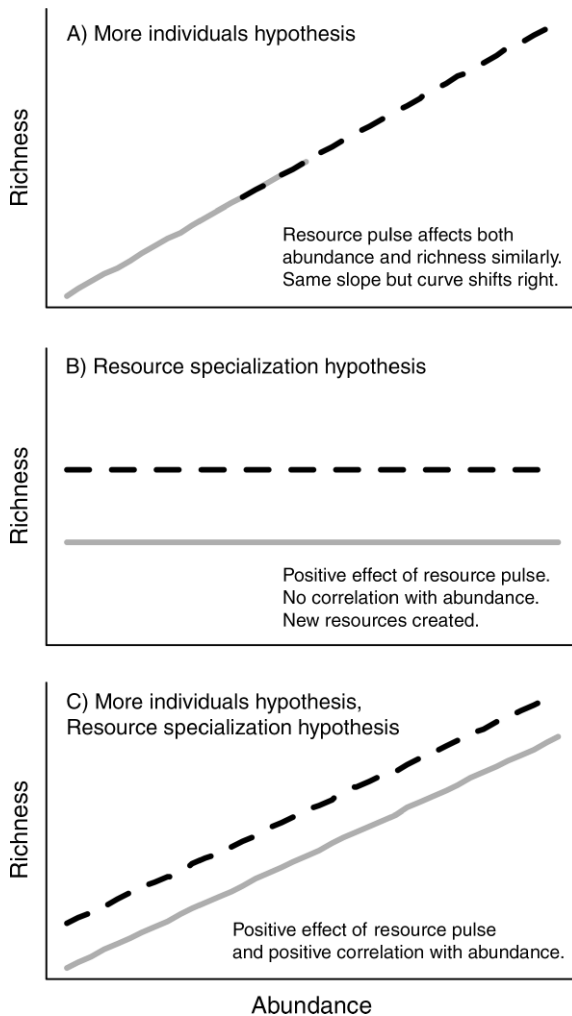
FIG. 1. Schematic of three scenarios of how a pulse in resource availability may change the relationship between species richness and abundance. Separate lines depict periods of differing resource availability (solid gray = normal conditions; dashed black = pulse conditions [high availability]). Panel labels denote possible hypotheses that explain observed patterns.

and the community regulation hypothesis (Hurlbert and Haskell 2003, Evans et al. 2006, Yee and Juliano 2007). Richness and abundance often covary positively, but the strength and shape of this relationship should be affected by resource supply (Hurlbert 2004). Three scenarios exist through which a resource pulse can affect richness (Fig. 1). In the first scenario (Fig. 1A), resources affect both abundance and richness, such that the slope remains unchanged but the curve slides to the right following the resource pulse. In this scenario, the resource pulse affects richness solely by increasing abundance, as would be expected if more species could be supported simply because more resources support more individuals (more individuals hypothesis; Srivastava and Lawton 1998). In the second scenario (Fig. 1B), the resource pulse results in an increase in richness but

not an increase in abundance. Species from the regional pool colonize in response to an increase in the number of types of resources available and not necessarily to an increase of resource quantity (resource specialization hypothesis; Keddy 1984, Hurlbert 2004). Such a dynamic where richness increases while abundance remains constant implies the creation of a novel resource that can be utilized by some, but not all, species that compete strongly for a second resource. Under this scenario, the production of a novel resource (e.g., tree cavities) creates colonization opportunities for cavity nesters from the species pool (Martin and Eadie 1999); these newly colonized species compete with other species in the local community for another resource (e.g., bark insects), potentially leading to strong density compensation and an increase in local richness without an accompanying change in abundance. This scenario is rarely noted in nature because richness and abundance usually covary strongly (Srivastava and Lawton 1998, Houlahan et al. 2007, Drever et al. 2008); we include it here for the sake of thoroughness. In the third scenario (Fig. 1C), the resource pulse affects the relationship between abundance and richness in a positive manner such that more species are noted for any given level of abundance, providing support for some combination of the more individuals hypothesis and the resource specialization hypothesis (Hurlbert 2004).

In forest ecosystems, resource pulses often are manifested as insect outbreaks, with direct and indirect consequences for local communities (Hahus and Smith 1990, Jones et al. 1998, Lovett et al. 2002, Yang 2004). Using an 11-year time series from interior British Columbia, Canada, we investigate responses of avian communities to an ongoing, large-scale outbreak of mountain pine beetles (MPB; *Dendroctonus ponderosae*). In light of this resource pulse, we explore relationships between abundance, richness, and community regulation in attempt to address whether the positive relationship between local richness and resource availability, well-documented across space, is upheld through time. Specifically, we address three related objectives. First, we investigate whether abundance within six avian foraging guilds varied in response to the MPB outbreak. Second, we evaluate support for the more individuals hypothesis and the resource specialization hypothesis by examining statistical relationships between richness and abundance within each foraging guild following the MPB outbreak. Third, we use a randomization approach to determine the extent to which richness of each foraging guild is regulated. We examine the effects of the MPB outbreak separately for each foraging guild because the local regulation hypothesized by Brown et al. (2001) should be strongest within guilds (i.e., groups of species that have similar requirements).

