**BIODIVERSITY RESEARCH**

# Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species

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## ABSTRACT

**Aim** Emerging infectious diseases present a major perturbation with apparent direct effects such as reduced population density, extirpation and/or extinction. Comparatively less is known about the potential indirect effects of disease that likely alter community structure and larger ecosystem function. Since 2006, white-nose syndrome (WNS) has resulted in the loss of over 6 million hibernating bats in eastern North America. Considerable evidence exists concerning niche partitioning in sympatric bat species in this region, and the unprecedented, rapid decline in multiple species following WNS may provide an opportunity to observe a dramatic restructuring of the bat community.

**Location** We conducted our study at Fort Drum Army Installation in Jefferson and Lewis counties, New York, USA, where WNS first impacted extant bat species in winter 2007–2008.

**Methods** Acoustical monitoring during 2003–2011 allowed us to test the hypothesis that spatial and temporal niche partitioning by bats was relaxed post-WNS.

**Results** We detected nine bat species pre- and post-WNS. Activity for most bat species declined post-WNS. Dramatic post-WNS declines in activity of little brown bat (*Myotis lucifugus*, MYLU), formerly the most abundant bat species in the region, were associated with complex, often species-specific responses by other species that generally favoured increased spatial and temporal overlap with MYLU.

**Main conclusions** In addition to the obvious direct effects of disease on bat populations and activity levels, our results provide evidence that disease can have cascading indirect effects on community structure. Recent occurrence of WNS in North America, combined with multiple existing stressors, is resulting in dramatic shifts in temporal and spatial niche partitioning within bat communities. These changes might influence long-term population viability of some bat species as well as broader scale ecosystem structure and function.

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## INTRODUCTION

One of the primary goals of ecology is to understand how biotic and abiotic factors interact to form and structure ecosystems (Smith, 1966). Community ecologists continue to debate generalized theories that have been proposed to explain community assemblage, dynamics and structure (Hastings, 1980; Tilman, 1982; Hubbell, 2001; Bell, 2001; Tilman, 2004). Regardless of the theoretical underpinning, there is abundant evidence that where suites of species occur

within a common area, trait-based ecological partitioning among co-occurring species commonly occurs (Connell, 1980, 1983; Schoener, 1983, 1986). This partitioning among species is explained by niche theory, whereby species within the community tend to partition resources provided two key general criteria are met: (1) interspecific competition remains above a certain threshold (such as the threat of intraspecific competition) and (2) the environment is stable and resources are limited (Hutchinson, 1957, 1978; Ricklefs, 1990).

Niche partitioning is most likely to occur in species assemblages that are diverse and highly structured by competition (Begon *et al.*, 1996), such as that displayed by insectivorous bat communities (Arlettaz *et al.*, 1997; Patterson *et al.*, 2003; Ashrafi *et al.*, 2011). Bats are among the most diverse and most recently expanded mammalian orders (Ray *et al.*, 2007). Insectivorous bats in particular exhibit unique wing and jaw morphologies, and sensory adaptations that should minimize interspecific competition by exploiting species-specific habitat or prey-base niches (Aldridge & Rautenbach, 1987; Barclay & Brigham, 1991; Siemers & Schnitzler, 2004; Siemers & Swift, 2006). Sympatric bat species might compete for auditory bandwidth and alter their echolocation call structure (Habersetzer, 1981; Ratcliffe *et al.*, 2004) in what has been termed an 'interspecific jamming avoidance response' (Necknig & Zahn, 2011). Additionally, bats are highly mobile and exhibit some flexibility in prey and habitat use, enhancing the likelihood of interactions and interspecific competition among sympatric species (Kunz, 1973; Ashrafi *et al.*, 2011). To limit interspecific competition for prey and auditory bandwidth, spatial niche partitioning is believed to be common in sympatric bat species, particularly at foraging areas where individual species exploit specific, fine-scale habitat conditions (Arlettaz, 1999; Arlettaz *et al.*, 2000; Patterson *et al.*, 2003; Nicholls & Racey, 2006; Razgour *et al.*, 2011). Though not as well documented, temporal niche partitioning within a night also occurs (Kunz, 1973; Reith, 1980; Castro-Arellano *et al.*, 2009) – particularly where multiple bat species prefer to utilize a limited resource simultaneously (e.g. water sources in arid environments; Adams & Thibault, 2006).

Niche partitioning as a result of interspecific competition can partially explain current patterns in bat community structure; however, natural or anthropogenic disturbance, whether stochastic or deterministic, also plays a key role in observed community structure (Shorrocks *et al.*, 1984; Tilman, 1987; Stewart, 1996). Disease outbreaks can impact population viability of species and have broader impacts on animal behaviour and community ecology (van Riper *et al.* 1986; Dobson & Hudson, 1986; Scheibling, 1986; Newman *et al.*, 2003; Holdo *et al.*, 2009). In particular, emerging infectious diseases have pronounced community-level impacts due to the rapid decline of certain species (Dobson & Hudson, 1986; Lips *et al.*, 2006). First documented in bats in a winter hibernaculum near Albany, New York, in 2006, white-nose syndrome (WNS) caused by the fungal pathogen *Pseudogymnoascus destructans* has spread rapidly across 23 states and five Canadian provinces in North America (USGS, 2013) resulting in the mortality of >6 million bats among 6 cave-dwelling species: big brown bat (*Eptesicus fuscus*; EPFU), eastern small-footed bat (*Myotis leibii*; MYLE), little brown bat (*Myotis lucifugus*; MYLU), northern long-eared bat (*Myotis septentrionalis*; MYSE), Indiana bat (*Myotis sodalis*; MYSO) and tri-coloured bat (*Perimyotis subflavus*; PESU). By contrast, there has been no documented occurrence of this disease in bat species that do not overwinter in cave or mine hibernacula (i.e. seasonally migratory tree-roosting species). Given the differential effect of WNS, not only is the disease likely to have a direct effect on conservation of individual bat species (e.g. Thogmartin *et al.*, 2013), but also an indirect effect on broader bat community structure as well (Frick *et al.*, 2010; Turner *et al.*, 2011).

Most conservation attention is focused on the ongoing WNS-associated population declines in some of North America's most abundant or endangered bat species such as MYLU and MYSO, respectfully. However, it is also critical to understand how all bat species are responding to the disease. For example, although there is evidence that rapid increase in certain bat species can suppress other resident bat species through interspecific competition (Arlettaz *et al.*, 2000), we do not yet have an understanding of whether the decline of certain bat species results in competitive release of other species. Currently, community-level investigations of WNS dynamics focus on disease transmission (e.g. Hayman *et al.*, 2012; Langwig *et al.*, 2012), and not the effects on remaining individuals. We hypothesize that dramatic changes in species abundance could lead to spatial or temporal alteration of their behaviour to exploit newly abandoned niche space.

