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The efficacy of common species as indicators: avian responses to disturbance in British Columbia, Canada

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Abstract Common species can be major drivers of species richness patterns and make major contributions to biomass and ecosystem function, and thus should be important targets for conservation efforts. However, it is unclear how common species respond to disturbance, because the underlying reasons for their commonness may buffer or amplify their responses to disturbance. To assess how well common species reflect changes in their community (and thus function as indicator species), we studied 58 bird species in 19 mixed conifer patches in northern British Columbia, Canada, between 1998 and 2010. During this time period two disturbance events occurred, stand level timber harvest and a regional-scale bark beetle outbreak. We examined relationships among densities of individual species, total bird density and overall species richness, correlations in abundance among species, and responses to disturbance events. We found three broad patterns. First, densities of common species corresponded more strongly with changes in total bird density and overall species richness than rare species. These patterns were non-linear and species with intermediate-high commonness showed similar or better correspondence than the most common species. Second, common species tended to be more strongly correlated with abundances of all other species in the community than less-common species, although on average correlations among species were weak. Third, ecological traits (foraging guild, migratory status) were better predictors of responses to disturbance than species commonness. These results suggest that common species can collectively be used to reflect changes in the overall community, but that whenever possible monitoring programs should

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be extended to include species of intermediate-high commonness and representatives from different ecological guilds.

Introduction

Land managers trying to maintain biodiversity need to balance the conflicting needs of different species in addition to providing for anthropogenic land uses. The complexity of these systems means it is critical to monitor the effectiveness of management practices to ensure that biodiversity objectives are being met (Lindenmayer and Franklin 2002). However, it is often not possible to monitor or actively manage all species, so indicator species are frequently used. Indicator species may be defined as "a species whose presence indicates the presence of a set of other species and whose absence indicates the lack of that entire set of species," and also as "a species that reflects the effects of a disturbance regime or the efficacy of efforts to mitigate disturbance effects" (Lindenmayer et al. 2000).

Historically ecosystem management has focused heavily on rare and threatened species. While areas retained for rare species can adequately provide for other taxa in some areas (Lawler et al. 2003), often the habitat requirements or distribution of rare species can be different from the majority of other species in the region (Gregory and Gaston 2000; Orme et al. 2005; Pearman and Weber 2007). Alternative approaches for selecting surrogate or "indicator" species are being promoted that attempt to better reflect the requirements of the entire community. Criteria for selection can include sensitivity to disturbance, degree of threat, known importance to the ecology of the system, and abundance or ease with which the species can be monitored (Lambeck 1997; Carignan and Villard 2002; Bakker 2008; Amici and Battisti 2009).

There is increasing literature on the importance of managing and monitoring common species (Gaston 2008; Gaston and Fuller 2008). Common species make significant contributions to biomass and often to ecosystem function (Gaston and Fuller 2008), and can be major drivers and indicators of species richness patterns (Lennon et al. 2004; Pearman and Weber 2007; Mazaris et al. 2010). Because common species distributions correspond with overall species richness, common species themselves may be good indicators of the richness of, or changes to systems (Gaston 2008). A number of broad scale monitoring programs have been or are being established which have greater statistical power to monitor common species than rare species (Sundt 2002; Mattfeldt et al. 2009; Nielsen et al. 2009).

Common species are frequently defined as those that are widespread, which generally equates to being locally abundant (Lennon et al. 2004; Pearman and Weber 2007; Gaston 2008). Common species may be common for a number of reasons; because they are habitat or foraging generalists, use the most commonly available resources, have greater effective fecundity, or are resilient to change (Gregory and Gaston 2000; Münzbergová 2005). Therefore, common species may respond to disturbance similarly to rarer species, or they may show less severe or delayed responses (Githiru et al. 2007), or no response to disturbance events that have strong effects on less-common species. Consequently, it is important to assess how well monitoring programs that focus on the patterns for common species can reflect trends of other less-common species and the overall community.

Birds may be suitable indicator species because their ecology is well understood, they respond to habitat changes at multiple spatial scales, they include a wide range of trophic

guilds, and they are easily detected (Carignan and Villard 2002; Padoa-Schioppa et al. 2006). We studied bird populations in mixed forest stands in interior British Columbia, Canada, affected by two major disturbance events; timber harvesting and insect outbreak. The recent outbreak of a native bark beetle (mountain pine beetle, *Dendroctonus ponderosae*) over much of western North America has resulted in the mortality of large areas of mature lodgepole pine (*Pinus contorta* var. *latifolia*) (Bentz et al. 2010; Coops and Wulder 2010). Both harvesting and the recent bark beetle outbreak are known to affect the population densities of bird species at these forest stands (Drever and Martin 2010; Norris and Martin 2010), providing an opportunity to examine how responses to disturbance vary between common and rare species.

This paper examines the potential and the particular conditions for common species to function as good indicator species. First, we examined how well species densities corresponded with changes in the total abundance and species richness of the community as they experienced disturbance by harvesting and insect outbreak, and whether the strength of the correspondence varied with species commonness. Second, we assessed how strongly species densities were correlated with each other, and whether common species were more strongly correlated with all other species than less-common species. Third, we assessed how all species in the community responded to disturbance and whether the type and magnitude of the response was related to species commonness or to other ecological traits.

Methods

Study sites

This study was conducted between 1998 and 2010 at 19 forest sites (15–32 ha) in the Williams Lake area of British Columbia, Canada (52°08′30″N, 122°08′30″W). All sites were dominated by conifer species, but varied in the relative proportions of lodgepole pine, Douglas fir (*Pseudotsuga menziesii*), hybrid white-Engelmann spruce (*Picea glauca* × *engelmannii*), and the deciduous trembling aspen (*Populus tremuloides*). All sites were initially mature forest (80–120 years old) but nine sites were commercially harvested during the study; one site in 1998, one in 2000, four in 2001, two in 2002 and one in 2004. Harvesting was done according to standard silvicultural prescriptions and ranged from a "partial harvest" where 15–30% of trees were removed, to "clearcut with reserves" where 50–90% of the trees were harvested. Trees retained after harvest were mostly aspen and veteran Douglas fir. Further details on the study sites can be found in Drever and Martin (2010) and Edworthy et al. (2011).