A "regulated" guild should exhibit compensatory colonization and extinction dynamics in that whole-guild rates of colonization are expected to increase when local richness falls below the long-term mean, while

whole-guild rates of extinction are expected to increase when local richness exceeds the long-term mean (Goheen et al. 2005, 2006). Thus, a regulated guild should exhibit less variance in richness about the long-term mean than expected under a random walk process. In our study, the community regulation hypothesis makes straightforward predictions: guilds most reliant on bark invertebrates, in which abundance and/or richness change in response to the MPB outbreak, are expected to show the least evidence of regulation because colonizations from the regional pool should override local extinctions. Similar levels of regulation between guilds, regardless of their response to the MPB outbreak, would directly falsify the hypothesis. Only weak inference can be made from guilds that do not respond to the MPB outbreak: guilds that do not respond to the resource pulse but show evidence of regulation suggest that colonization–extinction dynamics may be influenced by other resources not encompassed by the MPB outbreak, whereas those guilds that do not respond to the MPB outbreak and exhibit no evidence of local regulation suggest that regional factors drive colonization and local extinction.

METHODS

Study sites

Data on avian richness and vegetation structure were collected at 10 study sites in the Cariboo-Chilcotin region of British Columbia, all located within 50 km of the City of Williams Lake (52°08′30″ N, 122°08′30″ W). The sites were 15–35 ha in area, and were all mature unharvested forest stands (80–100 years old). Site composition varied between mixed deciduous/coniferous forest surrounded by grasslands, shallow ponds, and wetlands, to sites composed predominantly of dry coniferous forest with deciduous riparian zones. Composition of tree species varied among the 10 sites, with lodgepole pine (Pinus contorta var. latifolia) being the most common species (mean 39%, range [1–86%]), followed by Douglas-fir (Pseudotsuga menziesii, mean 34%, range [4–82%]), trembling aspen (Populus tremuloides, mean 19%, range [3–73%]), and hybrid white-Engelmann spruce (Picea glauca × engelmannii, mean 14%, range [0–32%]).

The MPB outbreak is the largest ever recorded in the province, and has resulted in widespread mortality of conifers, primarily lodgepole pine, >9.2 million ha in British Columbia in 2007 (Aukema et al. 2006, BCMFR 2007). Mountain pine beetles lay their eggs inside the inner bark of conifers, and their developing larvae, as well as the adults themselves, can be an important food source for insectivorous birds, with resultant increased abundances during outbreaks (Koplin 1969, Bull 1983, Bergvinson and Borden 1992, Martin et al. 2006, Drever et al. 2008). Following attack by MPB, dead and dying pines are colonized further by secondary bark beetles (e.g. Ips; Paine et al. 1997) and wood-boring beetles (Buprestidae and Cerambycidae), an additional food source for several avian bark insectivores (Murphy and Lehnhausen 1998, Powell et al. 2002). As such, food becomes temporarily available at dramatically high levels, constituting a resource pulse for some, but not all, of the avian guilds comprising the community depending on their foraging habits (Ehrlich et al. 1988, Appendix A).

Point counts and estimation of avian richness

Bird populations were enumerated using standardized point counts (Hutto et al. 1986) and playbacks (Johnson et al. 1981), conducted twice annually at the same stations during May and June, from 1997 to 2007. Point count stations were spaced 100 m apart, and varied in number from 10 to 26 per site. Point counts were completed at each station from 05:00–09:30 hours, and lasted 6 min, during which every bird seen or heard within a 50 m radius (0.79 ha) was recorded. We also used playbacks of woodpecker calls at every second point count station. After the initial 6-min count period, the call of each woodpecker species was played twice, each call followed by 30 s of listening time, for a total of 13 min observation time. We noted the species and number of woodpeckers seen or heard calling, singing, or drumming, as well as any other bird species detected, during both the initial 6-min observation and the playback periods within the 50 m radius. Raptors and waterfowl were excluded from analyses.

All birds recorded during point counts were classified into one of six foraging guilds using its main prey type and foraging technique reported in Ehrlich et al. (1988) and Poole and Gill (2000). Aerial insectivores captured prey during aerial pursuits or hawking. Bark insectivores gleaned prey from tree trunks and branches. Foliage insectivores gleaned prey from foliage and occasionally from branches. Ground insectivores fed on the forest floor. Herbivores fed on seeds, greens, nuts, fruit, and nectar. Omnivores fed on a variety of plant and animal prey, none of which comprised less than one-third of their diet. We expected the MPB outbreak would have the strongest effects on bark insectivores because all species within the bark insectivore guild eat MPB. The other three insectivore guilds contained at least one species known to prey on MPB (Appendix A).

