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Community occupancy before-after-control-impact (CO-BACI) analysis of Hurricane Gudrun on Swedish forest birds

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Abstract. Resilience of ecological communities to perturbation is important in the face of increased global change from anthropogenic stressors. Monitoring is required to detect the impact of, and recovery from, perturbations, and before-after-control-impact (BACI) analysis provides a powerful framework in this regard. However, species in a community are not observed with perfect detection, and occupancy analysis is required to correct for imperfect detectability of species. We present a Bayesian community occupancy before-after-control-impact (CO-BACI) framework to monitor ecological community response to perturbation when constituent species are imperfectly detected. We test the power of the model to detect changes in community composition following an acute perturbation with simulation. We then apply the model to a study of the impact of a large hurricane on the forest bird community of Sweden, using data from the national bird survey scheme. Although simulation shows the model can detect changes in community occupancy following an acute perturbation, application to a Swedish forest bird community following a major hurricane detected no change in community occupancy despite widespread forest loss. Birds with landscape occupancy less than 50% required correcting for detectability. We conclude that CO-BACI analysis is a useful tool that can incorporate rare species in analyses and detect occupancy changes in ecological communities following perturbation, but, because it does not include abundance, some impacts may be overlooked.

Key words: *Bayesian framework; before-after-control-impact study; community stability; forest birds; Hurricane Erwin; Hurricane Gudrun; perturbation; resilience; Swedish bird survey.*

INTRODUCTION

Ecological communities are composed of species interacting with one another through both direct and indirect relationships. Community stability defines the persistence of an ecosystem in a particular state or attractor region, such as its species composition, while community resilience characterizes the ability of an ecosystem to return to its original state following a perturbation (Halpern 1988). Ecological communities are regularly subjected to perturbations to which they must bear resilience or otherwise adapt (e.g., LaDeau et al. 2007). Resilience to such perturbations will depend on both the scale and magnitude of the disturbance event, and, particularly, whether the perturbation is a press or pulse event (Bender et al. 1984). Although perturbations occur naturally, the frequency and magnitude with which they occur is increasing with widespread human-driven global change (Root and Schneider 1995). Examples include elevated rates of habitat alteration, species introductions, and climatic

change, often by orders of magnitude compared to background levels (Vitousek et al. 1997). For ecological communities to persist, it is necessary that they demonstrate resilience to perturbations, regardless of the perturbation's origin (Graham and Grimm 1990). There is widespread evidence, however, that ecological communities are suffering in the face of ongoing disturbance (Simberloff et al. 2012) and, furthermore, that major disturbances can create wholesale regime shifts in ecological communities (Chavez et al. 2003). Community stability and resilience are thus vital in a changing world where habitat is shrinking and large perturbations are increasingly common. If communities are not resilient to these changes then they risk the loss of species, preventing them returning to any original state.

Ecological communities are commonly monitored in order to detect, and, where necessary, respond to, effects of perturbations as early as possible (Yoccoz et al. 2001). Monitoring programs continue to increase in both their scale and the sophistication of data being collected (Michener and Jones 2012). These large datasets present challenges for analysis, and different models and analytical methods are now available to identify important patterns and processes occurring in

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community datasets (Clark and Gelfand 2006). For communities over large spatial scales comprising many species, often the only data that can be efficiently and reliably collected are the presence or absence of species, which yield a measure of species distribution. Presence-absence data can be expected to be more robust to variation in observer effort and skill, which is an important consideration when the scale of monitoring requires many data collectors. Nonetheless, species presence-absence data are susceptible to imperfect detection (Roberge and Svensson 2003). Occupancy models (MacKenzie et al. 2006, Zipkin et al. 2012) provide a well-developed framework with which to analyze species distribution data while accounting for imperfect detection of species, providing more reliable estimates of species occupancy for wildlife management (Russell et al. 2009) and conservation planning (De Wan et al. 2009). Although presence-absence data can be used to estimate individual abundances, assuming an abundance-occupancy relationship, model assumptions of the abundance-occupancy relationship can be restrictive and are likely violated over large spatial and temporal scales (Royle and Nichols 2003, Wenger and Freeman 2008).

Monitoring data are collected in the hope that they can indicate when a significant change has occurred in an ecosystem, above and beyond that expected under normal circumstances. Before-after-control-impact (BACI) studies are a commonly used analytical framework for determining the size and direction of any perturbation at any number of sites, against a backdrop of natural variation monitored at control sites, both before and after the perturbation being investigated is likely to have manifested. Control site data allow us to estimate community stability (i.e., constancy), while impact site data allow us to estimate community impact and resilience (i.e., recovery post perturbation). In this paper, we propose a unified approach to community occupancy analysis and before-after-control-impact analysis. Community occupancy models have previously been developed for analyzing datasets of multiple species over large scales, and can be used for investigating community traits such as species richness or turnover (Kéry and Royle 2008, Zipkin et al. 2009), and the impact of climatic events (Russell et al. 2009, Mutshinda et al. 2011) or conservation actions (Zipkin et al. 2010, Sauer et al. 2013). A BACI design has been developed and implemented using a frequentist framework for dynamic occupancy models of a single species that explicitly incorporates colonization and extinction probabilities (Popescu et al. 2012), and implemented implicitly in an occupancy model of multiple species (Russell et al. 2009). We present an explicit BACI analytical design for simultaneously investigating changes in detection and occupancy of constituent species in a community that has been subjected to some kind of perturbation. This community approach is important because, for many of the rare species most vulnerable to