To examine potential indirect effects of large-scale population declines associated with WNS on community structure, we evaluated a long-term acoustic dataset that assessed nocturnal foraging bat activity from prior to (2003–2007) and following arrival (2008–2011) of WNS at Fort Drum Military Installation, New York, USA. Interspecific competition within our study area was likely to be greatest within the genus *Myotis* because they are known to occupy similar foraging niche space and exhibit a tendency towards temporal niche partitioning (Kunz, 1973; Arlettaz *et al.*, 1997; Siemers & Schnitzler, 2004; Siemers & Swift, 2006; Adams & Thibault, 2006). Further, even sympatric species with differing foraging strategies can be impacted by the presence of an abundant competitor (Arlettaz *et al.*, 2000). Therefore, we hypothesized that declines in dominant bat species as a result of WNS would cause changes in bat community structure and spatial and/or temporal niche partitioning.

## METHODS

### Study area

We conducted our study at Fort Drum, a 43,000 + ha U.S. Army installation in Jefferson and Lewis counties, New York, USA. Located in the north-western portion of the state, Fort

Drum lies at the intersection of the Tug Hill Plateau, the St. Lawrence/Great Lakes Lowlands and the foothills of the Adirondack Mountains. Topography is rolling with some incised water-courses along the Black River and Indian River drainages. Elevations range from 125 to 278 m. Approximately, 57% of the landscape was made up of forested habitat dominated by northern hardwood associations. Small lakes, ponds and open wet meadows covered approximately 20% of the landscape. While some small successional change in forested environments did occur over the course of our 8-year study, the habitat conditions within the riparian areas where we focused our study were relatively unchanged. Development was spatially concentrated in the south-eastern corner of the installation, with the remainder of the installation consisting of 18 training areas, an airfield and a large, centralized ordnance impact zone that are all largely undeveloped (Dobony et al., 2011; Ford et al., 2011).

Nine bat species have been documented on Fort Drum, including: MYLU, MYSO, MYSE, MYLE, silver-haired bat (Lasionycterius noctivagans, LANO), PESU, EPFU, eastern red bat (Lasiurus borealis, LABO) and hoary bat (Lasiurus cinereus, LACI). During the winter of 2007–2008, WNS appeared in area hibernacula, resulting in mass overwinter mortality and dramatic declines in summer activity by at least 3 of the most commonly encountered bat species (MYLU, MYSE and MYSO) since 2008 (Ford et al., 2011). In particular, MYLU suffered a precipitous population decline post-WNS (Dobony et al., 2011; Ford et al., 2011).

## Bat monitoring

From 2003 to 2011, we placed frequency-division Anabat II bat detectors (Titley Scientific, Ballina, Australia)[1] to passively record bat echolocation passes at 70 pre-determined, fixed study sites. Although spatially balanced, stratified random sampling designs are ideal for making inference to a larger area (e.g. Rodhouse et al., 2011), these designs are difficult to implement over a large area and often need to be balanced with low probability of detection of many bat species in certain habitat types within heterogeneous landscapes (Johnson et al., 2010; Coleman, 2013). Accordingly, to maximize detection of multiple species in our study area, we prioritized selection of study sites within or near (<100 m) riparian areas based on: (1) findings from previous studies suggesting summer bat activity is generally positively correlated with riparian habitat (Vaughan et al., 1997; Ford et al., 2005; Menzel et al., 2005b; Rogers et al., 2006) and (2) placement of acoustical devices in riparian areas has been shown to maximize detection probabilities for a variety of bat species present within Fort Drum (Owen et al., 2004; Menzel et al., 2005a). Thus, our placement of acoustical detectors within riparian areas was strategically based on the availability of open habitat near water sources where bat for-

aging activity and probability of detection would be maximized.

All acoustic surveys were conducted during the summer season (June–September) when bats were present on the landscape prior to, during and immediately following the maternity season. We programmed Anabat detectors to record from dusk to dawn. We were not able to sample all sites during all months and all years. We surveyed a total of 70 sites during our 8-year study. We visited 61 of the 70 sites at least once between 2003 and 2007 (pre-WNS) and 53 of the sites at least once between 2008–2011 (post-WNS). Overall, we visited 45 of the 70 sites once both pre- and post-WNS. We attempted to equally distribute our sampling across the summer period of peak activity, and to account for potential seasonal effects, attempted to revisit individual sites post-WNS within 2 weeks of the date used pre-WNS.

We downloaded, identified and tallied the number of species identifications per hour for each site on each sample night (see Ford et al., 2011 for specific echolocation pass identification methodologies). The resulting echolocation tallies commonly are used as an index of bat activity that in turn serves as a surrogate for bat relative abundance (Hayes, 1997; Law & Chidel, 2002; Gehrt & Chelsvig, 2004; Owen et al., 2004). Such activity indices fail to account for error associated with variation in species-specific differences in detection probabilities (MacKenzie et al., 2006); however, by standardizing methods across years and controlling for sampling conditions (as herein), indices still can provide inference to trends in population dynamics over time (Link & Sauer, 1998). Therefore, despite the shortcomings of using an index for making ecological inference (Anderson, 2001, 2003; Thompson, 2002), hourly rates of detection resulting from automated acoustical sensors currently provide the most reliable, repeatable and biologically relevant metric for quantifying presence and competition in studies of bat community ecology (Razgour et al., 2011).

## Analysing temporal and spatial niche partitioning

We evaluated whether temporal and spatial niche partitioning was altered pre- vs. post-WNS by comparing activity of each bat species to corresponding intensity of activity by one of the predominant bat species seemingly most affected by WNS across our study area and much of eastern North America, MYLU (Dzal et al., 2011). Prior to WNS, MYLU activity was 5–52 times higher on average than all other species (Table 1), and this species was consistently detected during the early evening period (i.e. within the first 4 h after sunset) across all study sites. Following WNS, MYLU activity declined precipitously across the entire study area (Ford et al., 2011).

In response to decreasing MYLU activity, a variety of complex species-specific responses could occur ranging from no response to positive or negative effects of MYLU activity at a site post-WNS. Preliminary analysis of the data using a correlation matrix (and thus not accounting for the repeated

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[1]The use of any trade, product or firm names does not imply endorsement by the US government.