For each year/site combination, we calculated a measure of abundance as the density of birds (the mean number of individual detections from each foraging guild seen per point count). Measures of richness depend strongly on survey effort (Lande et al. 2003), and survey effort varied with site area. We therefore standardized richness (S) for effort using sample-based rarefaction (Gotelli and Colwell 2001). Richness for each site/year combination for each foraging guild was estimated as the mean number of bird species accumulated in 20 randomly selected point counts from 1000 permutations of the data. In addition, we calculated richness as the total number of species recorded each year across all 10 sites. Effort varied slightly by year (range: 336–350
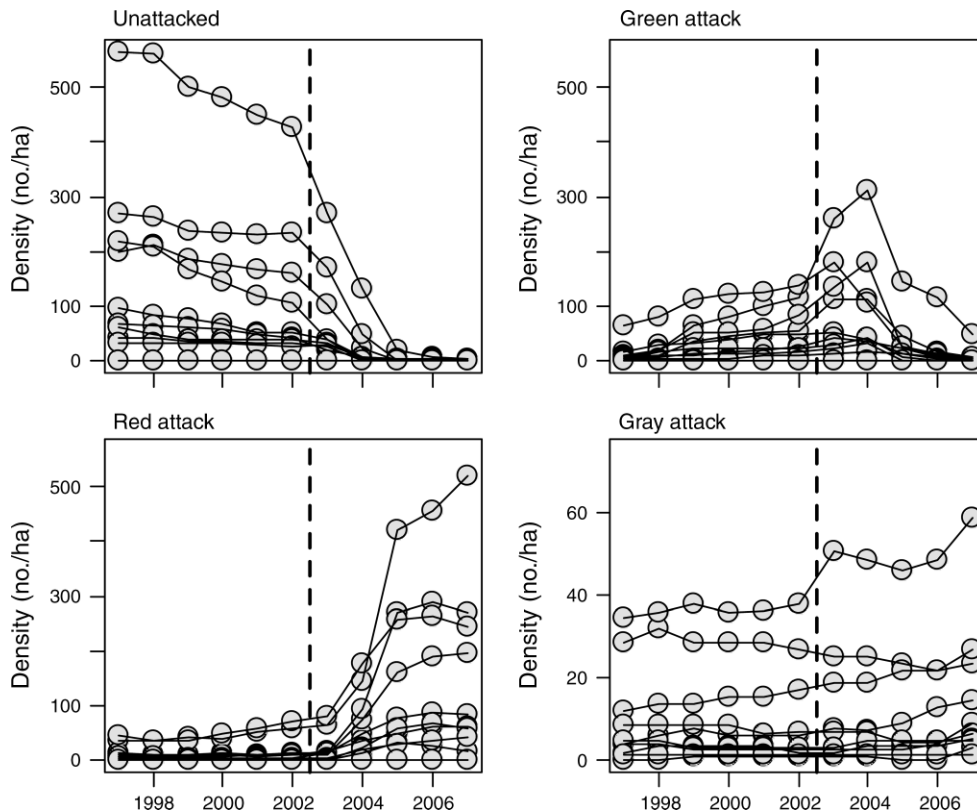
FIG. 2. Changes in densities of lodgepole pines in different phases of attack by mountain pine beetles at 10 forest sites in interior British Columbia, 1997–2007. See the *Methods* for definitions. The vertical dashed line indicates the dividing line between "pre-outbreak" years and "outbreak" periods. Note the different *y*-axis scale for "gray-attack" pines.

counts), and we thus standardized richness to the number of species detected in 300 point counts. These calculations were conducted using the vegan package (Oksanen et al. 2008) in R (version 2.6.1; R Development Core Team 2007).

Changes in habitat measures related to the MPB outbreak

We collected annual data on forest stand characteristics at 11.2 m radius vegetation plots (0.04 ha) centered on each point count station. We measured dbh (diameter at breast height [1.3 m]), and recorded tree species, decay class, and any signs of disease or damage for all trees with dbh ≥ 12.5 cm. Decay class of trees ranged from 1 to 8, according to a classification system where 1 was a healthy tree, 2 was a live tree with evidence of disease or insect damage, 3 was a recently dead tree, 4–8 were dead trees in increasing conditions of decay (Martin et al. 2006). Decay classes 4–8 were uncommon in the data set, and these trees were grouped into one decay class (4+).

Habitat measures related to the MPB outbreak were calculated for each site/year combination. These measures were overall density of lodgepole pine (number of stems per hectare) and density of MPB-attacked pines in decay classes 1, 2, 3, and 4+ (number of stems per hectare). Respectively, these decay classes corresponded

to pines whose names referred to phases of needle color changes that occurred in a sequence when lodgepole pines were attacked and killed by MPB (Safranyik et al. 1974). "Unattacked" pines had no evidence of beetle attack. "Green-attack" pines had green needles, but had evidence of beetle attack (pitch tubes). "Red-attack" pines had red needles, which typically occurred one year after MPB attack, and indicated the tree was dead. Beetle larval densities under the bark can reach high densities in the summer prior to the foliage turning red (Raffa and Berryman 1983, Safranyik and Wilson 2006). "Gray-attack" pines had needles that were falling off, which typically occurred one year following the red-attack stage. In addition, we categorized the time series into two periods: years 1997–2002 were categorized as "pre-outbreak" and years 2003–2007 were categorized as "outbreak" (Fig. 2).