perturbation, power is lacking to reliably detect any impact if the species was analyzed in isolation of the community. There is also some degree of arbitrariness in focusing on only one species to detect any perturbation, when conservation should focus on a whole-ecosystem context (Zavaleta et al. 2001). The occupancy approach further addresses previous concerns about zero-inflation (false absences) in BACI analyses (Smith et al. 1993).

Specifically, we are interested in investigating the impact of a large hurricane on the Swedish forest bird community. On 8 January 2005, northern Europe was struck by the storm alternatively named Erwin or Gudrun (German Weather Service and Norwegian Meteorological Institute, respectively). Sustained wind speeds of 126 km/h with wind gusts of 165 km/h were measured in Hanstholm, Denmark, the equivalent strength of a Category 1 hurricane. This was the worst storm in at least 40 years in the region, and killed 17 people (Suursaar et al. 2006), and, in Sweden, caused widespread losses to the forest industry equivalent to the total annual harvest and a value of 20 billion euros (Björheden 2007). Cyclones, hurricanes, and other wind-related meteorological phenomena, in particular, are forecasted to increase with climate change (Webster et al. 2005). The environmental devastation following such catastrophic events, such as widespread destruction of habitat, is rapidly observed and recorded (e.g., Boose et al. 1994, Björheden 2007). These perturbations have repercussive consequences on biological communities (Spiller et al. 1998, Simberloff 2000), but the impacts of such events on mobile species can be much harder to measure or detect, among other factors operating in the system (e.g., Schoener et al. 2001, 2004).

We are interested in quantifying any hurricane impact, and its form, on the detectability and occupancy of the Swedish forest bird community most likely to be impacted by loss of forest habitat. We do this by quantifying the short-term (pulse) impact of the storm on the detectability and occupancy of selected species from the Swedish forest bird community. Here, we interpret occupancy as a measure of range or distribution in our community and its constituent species, and detectability as some function of species identity and abundance. Our response variables are the site occupancy and detectability of each species across Sweden. We compare the distribution of a representative forest bird community for the two years both before and after Gudrun (the storm name used in Sweden and hereafter), where the strongest hurricane impact was in southern Sweden sites; and we can use northern Sweden sites as our control. Our model allows us to utilize a BACI design, while correcting for other known covariates of bird distribution. This framework also allows us to test sensible a priori predictions of species response to the hurricane, such as a reduction in either occupancy or detectability, or other predicted associations with habitat covariates (e.g., Angelstam et al. 2004).

METHODS

Model formulation

Following previous work, we formulate a community model based on species occurrence, whereby we can estimate the probabilities of species occupancy, ψ , and detectability, p , across the landscape, correcting for false absences where species are present but not detected by observers. This model is composed in a robust design that includes a long-term open population temporal component (e.g., seasons or years) in which, within each closed population time period, multiple species surveys take place. For i species over j sites, k surveys, and m times, we treat $X_{i,j,k,m}$ as the binary detection matrix for the i th species at the j th site on the k th survey in the m th time, and $Z_{i,j,m}$ as the underlying binary state matrix of presence or absence at a site. Thus, for our occupancy process model, we have the relationship

$$Z_{i,j,m} \sim \text{Bernoulli}(\psi_{i,j,m}).$$

And, for our detection model, we have the relationship

$$X_{i,j,k,m} \sim \text{Bernoulli}(p_{i,j,m} \times Z_{i,j,m}).$$

We can then estimate the effects of species, site, and time using a logistic generalized linear model of each of ψ and p . We treat species identity as a normally distributed random effect, time as an independent fixed effect, and include species-specific site covariates as follows

$$\text{logit}(\theta_{i,j,m}) = \sigma_i + \alpha_m \times I(m) + \delta_{i,h} \times S_{j,h}$$

where $\theta = \psi$ or p , σ_i is the random effect for species i , α_m the fixed effect for time m , given the indicator function $I(m)$, and $\delta_{i,h}$ is the effect of site covariate h on species i , given a matrix S of h site covariates for j sites.

For homogenous landscapes where site-level covariates are not important, or to incorporate additional unspecified variation, site effects may be treated as a random effect, σ_j . For parsimony, we do not model higher-order interactions among fixed effects.