Mountain pine beetle outbreak

An outbreak of mountain pine beetle (MPB) occurred in this area, peaking in 2004 and killing almost all lodgepole pine (Drever et al. 2009; Edworthy et al. 2011). MPB emerge and fly to new areas during summer. They deposit eggs into the bark of live pine, and the larvae burrow under the bark over winter. Females release pheromones which attract males and encourage mass attacks on the tree. During an outbreak all mature pine trees in a local area tend to be colonized by beetles over a short time period. Trees attacked by MPB typically die one or two years after infestation. Dead trees are colonized by other wood-boring invertebrates, which are generally found deeper in the wood than MPB (Paine et al. 1997). Bird populations may change during the outbreak due to increases in the availability

of MPBs, dead trees, and other invertebrates colonizing the dead trees. The increase in invertebrates and dead trees resulted in higher woodpecker populations, consequently cavity availability also increased after the outbreak (Drever and Martin 2010; Edworthy et al. 2011). The eventual collapse of beetle-affected trees and the subsequent change in forest structure may have also affected bird populations.

We established between 9 and 32 point count stations (median = 20) at 100 m intervals on each site. Each year vegetation surveys were done in an 11.3 m radius around every point count station. Details of the vegetation surveys can be found in Drever et al. (2008), but they involved measuring the diameter at breast height [dbh (1.3 m)] of all lodgepole pine $\geq$ 12.5 cm dbh and surveying all trees for evidence of attack by boring invertebrates. We calculated the basal area of pines in the 0.04 ha plot at each point count station, averaged the results for each site-year combination and converted the results to a per hectare estimate. As a measure of beetle outbreak we calculated the proportion of all pines (alive or dead) that had evidence of beetle attack.

Bird density and species richness

From 1998 to 2010 each point count station was surveyed for birds twice annually during the summer months (May–mid-June). Surveys were conducted between 5:00 am and 10:30 am. During each survey the species and abundance of all birds observed or heard within a 50 m radius (0.79 ha) of the point count station were recorded. Each station was counted with one regular survey that was 6 min long, and a second that included a playback of woodpecker calls and was 13 min long. Playbacks involved broadcasting a recording of the call and drum of each of seven woodpecker species twice, then listening for a 30 s interval. Playback surveys were done on every second station to reduce double counting of woodpeckers. We assumed detection probability did not change with harvest as has been found in other similar studies (Mahon et al. 2008).

For all analyses in this paper we only considered passerine birds that were observed during surveys on at least ten separate site-years (58 species). Density estimates were obtained by dividing the total number of individuals detected at a site-year by the number of surveys done, and then dividing the result by 0.79 to convert it to a per hectare estimate. We assessed the commonness of each species by averaging density estimates across all site-year combinations. A summary of species four-letter codes, common names, scientific names, average density (commonness) and general ecological categories (foraging, migratory and cavity-using) are provided in Appendix 1. We refer to species with a relatively high average density as being "common".

Species richness estimates vary with sampling intensity, so we used sample based rarefaction (Gotelli and Colwell 2001) to standardize estimates by the number of surveys done. Rarefied species richness for each site-year was estimated by averaging the number of species seen in 1000 permutations of 18 randomly selected point count surveys using the vegan package (Oksanen et al. 2010) in R (R Development Core Team 2010). The threshold was set to 18 point counts because this was the minimum number of surveys done at any of the sites.

Data analyses: species' correspondence with community-level parameters

To establish how well each species corresponded to changes in the community we correlated the density of each species in a site-year with both rarefied species richness and total bird density. Species at high densities may strongly affect patterns of total bird

density, so total bird density values were calculated using all species considered except the species with which the correlation was done. We used rank-based Kendall's correlation because the data were not normally distributed and to account for nonlinear relationships. Our data were potentially autocorrelated through time and space so we repeated the correlations excluding each site and year one at a time. We used the median of these accumulated correlation coefficients as an estimate of the true correlation coefficient. To assess whether common species reflect changes in the community better than less-common species we regressed the median of the correlation coefficients for both richness and total bird density against the average density of each species across all site-years. We had no a priori expectation of the form the relationship might take so we constructed a linear regression, a quadratic regression, and a linear regression using the log of species average density. The relative support for three models provided by the data was determined by calculating the Akaike weight (w_i) for each model, which is exp ($-0.5 \times \Delta$AICc score for that model) divided by the sum of these values across all three models. ΔAICc is the difference in AICc values between each model and the best model (the model with the smallest AICc value) (Burnham and Anderson 1998).

Data analyses: species correlations

There are limitations with using species richness as a means of monitoring change within ecosystems because changes in the species composition of a community may not be detected (Lindenmayer 1999; Azeria et al. 2009). Furthermore, it has been argued that the spatial relationship between common species occurrence patterns and richness may be at least partially attributed to statistical factors rather than just biological factors, driven by the species richness distribution among sites (Sizling et al. 2009). We therefore examined how well common species reflect the patterns of other species by correlating the density of all species-pairs for each site-year combination. As for the community-level assessments, we repeated the correlations excluding each site and year one at a time to account for the random effects. We took the median of the accumulated coefficients for each species pair as an estimate of the true correlation coefficient. To determine how well each species correlated on average with all other species, we then took the geometric mean of the absolute value of all the correlation coefficients that included that species. The geometric mean is the exponential of the mean logged-values and was used because of the skewed distribution of correlation coefficients for some species. We will refer to this geometric mean for each species as the "averaged correlation coefficient". We regressed the averaged correlation coefficient of each species against their average density to determine whether common species correlated more strongly with other species than less-common species. Again we constructed a linear regression, a quadratic regression, and a linear regression using the log of species average density and used Akaike weights (w_i) to examine the relative likelihood of the three models.

Data analyses: responses to disturbance

We used mixed-effect models to establish how each bird species responded to disturbance. For each species we included only data from sites where the species was seen at least once during the study (sample sizes are indicated in Appendix 2). Sites with no detections during the entire study were assumed to provide unsuitable habitat. The dependent variable used in the models was the total number of individuals observed during all surveys at a site in a particular year. For woodpeckers we only used data from the playback surveys. The models

included the number of surveys conducted in a site-year as an offset. All models used a Poisson distributed error structure that catered for overdispersion (i.e. quasipoisson) and included site and year as categorical random effects. Models were fitted with maximum likelihood methods using the lme4 package in R (Bates and Maechler 2010). Five models were constructed for each species:

- The null model included only an intercept.
- The harvest model included whether a site was harvested or not.
- The pine model included the average basal area (m^2/ha) of lodgepole pine for a particular site-year.
- The MPB model included the proportion of pine (alive or dead) that were affected by MPB, and the basal area of pine.
- The MPB-harvest model included the proportion of pine (alive or dead) that was affected by MPB, the basal area of pine, and whether the site was harvested.