Correlation between abundance and the MPB outbreak

We estimated the correlation between bird abundances for each foraging guild and MPB-related habitat features by comparing a series of six mixed-effects models (Pinheiro and Bates 2000) under an information-theoretic framework (Burnham and Anderson 2002). Site was included as a categorical random effect in all models, which allowed us to treat the site/year

combinations as individual replicates, and to account for the repeated sampling of sites over time. We first fit an intercept-only model to serve as a baseline null model. Densities of MPB-attacked pines at each site depended on the density of available pine trees, and we thus fit a pine density model, which had the overall density of pines at each site as a fixed effect. This model represented the potential for observed patterns of avian richness to vary with stand composition, rather than to the time-varying effects of the beetle outbreak. We then fit four models, each with a different fixed effect: unattacked pines, green-attack pines, red-attack pines, and gray-attack pines. The strength of evidence for each model was evaluated using Akaike's Information Criterion corrected for small sample sizes (AIC_c), and Akaike weight (w) for each model, which serves as a measure of the relative support for each model given the data (Burnham and Anderson 2002). For each site/year combination, we log-transformed bird abundance (N), such that $Y = \ln(N + 0.05)$, which resulted in normally distributed residuals for each model. All models were fit using the maximum likelihood method in package nlme in R (R Development Core Team 2007).

Changes in the relationship between abundance and richness during the MPB outbreak

For each foraging guild, we compared three mixed-effects models representing the alternative scenarios (Fig. 1) through which richness and abundance might vary with the two periods of the MPB outbreak (evaluated as pre-outbreak [1997–2002] or outbreak [2003–2007]). The power function is the canonical relationship between richness and abundance, where richness $= a \times$ abundance^b (Preston 1962, Srivastava and Lawton 1998). This relationship can be linearized by log-transforming both richness and abundance, such that $\log(\text{richness}) = \log(a) + b \times \log(\text{abundance})$. We log-transformed the abundance and richness values, where abundance was transformed as $\ln(N + 0.05)$, and richness (S) was transformed as $\ln(S + 1)$, and fit this linearized relationship using linear mixed models, with log-transformed richness as the response variable, log-transformed abundance and period of outbreak as explanatory variables, and site as a categorical random variable. Model 1 (abundance only) contained only the effect of abundance, and inference was based on the degree that observed abundance overlapped between the two periods of the MPB outbreak (Fig. 1A). Model 2 (outbreak only) included a parameter for an effect of the MPB outbreak on richness, and assumed no correlation between richness and abundance (Fig. 1B). Model 3 (combined) included parameters for both the effects of abundance and the MPB outbreak (Fig. 1C). All models had normally distributed residuals and random effects.

We estimated parameters and their standard errors for effects of abundance and the MPB outbreak on richness based on all three models through model averaging, where parameter estimates and their varianc-es are calculated as weighted averages over all models (Burnham and Anderson 2002). In addition, we used a graphical approach to aid in interpreting results: using a range of observed values for abundance, we calculated predicted values of richness for all guilds from the three models. These values were then averaged over the three models using the Akaike weights as weighting factors to calculate model-averaged predicted values. These model-averaged predicted values were back-transformed to match the original data, and were then plotted against abundance.

Assessing regulation of richness within guilds

Using richness values calculated each year across all 10 sites, we assessed community regulation separately within each foraging guild using a null model approach (Goheen et al. 2005). This approach randomizes observed changes in richness to generate the expected variability in richness through time, as if colonization and local extinction were occurring at random and without respect to richness in the local community. If the observed variability in species richness within a guild is less than expected under the null model, then richness can be viewed as regulated. We determined the observed distribution in annual net changes in species richness, and then randomly drew with replacement from this distribution to generate 10 000 time series of the same length as the observed time series for each guild (11 years). Each randomization was initialized with the same number of species recorded in the first year of the study (1997). The randomizations were bounded between 0 and the total number of species recorded for each guild throughout the course of the study. These randomized time series had the same mean number of species as the observed time series, but yielded variation in species richness expected in the absence of local regulation of species richness. We then calculated the coefficient of variation (CV) for each randomization, and compared the CV of the observed time series to this distribution of 10 000 CVs generated from the randomizations. The proportion of randomized CVs smaller than the observed value then provided a measure (P_{reg}) that the observed time series had reduced variability in species richness relative to a process of random colonization and extinction, and hence provided evidence of local regulation. We interpreted values of $P_{reg} < 0.05$ as strong evidence of regulation, $0.05 > P_{reg} < 0.20$ as weak evidence, and $P_{reg} > 0.20$ as no evidence of regulation. These arbitrary categories were meant as a heuristic device to aid the interpretation of results, and provide a conservative view of regulation because at $P_{reg} = 0.20$, 80% of the CVs from simulations exceeded that calculated from the observed data.

RESULTS

Changes in habitat measures related to the MPB outbreak

The number of unattacked pines at all sites declined gradually from 1997 to 2002, after which the incidence

TABLE 1. Akaike weights for six general linear mixed-effects models relating the abundances of forest birds, categorized into six foraging guilds, to densities of lodgepole pines in different health conditions related to an outbreak of mountain pine beetles (*Dendroctonus ponderosae*) at 10 forest sites in interior British Columbia, 1997–2007.