**Table 1** Bat species detected in Ft. Drum, New York, USA during our study (2003–2011) and percentage of nights when a species was detected at least once per night during summer sampling prior to ($n = 60$) and following ($n = 40$) white-nose syndrome (WNS) in winter of 2007–2008. The proportion of total detections that each individual bat species represents prior to ($n = 22308$) and following ($n = 6496$) WNS is given to further illustrate changes in bat community composition

| Species | Percentage of nights detected at least once | | Percentage of total detections | |
|---|---|---|---|---|
| | Pre-WNS (%) | Post-WNS (%) | Pre-WNS (%) | Post-WNS (%) |
| Little brown bat (*Myotis lucifugus*, MYLU) | 100 | 82.69 | 50.98 | 16.42 |
| Indiana bat (*Myotis sodalis*, MYSO) | 85.45 | 75.00 | 9.78 | 3.92 |
| Northern bat (*Myotis septentrionalis*, MYSE) | 83.64 | 34.62 | 3.36 | 0.73 |
| Eastern small-footed bat (*Myotis leibii*, MYLE) | 16.36 | 32.69 | 0.11 | 0.79 |
| Big brown bat (*Eptesicus fuscus*, EPFU) | 85.45 | 84.62 | 12.75 | 27.76 |
| Eastern red bat (*Lasiurus borealis*, LABO) | 72.73 | 82.69 | 10.14 | 12.86 |
| Hoary bat (*Lasiurus cinereus*, LACI) | 87.27 | 63.46 | 10.73 | 17.10 |
| Silver-haired bat (*Lasionycterius noctivagans*, LANO) | 47.27 | 76.92 | 0.96 | 16.85 |
| Tri-coloured bat (*Perimyotis subflavus*, PESU) | 38.18 | 38.46 | 1.19 | 3.56 |

**Table 2** Correlation matrix of hourly activity by nine bat species recorded at acoustic monitoring stations in Ft. Drum, New York, USA. Values below the diagonal reflect correlation values observed prior to white-nose syndrome (WNS) impacting the population (2003–2007), and values above the diagonal reflect correlation values observed post-WNS (2008–2011). Bat species we monitored included: little brown bat (*Myotis lucifugus*, MYLU), northern bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), eastern small-footed bat (*Myotis leibii*, MYLE), silver-haired bat (*Lasionycterius noctivagans*, LANO), tri-coloured bat (*Perimyotis subflavus*, PESU), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO) and hoary bat (*Lasiurus cinereus*, LACI)

| | EPFU | LABO | LACI | LANO | MYLE | MYLU | MYSE | MYSO | PISU |
|---|---|---|---|---|---|---|---|---|---|
| EPFU | 1 | 0.0805 | 0.2749 | 0.4044 | 0.0058 | 0.0603 | 0.2955 | 0.0909 | 0.0272 |
| LABO | 0.0380 | 1 | 0.1255 | 0.1128 | 0.1148 | 0.4006 | 0.0959 | 0.2507 | 0.1143 |
| LACI | 0.2669 | 0.2127 | 1 | 0.3854 | −0.0108 | 0.0421 | 0.0250 | 0.0657 | 0.0407 |
| LANO | 0.1026 | 0.2542 | 0.4249 | 1 | 0.0344 | 0.0581 | 0.0367 | 0.0023 | 0.0304 |
| MYLE | −0.0190 | −0.0191 | 0.0339 | 0.0041 | 1 | 0.1424 | 0.0038 | 0.1224 | 0.1443 |
| MYLU | 0.0346 | 0.1016 | 0.1236 | 0.1292 | −0.0195 | 1 | 0.1153 | 0.3249 | 0.1465 |
| MYSE | 0.1602 | −0.0251 | 0.0051 | 0.0146 | 0.0203 | −0.0305 | 1 | 0.2045 | 0.0027 |
| MYSO | 0.0114 | 0.0048 | −0.0241 | 0.0206 | −0.0056 | 0.1343 | 0.1907 | 1 | 0.0722 |
| PISU | 0.0051 | 0.5452 | 0.0150 | 0.0454 | −0.0104 | 0.0359 | 0.0306 | −0.0147 | 1 |

**Table 3** Matrix of hypothesized explanations for interactions between hourly activity rates of *Myotis lucifugus* (MYLU) and 8 other bat species we studied prior to and following white-nose syndrome (WNS) at foraging areas in Ft. Drum, New York, USA. Signs represent direction of relationship between activity by a bat species and MYLU activity

| | Post-WNS | | |
|---|---|---|---|
| | + | − | ~ |
| Pre-WNS | | | |
| + | No change | Competitive exclusion of MYLU possible | Relaxation of co-occurrence relationship with MYLU |
| − | Competitive release, co-occurrence with MYLU | No change | Partial competitive release |
| ~ | Competitive release, co-occurrence with MYLU | Competitive exclusion of MYLU possible | No change |

spatial and temporal nature of the data) supported our original hypothesis that compared with prior to WNS, MYLU activity was more strongly correlated with activity of most other bat species following WNS (Table 2). Specific to this study, we were concerned with species that exhibited activity patterns that were negatively or only weakly correlated with

MYLU activity pre-WNS, indicative of competitive exclusion (Table 3). For these species, we hypothesized that post-WNS, activity would show higher positive correlation with MYLU activity due to relaxed interspecific competition and utilization of newly available niche space.

To test these hypotheses, we developed a set of *a priori* candidate models for explaining patterns in activity (Table 4). To test the hypothesis that MYLU were spatially excluding other bat species, we included a fixed effect of MYLU activity in our models predicting activity for each of the eight other bat species. Further, because we hypothesized that competitive pressure was released post-WNS and the subsequent dramatic decline in MYLU, we included an interactive effect of MYLU activity and if sampling was conducting prior to or post-WNS.

We tested the effect of changing temporal niche partitioning by comparing hourly activity patterns pre- and post-WNS. Activity by a majority of North American bat species typically reaches a peak in the hours shortly after sunset (Kunz, 1973). However, peak times of activity can vary greatly among species, suggestive that temporal niche partitioning at a common site does occur (Adams & Thibault, 2006). Therefore, we tested the hypothesis that activity levels differed between hour intervals on a given night and that an interactive effect of time of night and MYLU activity influenced activity by other bat species. Moreover, due to the general decline of MYLU activity post-WNS, we hypothesized an interactive effect of both hour during the night and WNS on observed differences in activity whereby other bat species would be more likely to exploit the early, post-sunset period at these prime foraging areas following the decline of MYLU activity.