The five models for each species were compared using QAICc, which accommodates for overdispersion and small sample sizes (Burnham and Anderson 1998). The dispersion parameter for each model was calculated by summing the squared Pearson's residuals of the MPB-harvest model and dividing this value by the number of observations minus the number of model parameters (Zuur et al. 2009). If the data were under dispersed the model was fitted using a dispersion parameter value of one, producing a QAICc value equal to the AICc.

The results for each model are presented as the QAICc value relative to the best model in the set (i.e. ΔQAICc). A difference in QAICc value of two or more units provides strong support that the models differ in explanatory power (Burnham and Anderson 1998). We compared the QAICc value of each model to that of the next simplest model(s). The harvest and pine models were compared to the null models, the MPB models were compared to the pine models and the MPB-harvest models were compared to both the harvest and MPB models. If the difference in QAICc value ≥ 2.0, then we assumed the model with the lower value was better. If the better model contained one of the disturbance variables (MPB or harvest) we assumed that the species showed a strong response to this type of disturbance. The best model identified with this approach (i.e. lowest QAICc value of all models considered for a particular species) may include parameters that have only weak support (ΔQAICc < 2). Therefore we estimated the type and magnitude of species responses to disturbance by calculating the model-averaged coefficients for the effect of both harvesting and MPB (Burnham and Anderson 1998).

We used classification tree analysis to determine whether the response to disturbance by species varied with how common they were, or with other aspects of their ecology. Classification trees can model strongly nonlinear, unbalanced data with missing values and can test for high order interactions (De'Ath and Fabricius 2000). Classification trees explain variation in a single response variable by splitting the data into the most homogenous groups based on categorical or numerical predictor variables. The first split involves making all possible binary splits of the observations for each predictor variable. We set the limitation that each of the resulting groups had to contain at least five species. For each split the two resulting groups are defined by the dominant category and the error of the model is expressed as the rate at which observations are misclassified. The optimal split is the one with the lowest misclassification. This splitting is repeated for each sub-group to produce a dendrogram. The predictive accuracy of classification trees can be over-estimated by the misclassification rates and is better estimated from cross-validated relative error. Cross-validation is done by taking a random selection of 90% of the data and fitting a

model. This model is then used to predict values in the remaining 10% of data (De'Ath and Fabricius 2000). The rate at which the smaller sub-set of data is misclassified is averaged over 1000 permutations to determine the cross-validated error of the model.

To assess the response to disturbance, we constructed two classification trees; one for harvesting and one for MPB. In each case, we classified responses by species into one of four categories, depending on whether the species responded strongly or weakly to the disturbance event (as determined by the change in QAICc value from the relevant model comparison), and whether the response was positive or negative (as determined from the model-averaged coefficients). The four independent variables considered for all models were:

- Average species density (i.e. commonness).
- Foraging guild: aerial insectivore, bark insectivore, foliage insectivore, ground insectivore, herbivore, omnivore.
- Migratory: short-distance, long-distance or resident.
- Cavity-nesting guild: primary cavity-nester (i.e. excavator), weak primary cavity-nester, secondary cavity-nester or non-cavity-nester.

For both harvesting and MPB outbreak we identified the optimal model by selecting the tree size with the lowest cross-validated error (De'Ath and Fabricius 2000). We examined all alternative splits to determine whether there were any models with comparable explanatory power. All trees were constructed using the R package 'mvpart' (Therneau et al. 2010).

Results

Species' correspondence with community-level parameters

Common species were more strongly correlated with both total bird density and rarefied species richness than less-common species (Fig. 1). For total bird density, support for the
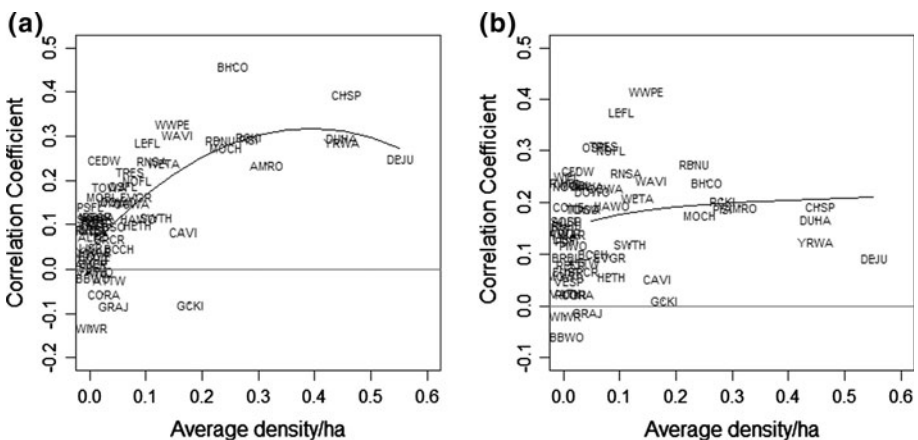

Fig. 1 Species average density (i.e. commonness) in relation to the coefficient of Kendall's correlation between the density of that species in a site-year and **a** total bird density and **b** rarefied species richness ($N = 58$ species). The *grey line* indicates a coefficient of zero. The *curved black line* is the predicted **a** quadratic and **b** lognormal relationship

quadratic model ($R^2 = 0.30$, $df = 55$, $P < 0.001$, $w_i = 0.53$) was comparable to the logged-density models ($w_i = 0.41$) and greater than for the linear model ($w_i = 0.06$). For species richness, support for the logged-density model ($w_i = 0.49$) was comparable to the quadratic model ($w_i = 0.48$) and greater than for the linear model ($w_i = 0.03$), although all models had low explanatory power ($R^2 = 0.10$, $df = 56$, p = 0.007 for the logged model, and $R^2 = 0.12$, $df = 55$, $P = 0.009$ for the quadratic model). The four most common species all had negative residuals for the logged model of species richness (Fig. 1b), indicating this model tended to over-predict correlations with species richness for the most common species.

Species correlations

Almost 25% of the correlations among species were significant at $P = 0.05$. Common species were more strongly correlated with other species on average than less-common species, although the strength of the relationship was weak for all species (averaged correlation coefficients < 0.08, Fig. 2). There was greater support for the log relationship ($w_i = 0.62$) than the quadratic ($w_i = 0.35$) and linear relationships ($w_i = 0.02$). Both the log and quadratic models had an R^2 of 0.2 and a P-value < 0.01 ($N = 58$).