Guild	Intercept only	Pine density	Un-attacked	Green attack	Red attack	Gray attack
Insectivore						
Aerial	0.22	**0.44**	0.09	0.07	0.08	0.10
Bark	0.01	0.00	0.02	**0.90**	0.00	0.07
Foliage	0.21	0.08	0.09	**0.34**	0.19	0.09
Ground	**0.22**	<u>0.20</u>	<u>0.21</u>	0.13	0.17	0.07
Herbivore	**0.32**	0.12	0.13	0.19	0.11	0.12
Omnivore	**0.26**	0.09	0.13	0.11	0.31	0.11

Note: The model with best support has the Akaike weight in bold, and underlined values refer to second-best models with nearly equal support.

of MPB-attacks increased sharply (Fig. 2). This decline was mirrored by an increase in the number of green-attack pines, which peaked in 2003 and 2004. The number of red-attack pines increased sharply following 2004, such that most sites had nearly 100% mortality of lodgepole pines by 2007. Beetle larvae and adult flying beetles are most abundant during the green-attack phase and in the transition to the red-attack phase (Safranyik and Wilson 2006), such that the resource pulse resulting from the MPB outbreak likely occurred between 2004 and 2005. The density of gray-attack pines, however, continued to rise to the end of the study period in 2007 (Fig. 2).

Correlation between abundance and the MPB outbreak

Abundances of most foraging guilds did not vary strongly with the MPB outbreak, with the exception of a strong positive correlation between abundances of bark insectivores with both green-attack and gray-attack pines, and a weak but positive correlation between foliage insectivores and green-attack pines. The intercept-only model had the strongest support for ground insectivores, herbivores, and omnivores (Table 1), indicating that abundance within these three guilds was unrelated to the MPB outbreak. The pine density model had the most support for aerial insectivores, and the 95% confidence interval for pine density indicated a negative correlation with abundance of this guild (slope = -0.0016, SE = 0.0007, CL: -0.003, -0.0001, all values are mean and 95% CL). The 95% confidence intervals for effects of MPB-related habitat parameters on the abundances of these four guilds all encompassed 0, consistent with the lack of an effect of the MPB outbreak on ground insectivores, herbivores, omnivores, and aerial insectivores. For bark insectivores, the Akaike weights for green-attack model and the gray-attack model sum to 0.97, indicating these two models account for the bulk of the support from the data (Table 1). The slope parameters for the effects of green-attack pines and gray-attack pines indicated a positive correlation between abundances of bark insectivores and densities of MPB-attacked pines (green-attack pines, slope = 0.0038, SE = 0.0011, CL: 0.0017, 0.0059; gray-

attack pines, slope = 0.022, SE = 0.009, CL: 0.005, 0.038). For foliage insectivores, the green-attack model received the most support, with an Akaike weight of 0.34 (Table 1). The slope parameter for the effect of green-attack pines on abundances of foliage insectivores was positive, but had a 95% confidence interval that encompassed 0 (slope = 0.0013, SE = 0.0007, CL: -0.0001, 0.0026).

Changes in the relationship between abundance and richness during the MPB outbreak

The effects of the MPB outbreak on the relationship between abundance and richness varied by foraging guild (Fig. 3; Appendix B). The best model for bark insectivores modeled richness as a combined effect of outbreak and abundance (Table 2). Predicted values of richness, averaged across all three models, indicated that richness of bark insectivores was highest in the outbreak period, when more species were detected for any given abundance than in the pre-outbreak period (Fig. 3). Abundances of bark insectivores were also highest during the outbreak, and shifted the richness/abundance curve to the right (Fig. 3).

Richness of the other five guilds did not change markedly between the pre- and outbreak periods. The "abundance only model" received the strongest support from the data for aerial insectivores, foliage insectivores, herbivores, and omnivores (Table 2), and the relationships between abundance and richness overlapped almost entirely during pre- and outbreak periods (Fig. 3). The best model for ground insectivores was the combined model (Table 2), although support for this model relative to the abundance only model was not strong ($w_3/w_1 = 0.58/0.42 = 1.4$). Model-averaged predicted values of richness indicated that richness of ground insectivores at any level of abundance was slightly lower during the outbreak period than during the pre-outbreak period (Fig. 3).