Although all of our study sites were within riparian habitat where all of the extant bat species at Fort Drum could be expected to occur (Ford *et al.*, 2011), fine-scale habitat differences such as proximity to forest edge or interior and uncluttered riparian areas could have influenced bat activity within our study (Coleman, 2013; Jachowski *et al.*, 2014). Therefore, we included fine-scale habitat measurements of both distance to forest edge and distance to open water or open moist field edge (after beaver abandonment) from the centre of each study site (i.e. location where Anabat acoustical detector was placed). Climatic patterns also are known to influence bat activity, with cooler temperatures and precipitation associated with decreased activity (Kunz, 1973). We focused our surveys during the relatively warm summer season and avoided acoustical monitoring during heavy rain; however, some fine-scale, among-night variability did exist in climatic conditions. We extracted nightly data on minimum temperature and total precipitation from a weather station centrally located within Fort Drum to relate these continuous metrics to bat activity.

We evaluated support for models containing each of our four primary hypothesized factors as well as seven models containing combinations of the four factors (Table 4), using an information-theoretic model selection approach (Burnham & Anderson, 2002). Because many sites were sampled at least twice, albeit during different years (i.e. one pre-WNS and one post-WNS), we fitted models using a mixed model approach, whereby site was treated as a random effect, and date (i.e. night within year) a site was sampled was treated as a repeated effect. We first used a restricted maximum-likelihood approach to identify the most appropriate covariance structure for our mixed model based on Akaike Information Criteria corrected for small sample size ($AIC_c$) ranking, which we determined to be autoregressive (Diggle *et al.*, 1994; Littell *et al.*, 2006). We then used a maximum-likelihood approach with autoregressive covariance structure to fit our linear mixed models [SAS PROC MIXED (Littell *et al.*, 2006)] and evaluated model support based on $\Delta AIC_c$ values (Burnham & Anderson, 2002).

**Table 4** *A priori* models used to evaluate competing hypotheses regarding the influence of climatic, habitat, as well as spatial and temporal niche partitioning on bat hourly activity rates in Ft. Drum, New York, USA. Bat communities were monitored prior to white-nose syndrome (WNS) impacting the population (2003–2007) and post-WNS (2008–2011).

| Model Number | Model* | Description |
|---|---|---|
| 1 | Time | Hour post-sunset |
| 2 | Time × WNS | Hour post-sunset × WNS |
| 3 | Time × WNS + MYLU | Hour post-sunset × WNS + activity of MYLU |
| 4 | Time × WNS + MYLU × WNS | Hour post-sunset × WNS + activity of MYLU × WNS |
| 5 | Time × MYLU | Hour post-sunset × activity of MYLU |
| 6 | Habitat | Site distance to water edge + Site distance to forest edge |
| 7 | Climate | Minimum night temperature + Total daily precipitation |
| 8 | Time × WNS + Temp | Hour post-sunset × WNS + Minimum nightly temperature |
| 9 | MYLU × WNS + Temp | Activity of MYLU × WNS + Minimum nightly temperature |
| 10 | Time × WNS + MYLU × WNS + Temp | Hour post-sunset × WNS + activity of MYLU × WNS + Minimum nightly temperature |
| 11 | Global | – |

*Model covariate description: MYLU = activity/hr of little brown bat (*Myotis lucifugus*); Time = hour post-sunset; Temp = minimum temperature of night sampled; WNS = bivariate value based on if sampling occurred prior to (0) or following (1) WNS.

We evaluated model performance by calculating percentage of variation in activity explained by each model. We calculated the percentage of variation explained using the maximum-likelihood covariance parameter estimate for each model, where

$$\%\text{variation explained} = \left| \left( \frac{\sigma^2_{\text{process}} - \sigma^2_{\text{residual}}}{\sigma^2_{\text{process}}} \right) \times 100 \right|$$

and $\sigma^2_{\text{process}}$ = variance component estimate for the intercept-only model, and the $\sigma^2_{\text{residual}}$ = variance component estimate for the model in question (Doherty *et al.*, 2010; Jachowski *et al.*, 2013).

## RESULTS

We detected 9 bat species prior to and post-WNS at Fort Drum (Table 1). However, activity levels declined greatly post-WNS for most species, particularly for three *Myotis* species believed most impacted by WNS (Table 1). Prior to WNS, we detected MYLU at all sites during all nights of surveying (Table 1), and on average recorded 8.12 detections per hour (SD = 23.69, range: 0–243). Following WNS, MYLU were still detected on most sites and nights (Table 1), but activity declined to an average of only 1.15 detections per hour (SD = 4.56, range: 0–56). For the other 8 bat species, we observed the most support for models that related activity as dependent upon the effects of hour past-sunset, activity of MYLU, and an interactive effect of those factors with WNS (Table 5). For *Myotis* species in particular, the interactive effect of MYLU activity and WNS was consistently retained within the top model (Table 5). The percentage of variation explained by our top models for predicting bat activity varied considerably depending on the species of interest. Two species (PESU and MYLE) were detected so infrequently (Table 1) that our ability to predict activity levels was limited (a result reflected in ≤1% per cent of variation being explained by the top-ranked models for these two species compared with 5–9% explained for all other species; Table 5). Therefore, we refrained from making further inference about these two species.

We observed support for including minimum temperature within top approximating models for all 6 bat species, but no support for inclusion of rainfall or the various habitat covariates (Table 5). Recorded low temperatures were similar between pre- and post-WNS periods, with minimum nightly temperatures on average being 15.24 °C (SD: 4.17, range: 7.22–26.11) during 2003–2007 and 14.31 °C (SD = 5.30, range: 3.89–22.78) during 2008–2011. A decrease in temperature was generally associated with decreases overall in bat activity, particularly for *Myotis* species. MYSE, MYSO and MYLU activities on average were predicted to decline 4% for every 1 °C decrease in minimum nightly temperature, and MYSE and MYSO activities were predicted to completely cease at temperatures below 10 °C (Fig. 1). Failure to find support for fine-scale habitat covariates was likely a result of all sites being placed in/near riparian areas and in close proximity to other habitat conditions relative to the high vagility of the bat species at Fort Drum.