Responses to disturbance

Species varied widely in their responses to timber harvest and the MPB outbreak. Of the 58 species examined, 45% showed no strong (i.e. ≥ 2 unit decrease in QAICc) change in density in response to the either harvesting or the MPB outbreak (Appendix 2). Almost half of the species showed a strong response to harvesting, with 34% increasing in density and 10% decreasing. Nearly half of species (47%) responded to the abundance of pine, with the majority of species decreasing in abundance as the basal area of pine increased. Fewer species (16%) had a strong response to the MPB outbreak with 7% of species increasing in density and 9% of species decreasing (Appendix 2).

How species responded to the disturbance events was more strongly related to their ecological traits than to their commonness. Classification tree analysis of the strength and direction of species' responses to disturbance indicated that foliage insectivores were likely to have a weak negative response to harvesting. Species in the other foraging guilds

Fig. 2 Species average density (i.e. commonness) in relation to the average correlation with other species ($N = 58$ species). For each species pair we correlated the density of birds for each site-year. The average correlation for each species is the geometric mean of the correlation coefficient for all pairings that included that species. The curved *black line* is the predicted log relationship
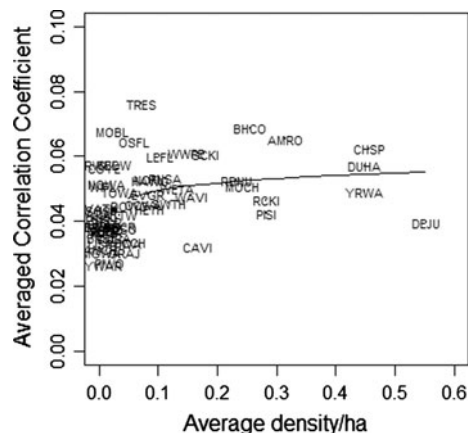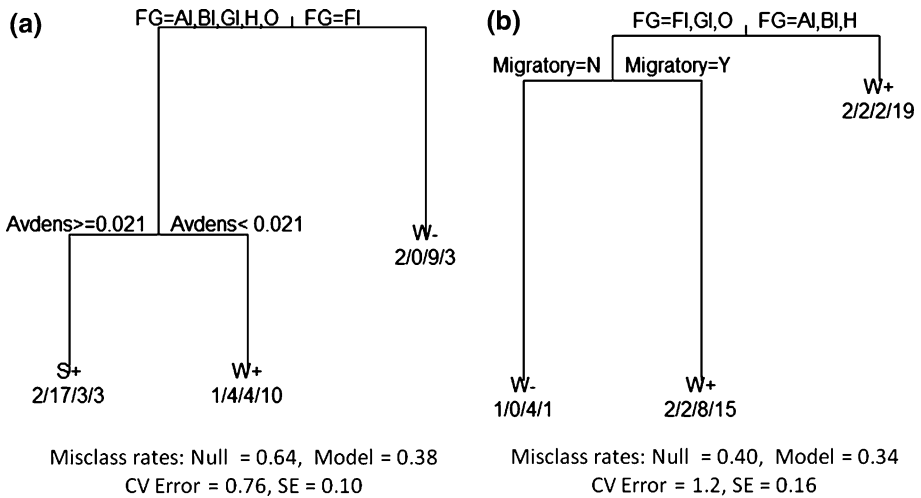
Fig. 3 The minimum classification trees for the result of the mixed-effect models for **a** harvesting and **b** mountain pine beetle (MPB; proportion of pine with evidence of beetle attack). Each mixed-effect model (Table 2) is classified as *S* strong or *W* weak, positive (+) or negative (−), where strength is defined as a decrease in QAICc by two or more units compared to the next simplest model and the sign of the model is determined from the model-averaged coefficient. The terminal end of each bar on the classification tree indicates the predicted classification for that group, and the number of models given that classification with results presented to indicate their true classification (W−/W+/S−/S+). The relative length of the *bars* indicates the relative contribution of the variable to the explanatory power of the model. FG indicates foraging guild, with the following categories: *AI* aerial insectivore, *BI* boring insectivore, *FI* foliage insectivore, *GI* ground insectivore, *H* Herbivore, *O* Omnivore. Avdens is the average density of the species across all site-years (i.e. commonness). Migratory indicates whether the species were migrants (*Y*) or residents (*N*). For the misclassification rates, the null rate is the misclassification error when the rule "go with the majority" is used. The model rate is the misclassification rate found from using the stated model. The CV error is the cross-validated error obtained by building the tree from a subset of the data and fitting it to the remaining data and SE is the standard error around the iterations

generally had a positive response to harvesting, but a strong result (ΔQAICc $\geq$ 2) was more likely for species of intermediate or high commonness ($\geq$0.021 birds/ha) (Fig. 3a). These two criteria (foraging guild and commonness) resulted in 62% of species responses being correctly classified. The cross-validation process indicated support for this model and there were no suitable alternatives. For the MPB outbreak, cross-validation indicated that the null model was optimal (the null model predicts that all species will have the response that was most prevalent in the data set, in this case weak positive responses). The next simplest model was within one standard error of the null, and so despite the low predictive ability of this model we present the results here to examine the traits that best differentiate species' responses to the MPB outbreak. Most species had a weak positive response to the MPB outbreak, except for resident foliage insectivores, ground-insectivores and omnivores that had primarily weak negative responses (Fig. 3b). These two criteria correctly classified 66% of species.

Common species tended to have less variable responses to disturbance than rare species, as evidenced by the decreasing range of coefficient values as species became more common (Fig. 4). The decreasing spread of coefficients with increasing commonness was less apparent for harvesting than it was for the MPB outbreak. Both common and less-common species were found to have strong responses (positive and negative) to harvest. Strong
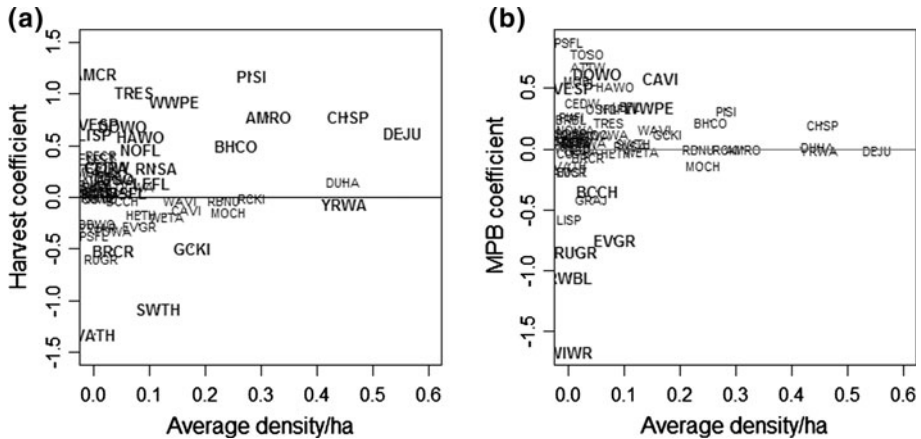
Fig. 4 Species average density (i.e. commonness) in relation to the model-averaged coefficients for **a** harvesting and **b** mountain pine beetle (MPB; proportion of pine with evidence of beetle attack). The *horizontal black line* indicates a coefficient of zero. Species codes are in *larger bold font* if the QAICc value of the model containing this variable was at least two units lower than the next simplest model, indicating support for the importance of this variable. $N = 58$ species

positive and negative responses to the MPB outbreak were found for species of interme-diate or less-common species (<0.2 birds/ha), but not for any of the most common species (Fig. 4b).