While estimating species occupancy and detectability in our regression equations, we can include BACI design terms that test for the interactive effect of time and impact, such that we determine whether there is an overall significant change in either the occupancy or detectability of the constituent species in the community at the sites that were impacted by some measure (either continuous or binary) of perturbation. Following from above

$$\text{logit}(\theta_{i,j,m}) = \dots + \beta \times P_j + \gamma_m \times P_j \times I(m)$$

where β measures any underlying (i.e., pre-impact) community differences among j sites subsequently impacted by some perturbation, P (binary or continuous), and γ_m is the interaction term measuring community perturbation impact across j sites at each time m . We assume any impact is consistent across the entire

community, but there is no reason constituent species cannot be grouped with regards to their response to any disturbance event (e.g., positive, neutral, or negative).

Following BACI design, a significant interaction term, γ_m , between time and impact, while correcting for background variability in the community over time, α_m , and any underlying differences in the community by level of impact at sites, β , and additional species-specific site variation, $\delta_{i,h}$, indicates the perturbation had a significant impact on the response variable of interest (i.e., occupancy or detectability) for the entire community simultaneously.

Following previous work (Dorazio and Royle 2005, Hurlbert and White 2007), we also include an ecologically plausible correlation between occupancy and detectability, recognizing that species with greater occupancy are also likely to be more detectable, given presumed greater abundance. Species-specific random effects, σ_i , for ψ_i and p_i are thus assumed to be bivariate normal with variances σ_ψ^2 and σ_p^2 and covariance $\sigma_\psi\sigma_p$. This assumption encourages shrinkage towards community means for occupancy and detectability, but allows inclusion of rare species with low values of ψ_i or p_i where data are sparse.

In one model, we, thus, estimate the detectability and occupancy of species within a predefined ecological community. Analysis of a single species is, thus, a special case of our model, but, by analyzing the community simultaneously, we can especially benefit from shared information among species.

Simulation

We test the power of our Bayesian community occupancy before-after-control-impact (CO-BACI) model on a simulated dataset. Due to the long computational time of the model, we only consider one dataset of similar dimensionality and design to our real data of interest. We simulate a community of 16 species distributed over 724 sites with eight annual surveys at each site over four years. Our 16 species have normally distributed occupancy, ψ_i , ranging from 0.2 to 0.8 and right-skewed detectability, p_i , ranging from 0.05 to 0.8, as observed in real communities. We order and couple ψ_i and p_i such that the rarest species has the lowest probability of detection, and the most common species has the highest probability of detection ($r=0.81$).

To simulate an acute perturbation to our community, at time period three we impose a 75% reduction in occupancy of all species at exactly half our sites, which recover in time period four to 95% of original occupancy, while species detectability is held constant. We are interested in verifying that our CO-BACI model is able to detect what we deem a significant crash in the community occupancy of all species, despite a rapid recovery. These simulation conditions are assumed quite similar to what may have happened to the Swedish forest bird community following Hurricane Gudrun.

TABLE 1. Forest bird species ($n = 16$ species) constituting a forest bird community and their average observed occupancy (ϕ_{obs}) using raw data over 2003–2006 (percentage of sites present from grid squares sampled) and predicted hurricane impact of spruce and pine loss based on species ecology.

Scientific name	English name	Swedish name	ϕ_{obs} (%)	Impact
<i>Phylloscopus trochilus</i>	Willow Warbler	Lövsångare	98.1	U
<i>Turdus philomelos</i>	Song Thrush	Taltrast	77.8	D
<i>Erithacus rubecula</i>	Robin	Rödhake	64.1	D
<i>Turdus merula</i>	Blackbird	Koltrast	60.7	D
<i>Dendrocopos major</i>	Great Spotted Woodpecker	Större hackspett	35.7	D
<i>Parus caeruleus</i>	Blue Tit	Blåmes	25.7	U
<i>Dryocopus martius</i>	Black Woodpecker	Spillkråka	22.1	D
<i>Garrulus glandarius</i>	Jay	Nötskrika	17.8	D
<i>Phylloscopus sibilatrix</i>	Wood Warbler	Grönsångare	17.4	D
<i>Parus ater</i>	Coal Tit	Svartmes	14.7	D
<i>Certhia familiaris</i>	Treecreeper	Trädkrypare	11.1	D
<i>Parus cristatus</i>	Crested Tit	Tofsmes	10.7	D
<i>Sitta europaea</i>	Nuthatch	Nötväcka	9.5	U
<i>Picus viridis</i>	Green Woodpecker	Gröngöling	9.4	U
<i>Lanius collurio</i>	Red-backed Shrike	Törnskata	5.1	U
<i>Perisoreus infaustus</i>	Siberian Jay	Lavskrika	3.1	D

Notes: An impact of U is unaffected and D is decline. *Perisoreus infaustus* was excluded from analysis due to low occupancy.

Data were prepared in R v.2.9.2 (R Core Team 2009), but all model fitting was done in OpenBUGS v.3.0.7 (Thomas et al. 2006). We ran two chains with a burn-in period of 10 000 iterations to allow convergence on a stationary process, followed by 50 000 more iterations to summarize posterior estimates. Prior distributions for species occupancy, ψ_i , and detectability, p_i , were Unif(0,1), their variance (on logit scale) Unif(0,10), and their correlation Unif(-1,1). Prior distributions for regression coefficients for time, α_m , impact, β , their interaction, γ_m , and covariates $\delta_{i,h}$, were Unif(-10,10). We interpret statistical significance in fixed effects when 95% credible intervals (CI) do not include zero, and, for such effects, we report posterior means and 95% credible intervals. We do not simulate a species-specific effect of any additional site covariates.