### Temporal niche partitioning

Temporal patterns in bat activity were altered for all bat species post-WNS. We observed support for an interaction between hour of the night sampled (i.e. time) and WNS within our top-ranked model(s) for all species (Table 5). By comparison, we observed no support for inclusion of an individual effect of time, or an interactive effect of MYLU activity and time, further suggesting that WNS had a large impact on bat temporal activity patterns. Prior to WNS, 6 of the 7 retained species were most active just after sunset, with MYLU being the most prominent bat species detected. Post-WNS, activity by MYLU and most other bat species, with the exception of LANO, declined in activity (Table 1) but generally still showed a peak in activity in the early evening. However, rather than showing identical patterns in hourly activity post-sunset (although at an overall reduced level), MYLU, MYSE, EPFU, LACI and LABO all illustrated more relaxed slopes of declining activity after sunset post-WNS (Fig. 2), suggesting that activity of these 5 bats was more widely distributed across the early evening hours post-WNS. In contrast, MYSO and LANO exhibited a shift in activity towards early evening activity post-WNS (Fig. 2).

### Spatial niche partitioning

We observed complex, species-specific shifts in the relationship between MYLU activity and activity of other bat species pre- vs. post-WNS indicative of a relaxation of spatial niche partitioning. We found strong support for the interactive effect of MYLU activity and WNS being retained in top predictive models for all species (Table 5), indicative of a difference in the relationship between MYLU activity and the activity of other bats at that site post-WNS. With the exception of MYSE and LANO, prior to WNS, we typically observed only a weak positive correlation between MYLU activity and activity of all other bat species (Fig. 3). In contrast, when MYLU activity was lowest post-WNS, we observed a much stronger positive effect of MYLU activity on activity by MYSO, MYSE, EPFU, LABO and LANO (Fig. 3). This suggests that most bat species were more likely to use locations with high MYLU activity post-WNS.

## DISCUSSION

Stochastic processes are inherently involved in ecosystem structure (Begon *et al.*, 1996), but novel invasive pathogens present a significant conservation problem, particularly when added to recent and legacy anthropogenic disturbance. For bats in North America, it is now well established that WNS has direct effects (i.e. mortality) on bat populations (Turner *et al.*, 2011), driving some species towards regional extirpation or

**Table 5** Support for models used to predict hourly activity levels by eight bat species in Ft. Drum, New York, USA. Support for each model in explaining activity by bat species was based on Akaike Information Criterion for small sample sizes. Only most supported models (i.e. within 4 $\Delta AIC_c$ units) are reported. Bat species we monitored included: little brown bat (*Myotis lucifugus*, MYLU), northern bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), eastern small-footed bat (*Myotis leibii*, MYLE), silver-haired bat (*Lasionycterius noctivagans*, LANO), tri-coloured bat (*Perimyotis subflavus*, PESU), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO) and hoary bat (*Lasiurus cinereus*, LACI)

| Species | Model* | log (l) | K | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight | $\sigma^2_{model}$† | Absolute variation explained (%) |
|---|---|---|---|---|---|---|---|---|
| LANO | Time × WNS | 7683.39 | 7 | 7697.39 | 0 | 0.34677 | 2.9008 | 9.30 |
| | Time × WNS + Temp | 7681.55 | 8 | 7697.55 | 0.1649 | 0.31932 | 2.9073 | 9.09 |
| | Time × WNS + MYLU | 7682.76 | 8 | 7698.76 | 1.3683 | 0.17495 | 2.9016 | 9.27 |
| | Time × WNS + MYLU × WNS | 7682.42 | 9 | 7700.42 | 3.0282 | 0.07629 | 2.9012 | 9.28 |
| | Time × WNS + MYLU × WNS + Temp | 7680.57 | 10 | 7700.57 | 3.1837 | 0.07058 | 2.9077 | 9.08 |
| LABO | Time × WNS + MYLU × WNS | 12440.2 | 9 | 12458.2 | 0 | 0.52765 | 81.5759 | 6.00 |
| | Time × WNS + MYLU × WNS + Temp | 12439.9 | 10 | 12459.9 | 1.7461 | 0.22039 | 81.7573 | 5.75 |
| | Time × WNS + MYLU | 12444.1 | 8 | 12460.1 | 1.947 | 0.19933 | 81.9317 | 5.55 |
| LACI | Time × WNS + MYLU | 10454.1 | 8 | 10470.1 | 0 | 0.59727 | 11.7750 | 7.47 |
| | Time × WNS + MYLU × WNS | 10454 | 9 | 10472 | 1.9411 | 0.22629 | 11.7826 | 7.41 |
| | Time × WNS + MYLU × WNS + Temp | 10453.9 | 10 | 10473.9 | 3.7976 | 0.08944 | 11.7726 | 7.49 |
| EPFU | Time × WNS + MYLU × WNS | 12315.1 | 9 | 12333.1 | 0 | 0.28288 | 28.0119 | 5.08 |
| | Time × WNS | 12319.1 | 7 | 12333.1 | 0.0748 | 0.2725 | 27.9874 | 5.17 |
| | Time × WNS + MYLU | 12317.7 | 8 | 12333.7 | 0.6656 | 0.2028 | 28.0217 | 5.05 |
| | Time × WNS + MYLU × WNS + Temp | 12314.8 | 10 | 12334.8 | 1.7678 | 0.11688 | 28.0574 | 4.93 |
| | Time × WNS + Temp | 12318.9 | 8 | 12334.9 | 1.8305 | 0.11327 | 28.0327 | 5.01 |
| PESU | TIME | 8124.23 | 5 | 8134.23 | 0 | 0.55454 | 3.3519 | 0.09 |
| | Climate | 8125.24 | 6 | 8137.24 | 3.0052 | 0.12342 | 3.3522 | 0.08 |
| | Time × WNS | 8123.87 | 7 | 8137.87 | 3.6371 | 0.08998 | 3.3549 | <0.01 |
| MYSO | MYLU × WNS + Temp | 12114.9 | 8 | 12130.9 | 0 | 0.73786 | 26.0485 | 5.94 |
| | Time × WNS + MYLU × WNS + Temp | 12114 | 10 | 12134 | 3.0958 | 0.15694 | 26.0605 | 5.89 |
| MYSE | Time × WNS + MYLU × WNS + Temp | 7662.89 | 10 | 7682.89 | 0 | 0.32331 | 2.6185 | 6.08 |
| | Time × WNS + Temp | 7666.98 | 8 | 7682.98 | 0.0856 | 0.30977 | 2.6217 | 5.97 |
| | Global | 7657.8 | 13 | 7683.8 | 0.9085 | 0.20528 | 2.6208 | 6.00 |
| | Time × WNS + MYLU | 7669.72 | 8 | 7685.72 | 2.8298 | 0.07855 | 2.6382 | 5.37 |
| MYLE | MYLU × WNS + Temp | 132.554 | 8 | 148.554 | 0 | 0.60194 | 0.06397 | 1.05 |
| | Time × WNS + MYLU × WNS | 132.155 | 9 | 150.155 | 1.6014 | 0.27028 | 0.06399 | 1.02 |
| | Time × WNS + MYLU × WNS + Temp | 132.135 | 10 | 152.135 | 3.5808 | 0.10046 | 0.06403 | 0.96 |