Assessing regulation of richness within guilds

Richness varied by foraging guild through time (Fig. 4). Richness of aerial insectivores, foliage insectivores, herbivores, and omnivores fluctuated, and showed no
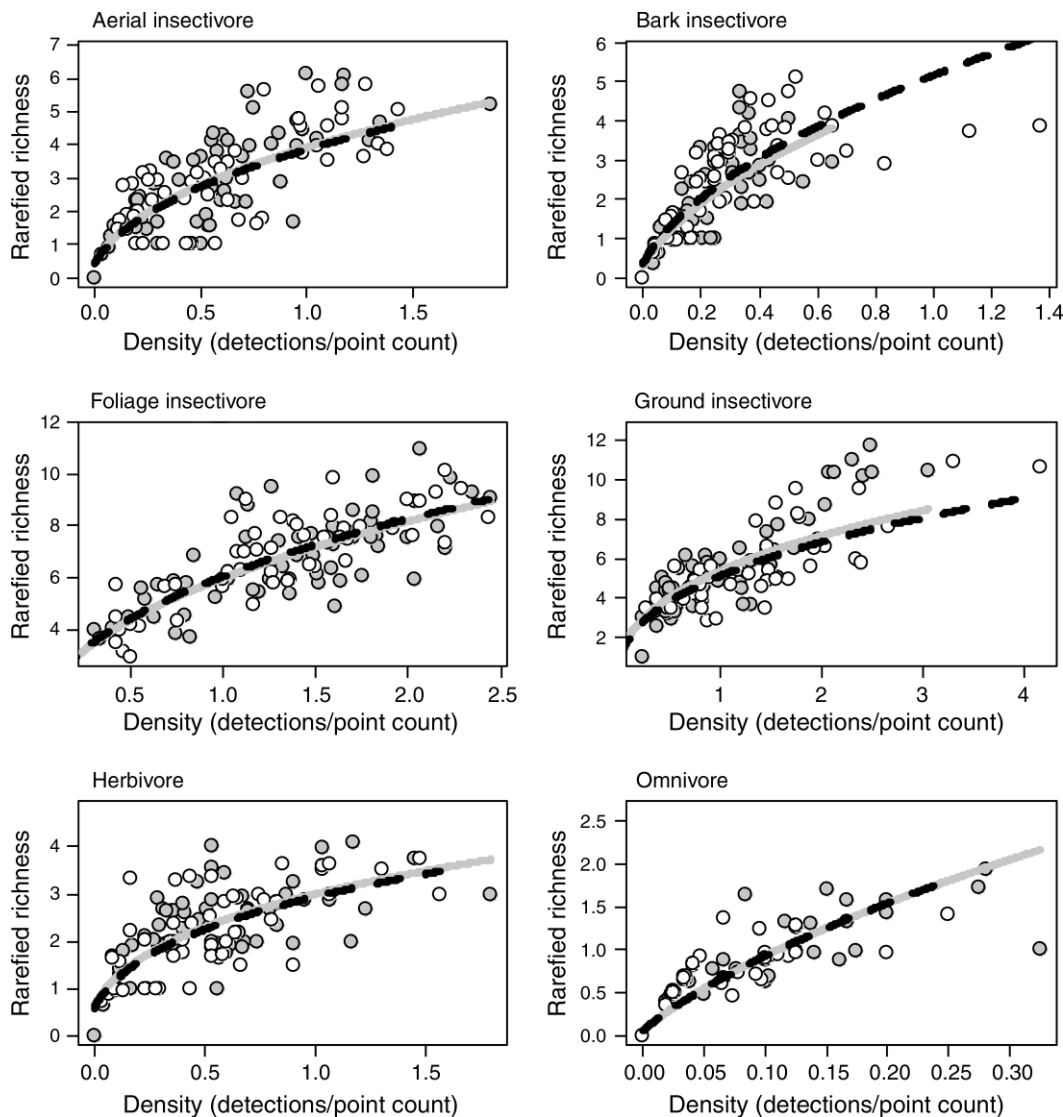
FIG. 3. The relationship between species richness and abundance of forest birds, categorized into six foraging guilds, in relation to an outbreak of mountain pine beetles at 10 forest sites in interior British Columbia, 1997–2007. Each point is a year/site combination, richness is rarefied as the number of species detected by 20 point counts, and abundance is measured as density (number of detections per point count; see the *Methods* for details). Gray-filled circles indicate data from the pre-outbreak period (1997–2002), and open circles indicate data from the outbreak period (2003–2007). Lines depict model-averaged predicted values for pre-outbreak (solid gray) and outbreak (dashed black) periods.

directional trend over the course of the study, while richness of bark insectivores increased, and richness of ground insectivores decreased. The CVs of species richness within the aerial insectivore, foliage insectivore, and herbivore guilds were more constrained than expected from the randomizations (Fig. 4), and provided weak evidence of regulation of richness ($P_{reg} < 0.20$). The observed CVs of the bark insectivores, ground insectivores, and omnivores provided little evidence of regulation ($P_{reg} > 0.20$, Fig. 4). The bark insectivores had the weakest overall evidence of regulation ($P_{reg} = 0.89$); the regulation shown by other five guilds had a mean P_{reg} value of 0.24 (SD = 0.197), and therefore the

level of regulation observed in bark insectivores was outside of the range of the regulation shown by other five guilds ($Z = -7.45$, $P < 0.0001$).

DISCUSSION

Our study provides mixed but generally positive evidence for the role of resource availability in driving the abundance, richness, and regulation of avian communities in mixedwood forests. Assuming that changes in MPB-related habitat features equated to changes food supply, we inferred that bark insectivores (and possibly foliage insectivores) experienced an increase in resource availability over the study period

TABLE 2. Akaike weights for three general linear mixed-effects models relating the richness of forest birds, categorized into six foraging guilds, to bird abundance and different periods of an outbreak of mountain pine beetles (MPB) at 10 forest sites in interior British Columbia, 1997–2007.