Swedish Breeding Bird Survey

We applied our CO-BACI model to investigate the impact of Hurricane Gudrun on the Swedish forest bird community. We combined two large Swedish data sets in order to do this; the extensive annual tree-fall forestry data available for all of Sweden (Gustafsson and Perhans 2010), with the long-term national Swedish Bird Survey (Ottvall et al. 2009). The Swedish national bird survey divides Sweden into 716, 25×25 km, grid squares, where a central 2×2 km sampling square within each larger grid square should be surveyed once a year. At each sampling square, five-minute bird counts are conducted at eight points located every 1 km around the perimeter. Grid squares are opportunistically sampled by a large number of volunteers, and so not all squares are sampled every year, nor randomly selected for sampling (e.g., southern squares around populous regions are more often visited), but differences among so many observers can be considered to have negligible

effects overall. Bird counts are standardized to occur on mornings in summer between mid-May (southernmost Sweden) to early July (northernmost Sweden) on days of fine weather. We treat our multiple spatial surveys within a grid square as equivalent temporal resurveys, assuming that the detection of a bird species at any of the eight points indicates its presence, and availability for detection, throughout the entire 2×2 km sampling square, i.e., any inference concerns presence or absence in the 2×2 km sampling grid square. This approach necessitates caution (Kendall and White 2009), but given the mobility and range sizes of the avian species constituting our community, and the close proximity of our sampling points, we believe this data treatment is acceptable.

We consider 16 representative species from the Swedish bird survey with a range of observed occupancies and selected for their forest dwelling habits and southern distribution, both hypothesized to predispose them to impacts from forest habitat loss associated with Gudrun, (Table 1). Eleven of our species are conifer tree specialists predicted to locally decline strongly following the hurricane. The remaining five are deciduous tree specialists predicted to be less affected following the hurricane. We typically expect occupancy of our species to be strongly correlated positively with forest, and negatively with latitude and elevation. We also expect detectability of our species to be correlated in a similar way, given correlation between occupancy and detectability. However, we finally exclude the Siberian Jay from analysis due to its very low detection rate with a northerly bias (only 58 counts). Our data then comprise 347 648 count records, of which 6.3% are species detections, 51.3% are species non-detections, and the remaining 42.4% are missing values (from where grid squares were not surveyed in a particular year). These