*Model covariate description: MYLU = activity/hr of little brown bat (*Myotis lucifugus*); Time = hour post-sunset; Temp = minimum temperature of night sampled; WNS = bivariate value based on whether sampling occurred prior to (0) or following (1) the white-nose syndrome.
†$\sigma^2_{model}$ = covariance parameter estimate.

possibly even extinction, including those species showing strong population recoveries pre-WNS (Thogmartin *et al.*, 2013). Our results suggest that WNS is not only limited to direct effects on certain infected bat species, but can also have indirect, but cascading effects on behaviour and interspecific interactions by those species directly not impacted by WNS. Collectively, our study provides evidence that introduced diseases can have dramatic impacts on wildlife populations not only in terms of population or species viability, but in terms of community structure.

Interspecific competition plays a prominent role in structuring bat communities, and our data suggest that disease outbreaks destabilize spatial and temporal niche partitioning in sympatric bat species. Previously, evidence of temporal niche partitioning based on capture studies has been mixed,

where the phenomenon is apparent in some bat assemblages (Kunz, 1973; Reith, 1980), but unapparent in areas where bats forage in different habitats (Saunders & Barclay, 1992) or on different prey items (Hickey *et al.*, 1996). Recent use of acoustical monitoring has revealed fine-scale temporal niche partitioning among sympatric *Myotis* species where a particular resource (e.g. water) is limited (Adams & Thibault, 2006). At our study site, riparian areas are relatively abundant and widespread. However, our fine-scale, hourly monitoring of bat activity illustrates that prior to WNS, temporal niche partitioning likely occurred within a diverse bat community at these riparian areas. Following WNS, rapid decline of one of the formerly most abundant bat species (MYLU) corresponded with dramatic temporal shifts in activity levels that varied depending on the species of interest. Collectively,
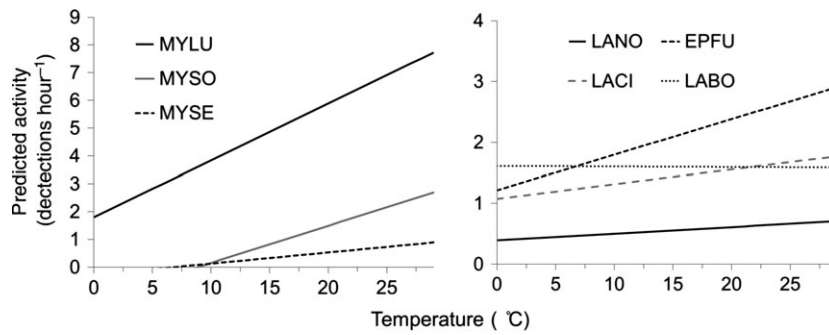
**Figure 1** Predicted effect of minimum nightly temperature on activity of 7 of the bat species we studied in Ft. Drum, New York, USA between 2003 and 2011 based on parameter coefficients from top-ranked models. Bat species we monitored included: little brown bat (*Myotis lucifugus*, MYLU), northern bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), silver-haired bat (*Lasionycterius noctivagans*, LANO), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO) and hoary bat (*Lasiurus cinereus*, LACI). Note that none of the 7 bat species are known to be active at temperatures below 0 °C.

these complex species-specific responses suggest that an overall reduction in interspecific competition and relaxation of temporal niche partitioning occurred post-WNS.

An abundance or density threshold likely exists prior to the relaxation of spatial niche partitioning, above which interspecific competition with the dominant bat species restricts activity of other bat species. Resource partitioning is known to be common in insectivorous bat species and *Myotis* in particular, whereby primary foraging habitats are largely thought to be species-specific (Arlettaz, 1999). However, our findings suggest that following a catastrophic disturbance such as WNS, such species-specific resource partitioning was less structured. Further, rather than taking advantage of sites where MYLU were reduced or extirpated post-WNS, other bat species generally were more likely to be active in areas where MYLU remained active. Although the causal mechanism for this enhanced correlation with MYLU activity for almost all bat species post-WNS remains unknown, there are at least two possible explanations for such an observed response. First, under optimal foraging theory (Emlen, 1966), patches of lowest foraging quality were likely the first to be abandoned by the surviving MYLU that remained post-WNS. Therefore, we hypothesize that rather than utilizing suboptimal riparian habitat that was abandoned or sparsely populated by MYLU post-WNS, other bat species could have taken advantage of reduced interspecific competitive pressure following WNS that allowed species to co-occur within optimal foraging patches. Second, calls of conspecific bats are known to influence the movement of individuals (i.e. conspecific attraction; Schöner *et al.*, 2010; Furmankiewicz *et al.*, 2011), and a similar interspecific attraction or 'eavesdropping' mechanism is known among sympatric bat species, resulting in mixed species foraging in high-quality habitats (Fenton, 2003; Gillam, 2007; Dechmann *et al.*, 2009; Übernickel *et al.*, 2013). Post-WNS, it is possible that this type of interspecific attraction was enhanced by MYLU generally being on a smaller number of sites, and by MYLU abundance overall being below a certain interspecific competition

abundance threshold that would otherwise limit activity of other species. A key area of future investigation will be to see whether changes in patterns of use in other habitat types might be more or less dramatic than those experienced in riparian areas. Although our focus was on the effect of MYLU activity, there is some evidence to suggest that for certain species, activity patterns are likely as strongly or more strongly correlated with species other than MYLU (Table 1). Therefore, shifts in activity by other species could similarly be impacting community assembly post-WNS and therefore are in need of future evaluation.