	Model		
Guild	Abundance only (A)	Outbreak only (B)	Combined (C)
Insectivore			
Aerial	**0.71**	0.00	0.29
Bark	0.35	0.00	**0.65**
Foliage	**0.63**	0.00	0.37
Ground	0.42	0.00	**0.58**
Herbivore	**0.64**	0.00	0.36
Omnivore	**0.75**	0.00	0.25

Notes: The model with best support has the Akaike weight in bold. Capital letters (in parentheses) following model names refer to models depicted in Fig. 1.

as evidenced by these guilds' positive correlations with green-attack and gray-attack pines. These changes affected richness of bark insectivores and foliage insectivores in a manner consistent with both the more individuals hypothesis and resource specialization hypothesis, suggesting an increase in both number and types of resources is driving abundance–richness relationships.

Bark insectivores showed the strongest response to the MPB outbreak; abundances were positively correlated with green-attack and gray-attack pines, and richness increased beyond that which would be expected by increases in abundance. During the study period, the Black-backed Woodpecker and American Three-toed Woodpecker, which specialize on dead and decaying coniferous trees (Dixon and Saab 2000, Leonard 2001), increased in abundance (Drever and Martin 2007). The appearance of these woodpeckers is consistent with an increase in the number of resource types resulting in tipping the balance of colonization/extinction processes.
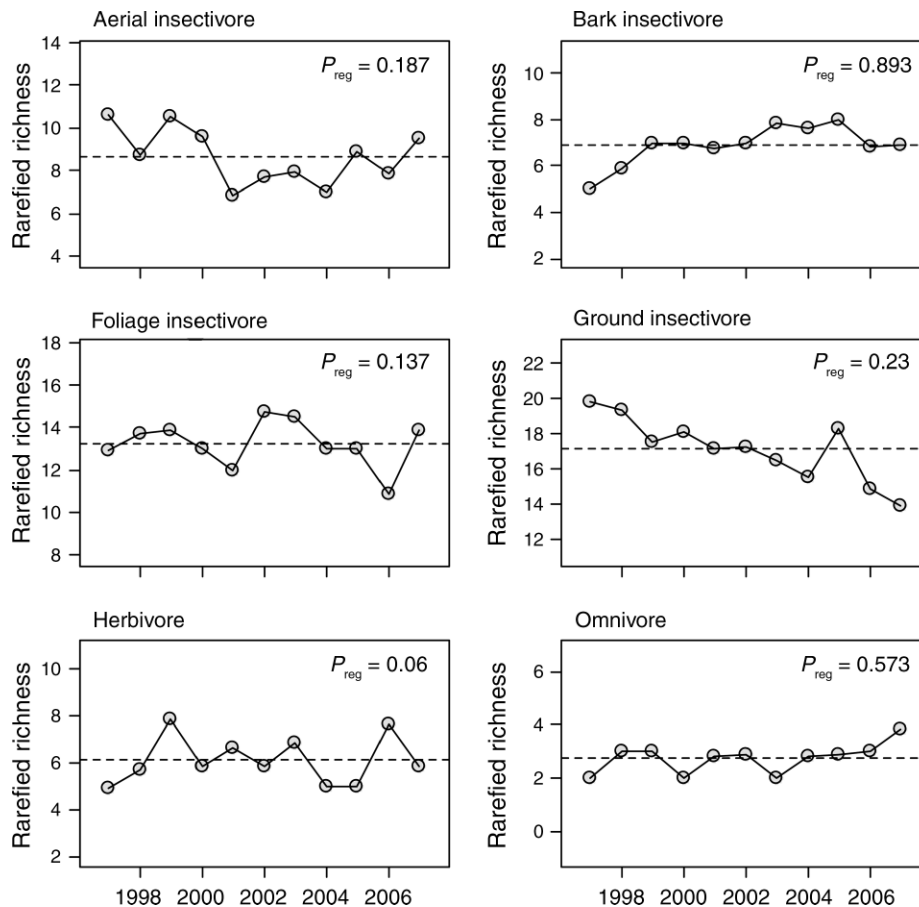

FIG. 4. Changes in species richness of birds categorized into six foraging guilds at 10 forest sites in interior British Columbia, 1997–2007. Horizontal dashed lines indicate mean species richness for each guild. Richness was calculated through rarefaction as the mean number of species seen in 300 point counts each year to account for differing yearly survey effort. P_{reg} indicates the result of a test for regulation of richness and indicates the proportion of CVs of simulated time series of richness that exceed the CV of observed time series. A small P_{reg} value indicates that observed richness is more temporally constrained than would be predicted by random fluctuations in richness.

TABLE 3. Number of species in species pool, mean richness (per year), observed coefficient of variation (CV) in species richness, and regulation of species richness of six avian foraging guilds, at 10 forest sites in interior British Columbia, 1997–2007, in relation to an outbreak of mountain pine beetles (MPB).