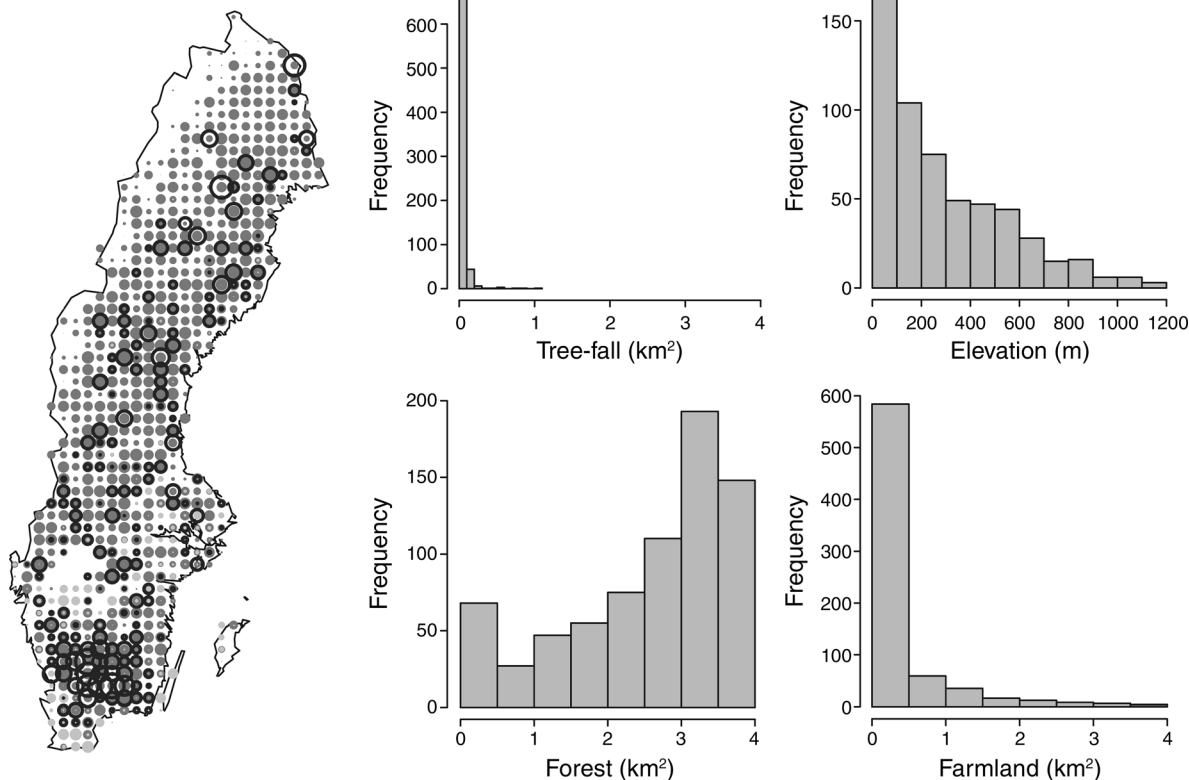


FIG. 1. Impact of Hurricane Gudrun and logging on Swedish forests in 2005. Black rings on the map are proportional to $\log_{10}(\text{tree-fall})$, measured in km^2 . Dark and light grays correspond to the amount of forest and farmland habitat in each grid square, respectively. Histograms of tree-fall, average elevation, forest, and farmland in grid squares (frequency is the number of grid squares in each category).

observations were collected from 679 grid squares (95%) from surveys during 2003–2006 ($n = 401\text{--}411$ grid squares each year), i.e., two summers each pre- and post-perturbation. Observations were made by 313 different volunteers over the four years (mean 3.9 grid squares, median 2 grid squares, range 1–81, per observer).

Data on latitude, elevation, and habitat were taken from the CORINE land cover project (Büttner et al. 2004). Elevation data were missing for 17% ($n = 120$) of our grid squares, and so were imputed as the average of all four adjacent squares. Habitat types are measured as the sum of either forest or farmland habitat within a 400-m radius of each of the eight survey points within any grid square (i.e., 4 km^2). Thus, fixed effect covariates for our j sites include latitude (δ_{lat} ; range 1500 km), elevation (δ_{elev} ; mean 290 m, range 0–1135), and the proportion of forest and farmland in each $2 \times 2 \text{ km}$ survey square (δ_{for} ; median 72%, δ_{farm} ; median 0.25%). The impact of Gudrun is similarly measured as a continuous variable for the sum of tree-fallen area at the end of 2005 in the same 400-m radius of each survey point of our grid squares (35% of grid squares). These tree-fall data also include intentional logging, which occurs throughout Sweden as part of silviculture, but could all reasonably be expected to contribute to avian

community disturbance (Fig. 1). All site covariates were normalized (subtract mean and divide by standard deviation) prior to analysis.

We follow the same protocols as for our simulation analysis, with additional prior distributions for normalized fixed effects $\text{Unif}(-10,10)$. Convergence was assessed by inspecting trace plots and using the Gelman-Rubin diagnostic statistic, which examines the variance ratio of the MCMC (Markov chain Monte Carlo) algorithm within and between chains across iterations. Total CPU time at the time of analysis (2007–2010) was in the order of one month.

RESULTS

Simulation

Our simulated values of ψ_i and p_i followed a nonlinear pattern (Fig. 2a). The CO-BACI model correctly detected the impact of a perturbation on the occupancy and not detectability of our simulated community, both immediately after impact (for occupancy $\gamma_3 = -0.58$ [95% CI: -0.75, -0.41]), and ongoing while the community recovered ($\gamma_4 = -0.23$ [95% CI: -0.40, -0.06]). Our simulation used known values of ψ_i and p_i from which we expected no temporal effects (i.e., $\alpha_m = 0$ for $m = 1, \dots, 4$), and negative gamma effects only after impact