Discussion

There are a number of appealing arguments why monitoring common species is practical, useful, ecologically meaningful and important (Gaston 2008; Gaston and Fuller 2008). Our results largely support the growing literature indicating that common species are relatively good at reflecting changes in the broader community, making common species potentially good indicator species. However, our study also highlights some potential concerns if monitoring programs were to focus exclusively on the most common species. These concerns could be addressed by including species of intermediate-high commonness and species representing the full range of ecological traits found in the community.

The first support we found for using common species as indicator species was the stronger correlation they had with both overall species richness and total bird density compared to rare species. The relationship was non-linear and the relative increase in correspondence decreased as intermediate to higher density species became more common. Our results are consistent with other studies demonstrating that common species contribute more to patterns of species richness than rare species (Lennon et al. 2004; Pearman and Weber 2007; Mazaris et al. 2010), although in our results all species had fairly weak relationships. The correspondence between common species and these community-level parameters may result from common species responding more strongly than rare species to increases in energy availability (Jetz and Rahbek 2002; Evans et al. 2005), which may drive changes in total abundance of the community. An alternative hypothesis is that common species may respond more to anthropogenic activities and potentially drive community composition (La Sorte and Boecklen 2005). Species in natural communities

often co-vary positively, which has been taken to mean that abiotic factors have a greater influence than competitive interactions on fluctuations in species abundances (Houlahan et al. 2007). This can explain why many studies observe a strong correlation between species richness and total abundance (Pautasso and Gaston 2005) and therefore why common species can track changes in both of these measures in a community.

Species with intermediate-high abundances had similar or better correspondence with community parameters than the most common species. For example, the relationship between species average density (commonness) and the correlation coefficients of each species' abundance with total bird density (Fig. 1a) was quadratic or log-linear in form. Further, a qualitative examination of the analogous relationship with rarified species richness reveals that correlation coefficients with overall species richness were lower for the four most common species compared to species of intermediate-high commonness (Fig. 1b), which may indicate that densities of these most common species fluctuated differently with species richness than other species. This may occur if common species are not sensitive or are less sensitive to disturbance events, for example if they are generalists and can adapt to changes in the system. In light of these results, we treat the statistical model of the positive decelerating relationship between species' commonness and overall species richness with caution and recommend that sampling programs include species of intermediate-high commonness whenever possible.

The second support for using common species as indicators was that correspondence between species was greater for common than less-common species. These results provide support for the use of common species as indicators when compared to less-common species. However, most of the relationships were weak and the poor correspondence between taxa stimulates the question of whether it is appropriate to use the indicator species concept at all, a topic which has been heavily debated (Niemi et al. 1997; Lindenmayer et al. 2000; Lindenmayer and Fischer 2003). An in-depth review of this debate is beyond the scope of this paper and has been adequately conducted elsewhere. We believe that multi-species monitoring is a critical part of biodiversity management programs, and our results suggest that examining single species will not capture all changes in the rest of the community. However, close correspondence between all species is not critical if indicator species are used to detect broad disturbance events that have multi-species impacts, rather than changes in all other species. Monitoring programs may address this low community-level correspondence by having multi-species surveys that includes species of intermediate to high commonness and representatives from all ecological guilds.

The third result we found supporting the use of common species as indicator species relates to how they responded to disturbance. Common species showed the full range of responses to harvesting that were displayed by less-common species (i.e. strong and weak, positive and negative responses), and the species' responses to disturbance were more strongly related to their ecology (foraging guild and migratory status) than their commonness. These results highlighted one of the advantages of using common species as indicators, which is that stronger evidence for effects of disturbance can be found for common species due to the greater statistical power that can be achieved. While species' responses to disturbance largely supported the use of common species as indicators, they also highlighted other concerns about monitoring only the most common species, including that none of the most common species showed a significant response to the MPB outbreak, and that the range of responses to disturbance (i.e. model coefficients) potentially decreased with species commonness.

Relatively few species (16%) showed a strong response to the MPB outbreak, so the lack of a strong response by the most common species may be due to chance. Alternatively,

the lack of a strong response could suggest that common species had greater resilience to this disturbance event. Although the MPB outbreak was a major disturbance event throughout the region, it had fewer immediate impacts than timber harvesting, and its effect varied with local forest composition. Suitable indicator species need to respond to all major disturbance events, not just the most severe ones, so the potential resilience of the most common species is a concern. However, this concern could be alleviated by extending the sampling program to include all ecological guilds and species of intermediate-high commonness, some of which showed a strong response to the outbreak.

The lower magnitude of response coefficients for common species (Fig. 4) raises the concern that significant but small proportional changes in populations may be ignored by land managers, as they would be expected to have only a minimal effect on the populations of common species. Yet if common species are used as indicators, small but significant changes in population densities may indicate an ecological change that has a greater impact on species with lower population sizes. Less-common species may be more prone to changes in abundance and more prone to extinction than more-common species (Robinson and Quinn 1988; Davies et al. 2000). We therefore argue that significant changes in populations of common species should be investigated fully, both for the potential implications for other species if common species are used as indicators, and for the loss of biomass and the potential impact on ecosystem function that changes in common species may represent.