Guild	No. species	Mean richness	CV	Effect of MPB outbreak on abundance	Effect of MPB outbreak on richness	Regulation of richness	
						Predicted	Observed
Insectivore							
Aerial	15	8.7	0.15	none	none	yes	weak
Bark	8	6.8	0.12	positive; green-attack and gray-attack pines	combined with effect on abundance	no	none
Foliage	17	13.2	0.08	positive (weak); green-attack pines	none	no	weak
Ground	27	17.1	0.11	none	combined with effect on abundance (weak)	yes	none
Herbivore	13	6.1	0.17	none	none	yes	weak
Omnivore	4	2.7	0.20	none	none	yes	none

In addition, Downy and Hairy Woodpeckers increased in abundance over the study period (Martin et al. 2006, Drever and Martin 2007), shifting the richness/abundance curve to the right (Fig. 3), consistent with an increase in the food supply for this guild during the MPB outbreak.

Abundances of foliage insectivores fluctuated with the densities of green-attack pines, and richness of this guild was weakly regulated, providing a combination of observations that potentially falsify the hypothesis of resource-limited regulation of richness in this guild (Brown et al. 2001). However, two considerations temper this potential falsification: first, the foliage insectivore guild is composed of 17 species, of which only five (29%) are known to feed on MPB. Second, the densities of green-attack pines rose and then returned to initial conditions by the end of the study period (Fig. 2). Therefore, changes in food supply resulting from the MPB outbreak may not have been borne out for the entire guild, or may not have lasted long enough to disrupt the balance of local extinction and colonization events.

Given these observations, we predicted that richness of bark insectivores and possibly foliage insectivores should show little evidence of regulation, whereas the other guilds should show evidence of regulation. These predictions were borne out for bark insectivores, aerial insectivores, and herbivores, but not upheld by foliage insectivores, ground insectivores, and omnivores (Table 3). Temporal patterns of richness from most foraging guilds provided evidence of weak regulation at best, and this weak regulation may be a general property of bird communities. Strong regulation due to food limitation would be expected in guilds that could be expected to deplete the food supply within one year. This depletion may occur within herbivores (Power 1992, Jefferies et al. 1994), the guild for which we found the strongest evidence of regulation ($P_{reg} = 0.06$), but may not occur as frequently within the insectivore guilds. For example, behavioral studies of foraging provide little evidence that food supply of aerial insectivores is depleted over the breeding season (Blancher and Robertson 1987,

Lovette and Holmes 1995). Breeding bird communities are composed of residents and migrants, whose respective richness may be controlled by different forces (Webster et al. 2002, Hurlbert and Haskell 2003), such that a large proportion of the bird community may be affected by changes on the wintering grounds. Most of the bark insectivores are winter residents, which may explain why this guild showed the strongest response to the MPB outbreak. The strong link between abundance and richness in these bird communities indicates that changes in richness are largely governed by changes in abundance (Fig. 3). If so, community dynamics of each guild should result from the combined population dynamics of their constituent species. The majority of species in our study were small to medium-sized passerine birds, which tend to have population dynamics characterized by weak density dependence with environmental stochasticity explaining large proportions of the variance in population growth rates (Sæther and Engen 2002). Evidence for regulation of richness has primarily come from studies in grasslands, oceans, or deserts (Collins 2000, Lekve et al. 2003, Goheen et al. 2005), simple habitats where interactions among species may be quite strong. In contrast, habitat complexity in forests may allow for greater resource partitioning among birds (Hurlbert 2004), resulting in decreased interaction strength. Parody et al. (2001) found that interannual differences in bird richness increased in magnitude as the Michigan landscape transformed from a grassland/agricultural matrix to mixed forest, consistent with weakened regulation in more complex habitats. For these reasons, we suggest weak regulation of richness may be a general feature of bird communities, and for forest birds in particular.

Forested habitats often have high avian richness (Hurlbert 2004), and the vast majority of species forage on insects (Appendix A). Thus, strong links exist between outbreaks of forest insects and avian biodiversity (Yang et al. 2008). Composition of local communities can vary markedly over time as species colonize and go locally extinct (Parody et al. 2001), and we have shown that resource pulses can affect rates of local

extinction and colonization. Resource pulses can reduce the rates of local extinction by allowing more individuals (and thus more species) to persist locally, or they can create novel resources, thereby facilitating colonization from the species pool. Both processes occurred for bark insectivorous birds during the mountain pine beetle outbreak. This connection between temporal variation in species richness and resource availability suggests the community regulation hypothesis of Brown et al. (2001) can be understood as a special case of species–energy theory (Wright 1983), in that local richness varies with resource availability, and is regulated only when resources are relatively constant. When coupled with long-term data, many of the concepts underlying theory on resource pulses (Nowlin et al. 2008, Yang et al. 2008) and community regulation (Brown et al. 2001) potentially can be unified under the auspices of species–energy theory.

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APPENDIX A

A list of species seen at 10 forest sites in interior British Columbia, 1997–2007 (*Ecological Archives* E090-071-A1).

APPENDIX B

Model-averaged parameter estimates for three models explaining variation in species richness of forest birds, categorized into six foraging guilds, as a function of bird density, and time period of an outbreak of mountain pine beetles (pre-outbreak and outbreak), in British Columbia, 1997–2007 (*Ecological Archives* E090-071-A2).