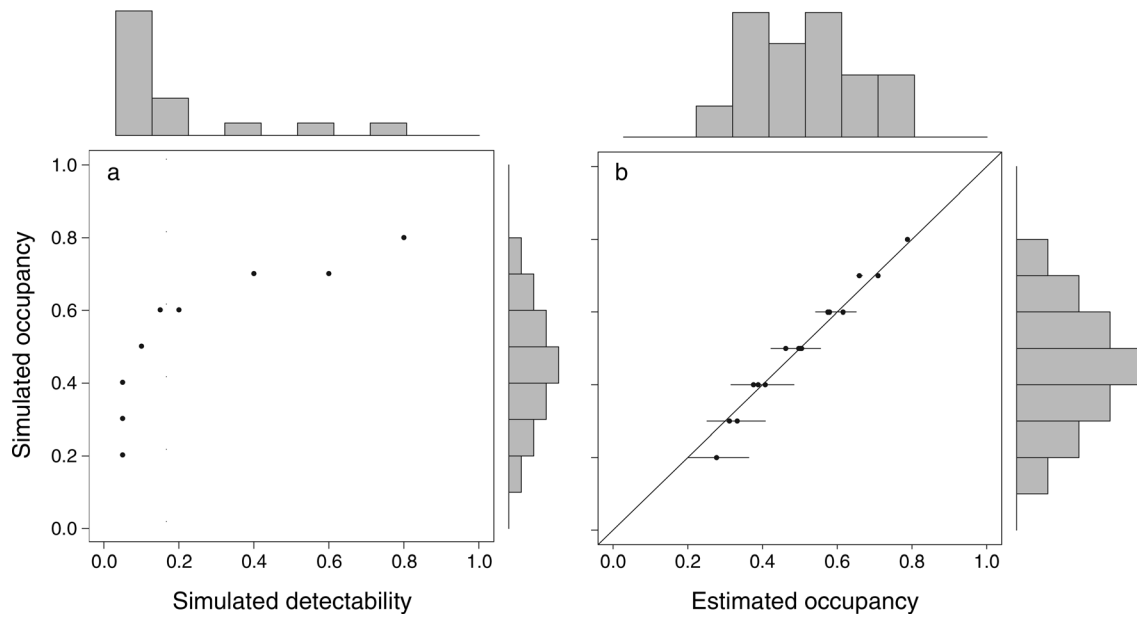


FIG. 2. (a) Simulated values of species occupancy (ψ_i) and detectability (p_i) to test the power of the Bayesian community occupancy before-after-control-impact (CO-BACI) model. (b) Estimated (pre-impact) and simulated values of ψ_i for the CO-BACI model. Error bars are lower and upper 95% credible interval estimates for parameters. The histograms show the distribution of data on each axis in one dimension.

(i.e., $\gamma_m < 0$ for $m = 3, 4$). Estimated occupancy (pre-perturbation) was correlated with simulated occupancy, but for species with extreme values of occupancy, the estimated occupancy did not include the true value in its 95% CI (Fig. 2b). Estimated detectability was identical to simulated detectability (results not shown).

Swedish bird detectability and occupancy

No significant interaction between time and impact (hurricane) was detected for either detectability or occupancy. No underlying difference between impacted

and control sites existed in either detectability or occupancy. No differences over time in bird detectability or occupancy occurred until the final year, when occupancy was significantly lower than previous years ($\alpha_{2006} = -0.32$ [95% CI: $-0.54, -0.09$]). Significant species-specific effects of covariates were detected (Table 2). Detectability generally decreased with latitude, elevation, and farmland, and increased with forest. Where affected, occupancy often strongly decreased with latitude, and also with elevation, while increasing strongly with farmland and forest. The Gelman-Rubin

TABLE 2. Direction and strength of significant species-specific covariate fixed effects on detectability and occupancy.

Species	Detectability				Occupancy			
	Latitude	Elevation	Farmland	Forest	Latitude	Elevation	Farmland	Forest
Willow Warbler			-	+		-		+†
Song Thrush	-			+	-		+	+†
Robin	-	-	-		-	-		+†
Blackbird	-	-	-		-†		+†	+
Great Spotted Woodpecker		-						
Blue Tit			-	-	-†	-	+†	
Black Woodpecker			-		-†	-†		
Jay				+	-†		+†	+†
Wood Warbler	-	-						
Coal Tit				+				
Treecreeper		-†	-					
Crested Tit								
Nuthatch				+	-†		+†	-†
Green Woodpecker	+†				-†			
Red-backed Shrike					-†			

Notes: Direction is positive (+) or negative (-). In the case of the Great Spotted Woodpecker and the Crested Tit, MCMC (Markov chain Monte Carlo) diagnostics indicate failure to estimate effects (Gelman-Rubin statistics > 2.5). Blank cells indicate there was no effect on species detectability or occupancy.

† Effect size > 1.