Conclusion

In the introduction, we outlined two possible definitions for indicator species provided by Lindenmayer et al. (2000), that indicator species may be "a species whose presence indicates the presence of a set of other species and whose absence indicates the lack of that entire set of species," or "a species that reflects the effects of a disturbance regime or the efficacy of efforts to mitigate disturbance effects". Our results provide little support for any species to function as indicator species according to the first definition if applied to the whole bird community, because all species showed poor correspondence with other species on average. However, our results do support the use of common species as indicator species according to the second definition, in that collectively they did respond to the disturbance events considered and thereby reflected changes to less-common species in the community. Similar studies will need to be conducted for different taxa and in different habitat types before general conclusions can be made about the adequacy of monitoring common species to reflect responses to disturbance events. Monitoring common species will not identify *all* important disturbance events as rare species are more likely to be habitat specialists and have habitat requirements dissimilar to the majority of other species (Gregory and Gaston 2000; Lawler et al. 2003). Thus, it is likely that some programs targeted to particular rare species will always be required. However, we suggest a suite of relatively common species could be used to monitor the impacts of broad disturbance events to take advantage of the statistical power these species provide. Ensuring the full spectrum of ecological guilds (e.g. foraging guilds, migrants and residents) are represented and including species of intermediate-high commonness would further improve any monitoring program that focuses on common species.

Appendix 1

See Table 1.

Table 1 Details on the four-letter code, common name, scientific name and ecological attributes of each species examined

Code[a]	Species name	Scientific name	Average density/ 100 ha	Cavity guild	Foraging guild	Migratory status
DEJU	Dark-eyed junco	*Junco hyemalis*	42.82	NCN	H	Migrant
DUHA	Dusky/ Hammond's flycatcher	*Empidonax hammondii* or *Empidonax oberholseri*	36.69	NCN	AI	Migrant
YRWA	Yellow-rumped warbler	*Dendroica coronate*	35.00	NCN	FI	Migrant
CHSP	Chipping sparrow	*Spizella passerine*	34.99	NCN	GI	Migrant
AMRO	American robin	*Turdus migratorius*	26.27	NCN	GI	Migrant
RCKI	Ruby-crowned kinglet	*Regulus calendula*	22.70	NCN	FI	Migrant
PISI	Pine siskin	*Carduelis pinus*	21.71	NCN	H	Short
BHCO	Brown-headed cowbird	*Molothrus ater*	19.68	NCN	GI	Migrant
RBNU[a]	Red-breasted nuthatch	*Sitta Canadensis*	19.11	WPCN	BI	Resident
MOCH[a]	Mountain chickadee	*Parus gambeli*	18.52	WPCN	FI	Resident
GCKI	Golden-crowned kinglet	*Regulus satrapa*	14.49	NCN	FI	Resident
WAVI[a]	Warbling vireo	*Vireo gilvus*	13.79	NCN	FI	Migrant
CAVI[a]	Cassin's vireo (solitary vireo)	*Vireo cassinii*	12.76	NCN	FI	Migrant
WWPE[a]	Western wood-pewee	*Contopus sordidulus*	11.71	NCN	AI	Migrant
WETA[a]	Western tanager	*Piranga ludoviciana*	9.80	NCN	FI	Migrant
RNSA[a]	Red-naped sapsucker	*Sphyrapicus nuchalis*	9.23	PCN	BI	Migrant
SWTH	Swainson's thrush	*Catharus ustulatus*	9.20	NCN	GI	Migrant
LEFL	Least flycatcher	*Empidonax minimus*	8.09	NCN	AI	Migrant
NOFL	Northern flicker	*Colaptes auritus*	7.79	PCN	GI	Migrant
HAWO	Hairy woodpecker	*Picoides villosus*	7.04	PCN	BI	Resident
OCWA	Orange-crowned warbler	*Vermivora celata*	6.92	NCN	FI	Migrant

Table 1 continued

Code[a]	Species name	Scientific name	Average density/100 ha	Cavity guild	Foraging guild	Migratory status
HETH	Hermit thrush	*Dendroica occidentalis*	6.48	NCN	GI	Migrant
EVGR	Evening grosbeak	*Coccothraustes vespertinus*	6.11	NCN	H	Migrant
TRES	Tree swallow	*Sturnus vulgaris*	5.81	SCN	AI	Migrant
OSFL[a]	Olive-sided flycatcher	*Contopus cooperi*	5.21	NCN	AI	Migrant
DOWO	Downy woodpecker	*Picoides pubescens*	4.83	PCN	BI	Resident
BCCH	Black-capped chickadee	*Parus atricapillus*	3.98	WPCN	FI	Resident
GRAJ	Gray jay	*Perisoreus Canadensis*	3.61	NCN	O	Resident
WIWA[a]	Wilson's warbler	*Wilsonia pusilla*	3.47	NCN	FI	Migrant
ATTW[a]	American three-toed woodpecker	*Picoides tridactylus*	2.79	PCN	BI	Resident
BRCR	Brown creeper	*Certhia Americana*	2.71	SCN	BI	Resident
TOWA[a]	Townsend's warbler	*Dendroica townsendi*	2.71	NCN	FI	Migrant
TOSO[a]	Townsend's solitaire	*Myadestes townsendi*	2.59	NCN	AI	Migrant
CORA	Common raven	*Corvus corax*	2.07	NCN	O	Resident
CEDW	Cedar waxwing	*Bombycilla cedrorum*	1.90	NCN	H	Migrant
MOBL[a]	Mountain bluebird	*Sialia currucoides*	1.76	SCN	GI	Migrant
PIWO	Pileated woodpecker	*Dryocopus pileatus*	1.55	PCN	BI	Resident
NOWA	Northern waterthrush	*Seiurus noveboracensis*	1.36	NCN	GI	Migrant
RUGR[a]	Ruffed grouse	*Bonasa umbellus*	1.09	NCN	H	Resident
RECR[a]	Red crossbill	*Loxia curvirostra*	0.99	NCN	H	Resident
COYE	Common yellowthroat	*Geothlypis trichas*	0.79	NCN	FI	Migrant
VESP	Vesper sparrow	*Pooecetes gramineus*	0.76	NCN	GI	Migrant
YWAR[a]	Yellow warbler	*Dendroica petechia*	0.68	NCN	FI	Migrant
PUFI	Purple finch	*Carpodacus purpureus*	0.59	NCN	H	Short
RUHU[a]	Rufous hummingbird	*Selasphorus rufus*	0.56	NCN	H	Migrant
WIFL	Willow flycatcher	*Empidonax traillii*	0.50	NCN	AI	Migrant
BBWO[a]	Black-backed woodpecker	*Picoides arcticus*	0.45	PCN	BI	Resident
BRBL	Brewer's blackbird	*Spizella breweri*	0.44	NCN	GI	Migrant
EUST	European starling	*Sturnus vulgaris*	0.41	SCN	GI	Migrant
MGWA[a]	MacGillivray's warbler	*Dendroica magnolia*	0.41	NCN	FI	Migrant
RWBL	Red-winged blackbird	*Agelaius phoeniceus*	0.39	NCN	GI	Migrant
SOSP	Song sparrow	*Melospiza melodia*	0.39	NCN	GI	Migrant
WIWR	Winter wren	*Troglodytes troglodytes*	0.39	NCN	GI	Migrant
ALFL	Alder flycatcher	*Empidonax alnorum*	0.34	NCN	AI	Migrant