Given that insect availability varies both spatially and temporally across the northern hardwood region where our study occurred (Belwood & Fenton, 1976; Clare *et al.*, 2011), observation of a relaxation of temporal and spatial niche partitioning across species suggests that a dietary shift could be simultaneously occurring. Although beyond the scope of our study, in addition to spatial and temporal niche partitioning, dietary niche partitioning occurs in sympatric bat species (Arlettaz *et al.*, 1997; Patterson *et al.*, 2003; Ashrafi *et al.*, 2011). MYLU are smaller in size compared with the non-*Myotis* species present and have a generalized diet focused on small aquatic insects (Belwood & Fenton, 1976; Edythe & Kunz, 1977). By contrast, the somewhat larger non-*Myotis* species have diets that tend to include larger insects including beetles (Coleoptera) and a wider array of moths (Lepidoptera) (Rolseth *et al.*, 1994; Whitaker, 1995; Agosta, 2002; Clare *et al.*, 2009). Post-WNS, the shift of almost all species to spatially and temporally overlap foraging activity with MYLU suggests these species could be similarly focusing their diet on abundant, relatively small aquatic insects. Therefore, although prey size and hardness have been correlated with bat size in the species we studied, at a fine-scale extensive dietary overlap can occur (Feldhamer *et al.*, 2009), and an overall reduction in dietary niche separation could be occurring between species post-WNS. Additionally, it remains unknown what effect these shifts in foraging activity could have on physiological condition or fitness of bat
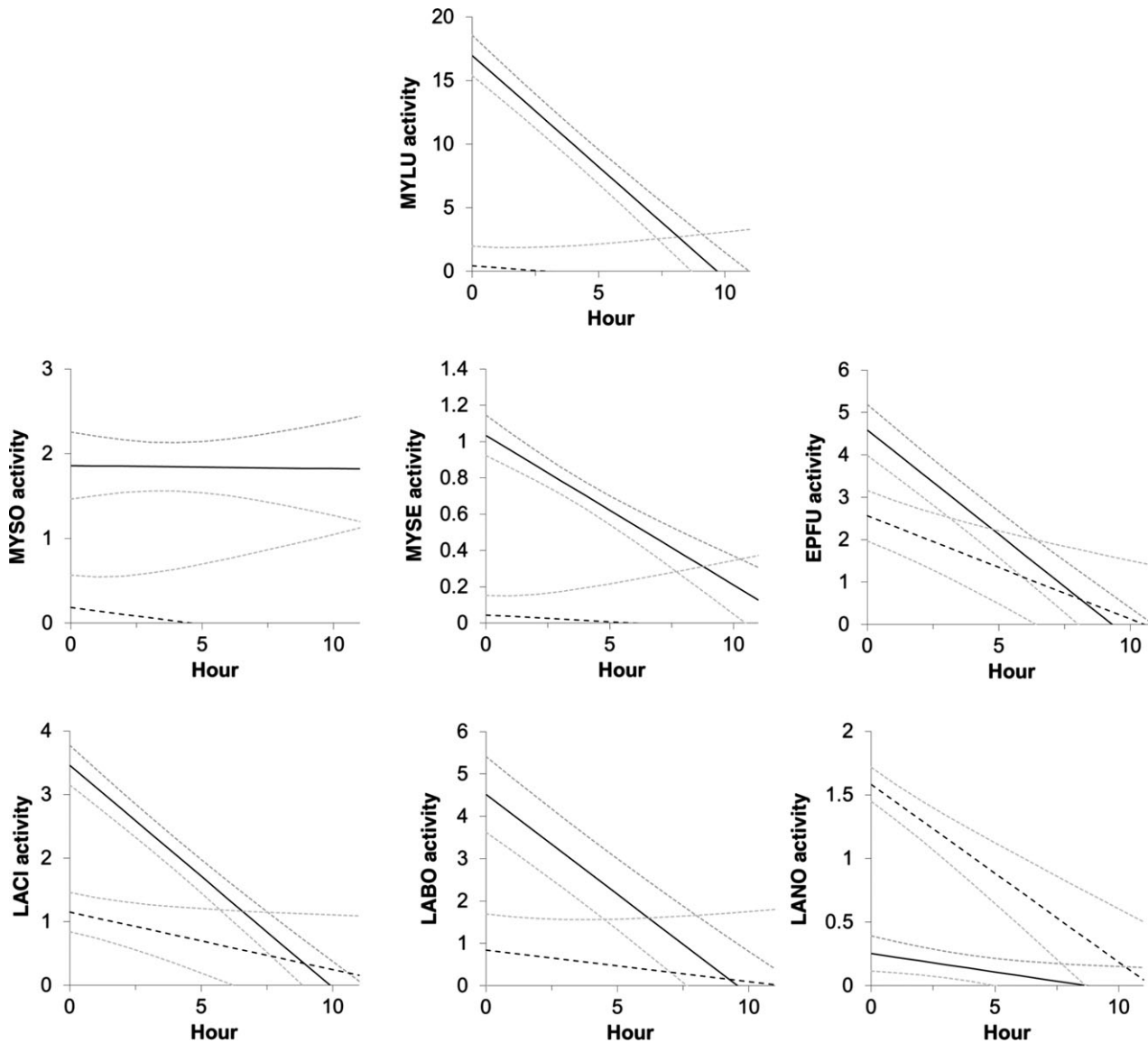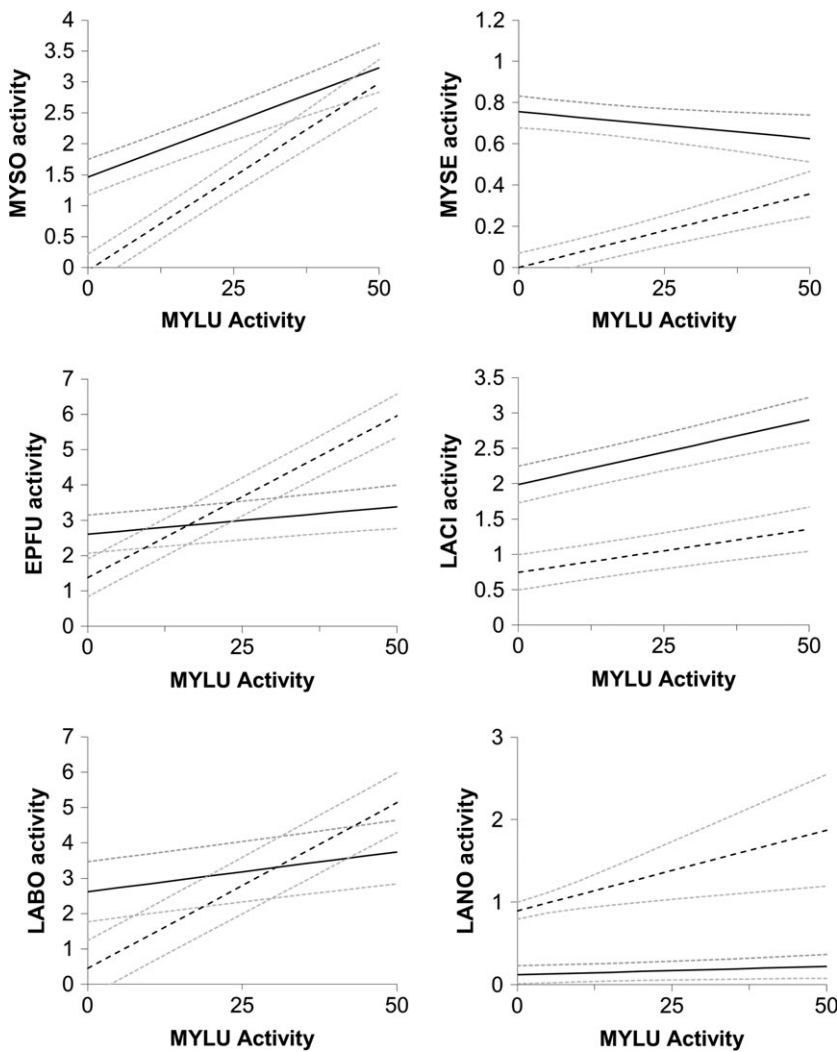
Figure 2 Predicted effect of hour post-sunset on activity (detections/hr) of 7 of the bat species detected in Ft. Drum, New York, USA based on parameter coefficients from top-ranked models. Predictive plots are divided into time periods prior to (solid line, 2003–2007) and following (dashed line, 2008–2011) white-nose syndrome (WNS) that occurred during the winter of 2007–2008 (light grey dashed bars represent extent of 1 standard error around predicted value). Bat species we monitored included: little brown bat (*Myotis lucifugus*, MYLU), northern bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), silver-haired bat (*Lasionycterius noctivagans*, LANO), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO) and hoary bat (*Lasiurus cinereus*, LACI). See Appendix S1 in supplementary information for hourly average summary of original data points.