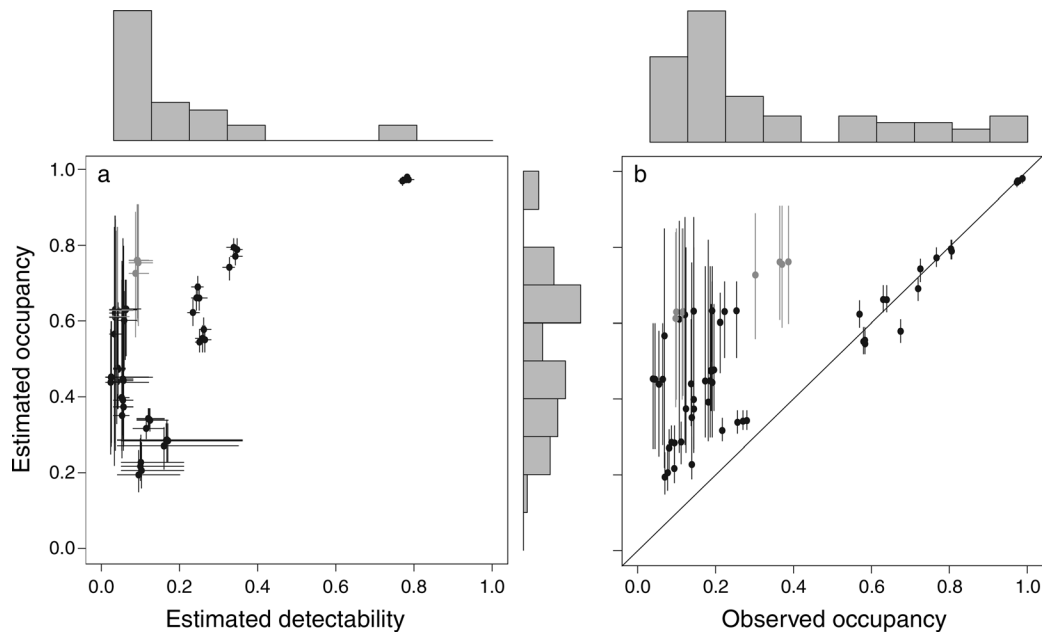


FIG. 3. (a) Estimated values of ψ_i and p_i for the CO-BACI model of Hurricane Gudrun on 15 forest bird species. (b) Estimated (pre- and post-impact) and observed (minimum) values of ψ_i for the CO-BACI model of Hurricane Gudrun on 15 forest bird species. Error bars are lower and upper 95% credible interval estimates for parameters. Gray data indicate species estimates failed. The histograms show the distribution of data on each axis in one dimension.

diagnostic statistic estimated all potential scale reduction factors were <1.5 , except for the correlation of detectability and occupancy; estimates involving the Treecreeper, where there was weak evidence of a lack of mixing (<2.5); and estimates involving the Great Spotted Woodpecker and Crested Tit, where there was strong evidence of a lack of mixing (>2.5), and hence estimation failure.

Species-specific estimates of detectability and occupancy across the four years of our study remained constant, notwithstanding a small drop in occupancy in the fourth year of our study. This fourth year drop in occupancy was most pronounced for the Nuthatch and Wood Warbler, where occupancy dropped by more than 10%. Additional unexplained heterogeneity in species detectability ($\sigma_p = 1.81$ [95% CI: 1.16, 2.84]) and occupancy ($\sigma_\psi = 3.21$ [95% CI: 1.92, 5.19]) was also detected.

Some positive correlation in detectability and occupancy was estimated ($\rho = 0.29$ [95% CI: $-0.37, 0.86$]), but the relationship was typically non-linear (Fig. 3a). Detectability and observed occupancy were right-skewed across the forest bird community, while estimated occupancy was more normally distributed. For species where observed occupancy using raw data is above 50%, observed occupancy is a good indicator of estimated occupancy (Fig. 3b). However, for species with observed occupancy using raw data less than 50%, estimated occupancy may vary greatly depending on probability of detection.

DISCUSSION

Our approach to investigating community impact from, or resilience to, perturbation required drawing upon and combining analytical methods. Occupancy analysis provided the framework with which to analyze multi-species national monitoring data, which was important, since these data were being collected independently of any anticipation to analyze community resilience. The BACI analysis provided a developed framework to test for any impact of a perturbation, while correcting for natural levels of spatial and temporal variability. Our community-level approach allows us to share data simultaneously across multiple species in one model, rather than constructing many species-specific models, in order to investigate an effect that simultaneously impacted the entire community (Russell et al. 2009). However, this comes at the cost of having to impose parametric constraints on our model. In particular, species-specific estimates of detectability and occupancy are treated as normally distributed (on logit scale) random effects around a community average (Dorazio and Royle 2005). This could lead to a dampening of the response by any particular species within the context of the overall community response. Furthermore, our model is conservative, in that it does not allow for species-specific effects over time, which would over-parameterize our already computationally intensive community occupancy model. Our simulation study suggested the CO-BACI model performed admirably and is capable of detecting significant occupancy

impacts on communities, and estimates species detectability well.

The BACI framework was particularly useful for analyzing the impact of Hurricane Gudrun on Swedish forest birds. Underlying natural variability required incorporation, because the impact of Hurricane Gudrun was restricted to the southern half of Sweden, which is at a more temperate latitude, lower elevation, and has greater farmland cover. Including natural and habitat variability among sites allowed us to correct for any a priori difference between sites impacted and not impacted by the hurricane. Similarly, including a temporal component allowed us to estimate natural background rates of variation in avian community detectability and occupancy, as a context for any potential impact from Hurricane Gudrun. We did not find a significant change in occupancy or detectability of the forest bird community at hurricane impacted sites compared to control sites after the event. However, we did detect a significant decrease in occupancy, but not detectability, for the avian community in the final year of our analysis, across all sites. This effect, independent of the hurricane, corroborates other work suggesting the Swedish bird community is rapidly responding to climate change (Davey et al. 2013, Lindström et al. 2013). Overall, we suggest there is little evidence at the scale we investigated that Hurricane Gudrun had a significant effect on the forest bird community occupancy, or detectability, for our fifteen representative forest bird species in Sweden. However, we did find clear evidence that habitat relationships of species matched a priori predictions on how those relationships might alter detectability and occupancy for individual species, encouraging the CO-BACI framework as a way to simultaneously investigate community and species ecology.