Table 1 continued

Code[a]	Species name	Scientific name	Average density/ 100 ha	Cavity guild	Foraging guild	Migratory status
AMCR	American crow	*Corvus brachyrhynchos*	0.33	NCN	O	Resident
VATH[a]	Varied thrush	*Ixoreus naevius*	0.29	NCN	GI	Migrant
LISP	Lincoln's sparrow	*Melospiza lincolnii*	0.27	NCN	GI	Migrant
PSFL	Pacific-slope flycatcher	*Empidonax difficilis*	0.26	SCN	AI	Migrant

Species are ordered by average density across all site-years, which is used to indicate how common a species is

The cavity guilds considered were *PCN* primary cavity-nester, *WPCN* weak primary cavity-nester, *SCN* secondary cavity-nester, and *NCN* non-cavity-nester. Foraging guilds considered were *AI* aerial insectivores, *BI* boring insectivores, *FI* foliage insectivores, *GI* ground insectivore, *H* herbivores, and *O* omnivores

Migratory status indicates whether the species are residents, long-distance migrants or short-distance migrants

[a] Proposed focal species (http://www.pifbcyukon.org/3b.html)

Appendix 2

The results of the models examining species responses to harvesting and MPB are outlined in Table 2, which is best explained using some examples. The second row of data is for the western wood-pewee (WWPE). Of the five models for this species the harvest model had the lowest QAICc value, and therefore the best explanatory power, as evidenced by the zero in the harvest column. The + indicates that harvesting had a positive effect on WWPE density. The QAICc value of the WWPE harvest model is at least two units less than the next simplest model, the null model (ΔQAICc $= 20.8 - 0 = 20.8$), so the text is bolded to indicate the strong support for an effect of harvesting. The pine model is also bolded, indicating that the QAICc value of this model is at least two units less than the next simplest model, the null model (ΔQAICc $= 20.8 - 11.4 = 9.4$). The + sign for the WWPE pine model is in brackets, indicating that the model-averaged coefficient for pine was positive but that the model that only included pine (i.e. not MPB or harvest) had a negative coefficient. The WWPE MPB model is also bolded, indicating strong support for an effect of MPB (ΔQAICc $= 11.4 - 8.7 = 2.7$). The MPB-harvest model has a low ΔQAICc value, comparable to the harvest model which is the best model overall. However the MPB-harvest ΔQAICc value is not bolded, indicating only weak support for this model. While the MPB-harvest model is better than the MPB model (ΔQAICc $= 8.7 - 0.1 = 8.6$), it is not better than the harvest model (ΔQAICc $= 0 - 0.1 = -0.1$). This result means that while MPB was found to have an effect when considered on its own, the effect of MPB was relatively weak when harvesting was taken into account.

Our second example is for the Dusky or Hammond's flycatcher (DUHA). Of the five models for this species the harvest model had the lowest ΔQAICc value, and therefore the best explanatory power, as evidenced by the zero in the harvest column. However, the zero is not bolded indicating there was only weak support for an effect of harvesting (ΔQAICc $= 0.5 - 0 = 0.5$). Similarly there was no support for an effect of pine or MPB on DUHA as these models have QAICc values greater than the null model.

Table 2 Results of the mixed-effect models between species density and harvesting, basal area of pine, and proportion of pine affected by MPB

Species	Average density (birds/100 ha)[a]	ΔQAICc					(%) Residual variance partitioned by site[b]	(%) Residual variance partitioned by year[b]	N
		Null	Harvest	Pine	MPB	MPB-harvest			S: Sites, T: Total
Aerial insectivores									
DUHA	44.9	0.5	0.0+	2.6 (+)	4.4+	1.5	29.7	2.6	S 19 : T 238
WWPE	14.7	20.8	0.0+	11.4 (+)[c]	**8.7+**	0.1	24.7	10.0	S 19 : T 238
LEFL	10.4	12.4	**3.1+**	**0.5−**	0.0+	1.7	58.8	4.8	S 18 : T 225
TRES	7.3	24.5	0.0+	**3.3−**	3.4+	1.3	44.0	5.5	S 19 : T 238
OSFL	6.1	11.0	**5.2+**	**0.7−**	0.0+	2.0	40.4	3.8	S 18 : T 225
TOSO	3.7	14.7	**5.0+**	**1.4−**	0.0+	0.5	17.6	29.6	S 19 : T 238
WIFL	0.6	0	0.8+	1.9−	3.8+	4.8	37.4	14.8	S 8 : T 100
ALFL	0.4	0	1.2+	1.8−	3.4+	5.1	6.5	54.6	S 9 : T 113
PSFL	0.3	0.9	2.7−	1.2−	0.8+	0.0	0.0	4.4	S 10 : T 126
Bark insectivores									
RBNU	23.3	0	1.5−	2.1 (−)	4.2+	5.4	6.0	13.6	S 19 : T 238
RNSA	11.3	8.6	0.1+	0−	1.9+	1.7	19.4	5.6	S 19 : T 238
HAWO	8.7	20.7	**2.9+**	**4.9−**	3.2+	0.0	9.2	6.7	S 19 : T 238
DOWO	5.2	12.7	**1.6+**	**6.5−**	**3.9+**	0.0	11.1	13.7	S 19 : T 238
BRCR	3.6	6.9	**0.4−**	0+	2.0−	0.9	17.8	34.7	S 17 : T 212
ATTW	3.6	12.9	14.6 (+)	**1.6+**	0.2+	0.0	0.0	15.8	S 17 : T 217
PIWO	1.8	0	2.1 (−)	1.5−	2.8+	4.5	35.4	2.0	S 17 : T 212
BBWO	0.7	0.4	0.8−	0+	2.1+	3.9	14.5	30.0	S 9 : T 108
Foliage insectivores									
YRWA	45.0	7.3	**2.2−**	0.0+	2.1−	3.8	10.1	6.1	S 19 : T 238
RCKI	28.3	0	2.0−	2.1−	4.2−	6.2	13.8	5.6	S 19 : T 238