species post-WNS. Clearly, further research is needed to assess whether such dietary shifts are occurring, the physiological implications of potential shifts, and any cascading effects thereof due to the important role bat species play as insectivores in ecosystems (Cleveland *et al.*, 2006; Kalka *et al.*, 2008).

Although our study provides initial evidence of alteration in spatial and temporal niche partitioning post-WNS, further investigations into bat community structure post-WNS will be necessary to fully quantify the scope and outcome of this ongoing phenomenon. Acoustical monitoring for bats is one

of the most frequently used and logistically feasible techniques for monitoring bat species activity and occurrence (O'Farrell & Gannon, 1999). However, the low amount of variation explained by our predictive models for these small, highly vagile mammals suggests that further, more detailed studies of bat community structure are needed. Further, changes in community structure that we observed might be interacting with larger-scale factors such as local and regional habitat alterations and/or naturally occurring successional processes in forest and wetland condition, and more recently, wind energy development. Six of the 9 species we observed

**Figure 3** Predicted effect of activity of the predominant bat species (little brown bat, *Myotis lucifugus*, MYLU) on activity (detections/hr) of 6 other bat species detected in Ft. Drum, New York, USA based on parameter coefficients from top-ranked models. Predictive plots are divided into time periods prior to (solid line, 2003–2007) and following (dashed line, 2008–2011) white-nose syndrome (WNS) that occurred during the winter of 2007–2008 (light grey dashed bars represent extent of 1 standard error around predicted value). Bat species we monitored included: little brown bat (*Myotis lucifugus*, MYLU), northern bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), silver-haired bat (*Lasionycterius noctivagans*, LANO), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO) and hoary bat (*Lasiurus cinereus*, LACI). See Appendix S2 in supplementary information for original data points.

(MYLU, MYSO, MYSE, MYLE, EPFU and PESU) are known to be susceptible and have had mortality events linked to WNS (Turner *et al.*, 2011). Accordingly, we observed the most drastic declines in activity of *Myotis* species that were most active pre-WNS (MYLU and MYSO). We also observed declines in activity of two species (LACI and LABO) not yet documented to succumb to the disease (Table 1). Cause of the decline in recorded activity of these two migratory bat species post-WNS is unknown, but could be attributed to the recent development of wind energy facilities in the eastern United States (Kunz *et al.*, 2007; Arnett *et al.*, 2008) some of which has occurred in the region near Fort Drum. However, an increase in activity rather than a decline was observed for the other migratory bat species commonly associated with wind energy fatalities (LANO; Kunz *et al.*, 2007; Arnett *et al.*, 2008). We encourage further research into the interactive effects of WNS and other anthropogenic disturbances on bat community structure.

In the face of climate change, continued presence of WNS, and increased or changing anthropogenic disturbance, bat species in North America face a critical, unprecedented conservation hurdle. Our results suggest that niche partitioning is relaxed post-WNS, allowing other species into formerly occupied niche space. The obvious question that remains to be answered is whether relaxed interspecific competition will eventually scale-up to demographic increases in species not directly impacted by WNS. Our relatively short-term (4 year) monitoring post-WNS and monitoring at other locations over a similar length of time post-WNS (Brooks, 2011) so far suggests that bat populations have yet to show any signs of recovery and rather still continue to decline. Further, species not directly impacted by WNS might not occupy abandoned niche space due to other stressors still operating on bat populations irrespective of WNS impacts. Although we are aware of the direct and indirect effects WNS is having on bat community assemblages and species interactions, the long-term and likely cascading effects of losing such diverse and abundant insectivores across much of North America remain unknown. Finally, it remains unclear whether and when niche partitioning will reappear within WNS-impacted bat communities, and at a minimum it is likely that movements and habitat associations of bats post-WNS will be less

structured than previously described. Therefore, we suggest that researchers reconsider existing knowledge of bat community ecology for WNS-impacted systems and that managers recognize that WNS-induced changes might render irrelevant the past data on bat habitat use, distribution and abundance commonly used as baselines in making land management decisions.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Average observed hourly activity levels for nine bat species detected at acoustic monitoring stations prior to (2003–2007) and following (2008–2011) arrival of white-nose syndrome (WNS) at Ft. Drum, New York, USA.

**Appendix S2** Observed hourly activity levels detected at acoustic monitoring stations prior to (2003–2007) and following (2008–2011) arrival of white-nose syndrome (WNS) at Ft. Drum, New York, USA, plotted as a function of activity by little brown bats (*Myotis lucifugus*, MYLU).

## BIOSKETCH

The research team composed of biologists with U.S. Army, U.S. Forest Service, U.S. Geological Survey and Virginia Tech have been monitoring and conducting field studies on bat community ecology, behaviour and conservation over the past decade.

Author contributions: D.J. and W.M.F. conceived idea for this manuscript; C.D. and L.C. collected data; D.J., W.M.F., L.C., E.B. and J.R. analysed the data; and D.J., W.M.F. and C.D. led the writing.

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