The impacts of hurricanes on bird communities can be diverse, and there are a number of reasons why the hurricane may not have had an impact on occupancy (Wiley and Wunderle 1993, Simberloff 2000). The impact of the hurricane was patchy across the landscape, as characterized by our covariate for hurricane damage. Essentially, the hurricane created a variably sized checkerboard pattern of habitat loss through southern Sweden. The relative micro-scale of these habitat losses may have had little impact on the overall range of species relative to our 2-km squares, and so, overall occupancy would not have changed. Reasonably high levels of unexplained heterogeneity in occupancy might also be explained by such micro-scale effects as forest type (Roberge and Angelstam 2006), or other effects not considered in this macro-ecology study. Alternatively, and non-exclusively, avian abundance may have been reduced across the landscape, but not sufficiently to cause any local population extinctions, and thereby reducing occupancy. Swedish bird communities appear to respond most strongly to climate change in abundance rather than distribution (Lindström et al. 2013).

The lack of a reduction in detectability after impact, then suggests abundance influences detectability only to a minor degree in our study system. Our analytical framework did not explicitly model abundance, but occupancy–abundance relationships could be included to make inferences on changes in abundance, should the computational power not be prohibitive and the parameters identifiable. We did find non-linear positive correlation between detectability and occupancy (i.e., the most widespread species were also more easily detected). It is also plausible that the forest bird community was simply not impacted significantly by the hurricane, and that, whereas habitat was destroyed and sedentary species unable to relocate to new habitat may have been impacted, highly mobile species would have been able to relocate, if only temporarily.

Encouragingly, the detectability and occupancy of our community did depend upon other a priori hypothesized covariates, such as latitude, elevation, and the presence of certain habitats (farmland or forest), which were included to correct for their effect (Stjernman et al. 2013). Elevation and latitude generally had a negative impact on detectability and occupancy for a number of the species, which is not surprising given these species were generally chosen for their niche preference to forest and southern Swedish localities, and hence, vulnerability to the impacts of Hurricane Gudrun. Whereas, detectability was increased for some species in forest habitat, it was reduced in farmland habitat, putatively a function of habitat-specific bird abundances or behavior. In contrast, occupancy increased for some species in both farmland and forest, which provides the most amenable habitat for these species compared to other categories (settlement, open, and mire). Trends for Swedish farmland bird species are also similar in both farmland and forest habitats, where forest dominates Sweden's landscape, and thus trends in bird monitoring indices (Stjernman et al. 2013). Effects of habitat covariates on occupancy were strong, but not significant, for Red-backed Shrike, the species with lowest occupancy and least detections of those analyzed (having discarded Siberian Jays). Unfortunately, parameter estimation in the community occupancy framework failed for two species, and covariate estimates could not be reliably obtained. Nonetheless, the long-term high quality Swedish forest and bird survey datasets provided a rich source of data with which to test for a pulse environmental impact, and even though none was detected, the datasets allow ongoing monitoring of bird and forest population dynamics in anticipation of future impacts, whether natural or anthropogenic, which might also take a longer-term press form through gradual decline (Lindström et al. 2013).

Whereas observed occupancy not correcting for detectability is usually right-skewed, correcting for detectability in estimates of occupancy produces a more normal-like distribution (Kéry and Royle 2008). Correcting for detectability of forest bird species, such as

these, is probably not required when landscape occupancy is greater than 50%, however the species with low occupancy, where correcting for detectability is required, are precisely the species for which data are sparse and a community approach is required. Despite widespread availability of occupancy methods, many studies of avian distribution continue to neglect a vital detectability component (e.g., Hurlbert and White 2007), which leads to confounding results when changes in distribution cannot be separated from changes in detectability. The community occupancy framework allowed us to convincingly demonstrate that there was a real drop in occupancy (and, therefore, probably abundance) in our Swedish forest bird community, and not simply a change in detectability, and that this was independent of any hurricane impact. This is important, as, had a significant drop in avian counts occurred in hurricane impacted sites after the event, it could plausibly be attributed to a reduction in detectability associated with habitat loss, rather than occupancy. It is clear that a measure of detectability can greatly improve the usefulness of analyses like ours, even though this will require some form of repeated measures sampling.

Further theoretical work should consider the power of the CO-BACI model under different impact scenarios (e.g., acute vs. chronic perturbations) and in incorporating species abundances by assuming an occupancy–abundance relationship (Wenger and Freeman 2008). Complementary approaches to detecting impacts might include modeling turnover metrics (MacKenzie et al. 2003) or directly modeling dynamic habitat relationships (Miller et al. 2012). For practical application, future developments might include interspecific variation in response to perturbation, such as grouping species with regards to their response, but such variation has been demonstrated elsewhere to be weak (Mutshinda et al. 2011). There is no reason that additional species-specific covariates cannot be included, such as trait measurements (e.g., Hurlbert and White 2007), nor temporal covariates, such as climatic variables. Additional variation among sites could be modeled with site heterogeneity effects (Royle 2006), or auto-logistic models incorporating spatial effects to provide a more nuanced estimate of species occupancy across a landscape (Hui et al. 2006). False positive detections could also be modeled when species identification is not perfect (Miller et al. 2011). Extensions to the model could include developing multivariate control chart approaches around attractor regions incorporating imperfect species detection for detecting when a perturbation may have occurred (Anderson and Thompson 2004).

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