Table 2 continued

Species	Average density (brids/100 ha)[a]	ΔQAICc					(%) Residual variance partitioned by site[b]	(%) Residual variance partitioned by year[b]	N S: Sites, T: Total
		Null	Harvest	Pine	MPB	MPB-harvest			
MOCH	24.2	4.5	6.5 (−)	**0.7−**	1.6−	0.0	8.9	3.7	S 19 : T 238
GCKI	17.8	61.4	**6.1−**	**4.0+**	5.8+	0.0	38.9	17.8	S 19 : T 238
CAVI	16.7	11.0	12.4 (−)	**4.2−**	0.0+	0.5	20.7	5.4	S 19 : T 238
WAVI	15.5	5.2	6.5 (−)	**0−**	0.9+	2.2	14.9	11.7	S 19 : T 238
WETA	13.2	0.0	0.8−	1.2−	3.2−	0.3	22.6	6.6	S 19 : T 238
OCWA	7.6	0.0	1.3+	1.0+	2.2+	1.1	6.4	10.6	S 19 : T 238
BCCH	5.2	0.1	2.1−	2.1−	0.0−	1.9	18.6	15.5	S 19 : T 238
WIWA	4.4	0.0	1.5+	0.9+	2.6+	0.7	15.4	30.9	S 19 : T 238
TOWA	3.6	0.7	0−	1.3+	2.8+	3.3	48.2	13.1	S 17 : T 212
COYE	1.0	0.0	2.2 (−)	1.6−	3.6−	5.3	33.6	15.3	S 9 : T 112
YWAR	0.9	0	0−	1.3+	3.5+	4.2	38.4	16.3	S 15 : T 186
MGWA	0.4	0	0.6+	2.0+	3.0+	2.6	15.7	18.4	S 14 : T 178
Ground insectivores									
CHSP	45.7	32.5	0.0+	**8.5−**	7.3+	0.1	23.4	5.2	S 19 : T 238
AMRO	31.6	23.5	0.0+	**13.7 (+)[C]**	15.8+	3.7	16.5	1.2	S 19 : T 238
BHCO	25.7	7.6	0.0+	**3.1−**	2.0+	1.3	51.2	4.4	S 19 : T 238
SWTH	11.8	19.2	0.0−	**10.2+**	12.2+	3.0	20.1	25.7	S 19 : T 238
HETH	8.6	0	0.2−	2.0−	4.0−	2.8	9.3	17.8	S 19 : T 238
NOFL	8.6	26.3	**5.1+**	**3.2−**	2.6+	0.0	14.9	3.4	S 19 : T 238
MOBL	2.4	15.8	0.0+	**8.8−**	6.9+	0.7	32.9	12.2	S 12 : T 152
NOWA	1.5	0.0	2.1 (+)	0.9+	1.7+	3.1	22	25.4	S 12 : T 156

Table 2 continued

Species	Average density (brids/100 ha)[a]	ΔQAICc					(%) Residual variance partitioned by site[b]	(%) Residual variance partitioned by year[b]	N S: Sites, T: Total
		Null	Harvest	Pine	MPB	MPB-harvest			
VESP	1.0	5.7	0.0	**2.9**–	**0.8**+	0.4	36.2	1.8	S 14 : T 178
BRBL	0.6	0.0	1.7+	1.5–	2.9+	5.1	10.7	69.0	S 10 : T 126
EUST	0.6	6.0	**1.4**+	0.0–	1.9–	2.5	4.8	56.4	S 11 : T 138
RWBL	0.5	1.2	3.2+	3.4–	0.0–	1.8	49.5	0	S 7 : T 91
SOSP	0.5	0.0	2.1+	2.1+	2.9+	4.6	25.9	10	S 11 : T 143
WIWR	0.5	3.8	5.9 +	5.5+	0.0–	1.7	28.8	16.4	S 11 : T 143
VATH	0.4	5.0	**0**+	**2.8**+	4.6–	3.6	32.5	25.1	S 8 : T 99
LISP	0.3	5.0	**0.9**–	0.0–	1.2–	3.2	15.2	56.4	S 6 : T 78
Herbivores									
DEJU	55.4	32.1	0.0+	**16.7**–	18.7–	4.1	6.8	4.9	S 19 : T 238
PISI	28.3	16.8	**5.1**+	18.8 (+)	18.9+	0.0	24.6	49.1	S 19 : T 238
EVGR	8.4	2.1	2.8–	4.1–	**0.2**–	0.0	26.6	40.8	S 18 : T 225
CEDW	2.6	5.0	**1.0**+	0.0–	0.9+	2.2	25.6	39.7	S 17 : T 212
RUGR	1.5	3.1	3.4–	4.6–	**2.6**–	0.0	23.2	21.7	S 17 : T 212
RECR	1.5	0.0	0.0+	2.1+	4.1+	3.9	21.2	62.6	S 13 : T 160
PUFI	0.7	0.0	1.9+	2.1+	2.0+	3.8	22.8	33	S 16 : T 204
RUHU	0.6	0.0	2.1 (–)	1.3–	3.0+	4.9	29.9	3.8	S 9 : T 113
Omnivores									
GRAJ	4.3	1.9	3.8 (+)	1.1+	0.0–	1.2	12.6	8	S 19 : T 238
CORA	2.5	2.3	0.0+	1.1–	3.2–	3.7	26	6.6	S 19 : T 238

Table 2 continued

| Species | Average density (brids/100 ha)[a] | ΔQAICc | | | | | (%) Residual variance partitioned by site[b] | (%) Residual variance partitioned by year[b] | N |
		Null	Harvest	Pine	MPB	MPB-harvest			S: Sites, T: Total
AMCR	0.3	4.4	0.0+	3.6–	5.1–	3.2	18.1	40.8	S 11 : T 143

The ΔQAICc is the difference between the QAICc value of the model in question, and the model for that species that has the lowest QAICc value (i.e. for each species the model with a QAICc value of zero is the most parsimonious fit to the data). ΔQAICc values are in bold font if the model is >2 units better than the next most simple model (i.e., the harvest and pine models are compared to the null model, the MPB is compared to the pine model, MPB-harvest is compared to both harvest and MPB). The sign (±) indicates whether the model-averaged coefficient for that variable was positive or negative. If the sign is in brackets then the simplest model containing that variable is the opposite sign, where model simplicity refers to the number of parameters. Species are ordered by foraging guild, and then by average density (commonness)

[a] Average density across all sites

[b] Reported for the MPB-harvest model

[c] These species had a positive model-averaged coefficient but a negative coefficient in the model that just contained the basal area of pine. The difference in direction of coefficients occurred for these species because pine contributed significantly in the pine models, but not in the models with the greatest weighting

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