Journal of Environmental Management 405 (2026) 129622

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Energy-sector footprints, subsequent disturbances and footprint reclamation determine the direction and rate of landbird community trajectories in boreal forests

Tharindu Kalukapuge [a,*], Christine M. Godwin [b], Kenneth R. Foster [b], James F. Saracco [c], Erin Bayne [a]

[a] *Department of Biological Sciences, University of Alberta, Canada*
[b] *Owl Moon Environmental Inc., Fort McMurray, Alberta, Canada*
[c] *The Institute for Bird Populations, Petaluma, CA, USA*

ARTICLE INFO

Keywords:
Bird communities
Disturbances
Divergence
Energy-sector
Footprints
Reclamation
Temporal dynamics

ABSTRACT

Understanding temporal dynamics of wildlife communities associated with energy-sector footprints is fundamental for land management and restoration. This is especially important in landscapes where footprints intersect with successive disturbances and human interventions, and where wildlife recovery is expected to follow vegetation succession. We monitored bird communities in the Athabasca oil sands region of Alberta, across 34 long-term monitoring stations representing multiple disturbance and reclamation scenarios for 5–14 years. We quantified the rate and direction of temporal dynamics at each station, then evaluated how these dynamics relate to disturbance and reclamation legacies. We hypothesized that, at the local scale, bird community composition would diverge rapidly in areas with higher footprint intensity and successive events that drive changes in vegetation. Temporal dynamics fell into three major trajectories: directional change, stable and convergent dynamics. These dynamics were strongly linked to disturbance and reclamation scenarios. Rapid directional changes were associated with higher footprint intensity, subsequent events and highly dynamic vegetation. Stable and convergent dynamics were observed in landscapes where energy-sector footprints and successive disturbances were limited. Successive events, including wildfire and reclamation, exerted substantial effects on temporal dynamics. Wildfire caused directional change, whereas effects of reclamation were varied. Bird communities at older reclaimed sites showed limited temporal variability, while younger reclaimed sites showed marked variation in species composition. We present a conceptual framework that uses spatio-temporal monitoring of communities and highlights that temporal dynamics of birds are influenced by both initial forest clearing and subsequent events; thus, understanding how each scenario should be managed is essential for restoration.

1. Introduction

Among the anthropogenic pressures that influence birds in the boreal forest of northeastern Alberta, oil sands mining and *in-situ* bitumen production (*hereafter* energy-sector activities) are increasingly recognized as a key concern. These energy-sector activities have been studied for their impacts on the abundance of birds at different organizational scales, including studies of individuals (Bayne et al., 2005a), populations (Saracco et al., 2022), and communities (Kalukapuge et al., 2024). Several studies have addressed how spatial scale influences avian responses to energy development (Bayne et al., 2005b; Mahon et al., 2019; Crosby et al., 2023). However, the temporal dynamics of bird communities in response to energy-sector disturbances in forest landscapes remain largely unexplored.

A challenge in understanding temporal dynamics of communities is disentangling responses to anthropogenic pressures from natural fluctuations (Magurran et al., 2010), particularly when disturbances interact across space and time (Buma, 2015). In general, energy-sector activities influence birds through habitat loss, edge effects, and potentially isolation. The magnitude of these impacts depends on footprint

---

[*] Corresponding author.
E-mail addresses: kalukapu@ualberta.ca, ktharindukrishan@gmail.com (T. Kalukapuge).

https://doi.org/10.1016/j.jenvman.2026.129622
Received 10 January 2026; Received in revised form 27 March 2026; Accepted 7 April 2026

attributes such as size of the disturbance and post-disturbance activities (e.g., industrial noise) (Ball et al., 2009; Bayne et al., 2005a; Kalukapuge et al., 2024). Changes in vegetation after the initial energy-sector disturbance are likely important but are only starting to be understood (Foster et al., 2017; Lankau et al., 2025; Wilson and Bayne, 2019). Disturbance legacies of energy-sector footprint are also characterized by successive disturbances and management activities. Wildfire is a common natural disturbance that has burned over many landscapes with a large energy footprint over the last decade. How fire influences vegetation conditions on energy footprint can vary. Typically, fire can erase energy footprints by setting all vegetation in an area to an early seral state. However, fire may also limit some birds in the immediate post-fire phase by reducing nesting or foraging opportunities (Hobson and Schieck, 1999; Schieck and Song, 2006). At the same time, management activities such as footprint reclamation through soil and vegetation restoration are intended to erase energy sector footprints directly. However, restoration is often implemented in areas with higher footprint intensity, and active vegetation clearing for new footprints is also occurring, potentially negating the effects of restoration at larger scales. Finally, time since reclamation is a key driver of vegetation structure, and it is likely that recently reclaimed footprints may have different bird community responses than footprints restored less recently (Azeria et al., 2020; Hawkes and Gerwing, 2019; Wilson and Bayne, 2019).

Given the complexity of vegetation change in energy-sector landscapes with multiple disturbance agents, and the likelihood that birds respond nonlinearly or with lags, it is important to assess how bird communities are reacting using complementary approaches (Magnuson, 1990; Lindenmayer et al., 2012). Studies from energy-sector footprints report limited impact on bird abundance and local species richness (Lankau et al., 2025; Fleming, 2001). One reason may be that the widely used space-for-time substitution approach, which has been used to assess energy-sector impacts, may not adequately explain bird responses to environmental change, especially in nonstationary environments (Damgaard, 2019). We argue that spatio-temporal monitoring of beta diversity has the potential to capture far more complex community dynamics such as stable states or cyclical and directional patterns (Collins et al., 2000; Kampichler et al., 2012). Directional dynamics occur when the composition of bird communities shifts in the same direction over time (Magalhães et al., 2007; Buckley et al., 2018). These changes arise from deterministic, niche-based processes such as environmental filtering operating through mechanisms like disturbance and succession (Vellend, 2016; Keddy, 1992). Directional change overlaps with the concept of divergence and describes cases where, over time, community composition becomes increasingly dissimilar to an initial state. Convergent dynamics operate in situations where an assemblage becomes more similar to a previous compositional state in a time series (Collins, 2000, Buckley et al., 2021), which can be expected during community recovery. Temporal stability can arise either when fluctuations in species composition occur in a repeatable fashion, or when communities maintain a similar overall structure through a "loose equilibrium" despite stochastic annual variations in composition and abundance (Collins, 2000). Temporally stable bird communities have most often been observed in forests where anthropogenic or natural disturbances are minimal (Wesołowski et al., 2010; Enemar et al., 1994).

Using a temporal perspective for understanding changes in bird communities in energy-sector dominated landscapes has the key advantage of providing quantitative insights into resilience and recovery by indicating whether communities resist change (i.e., stable dynamics) or return towards their initial or reference state over time (Bagchi et al., 2017). In addition, the "field of dreams" hypothesis (Palmer et al., 1997), which suggests wildlife will return passively following vegetation recovery in a consistent linear way, is not always true. Bird communities may change through time in ways that are not directly parallel to vegetation succession after perturbations as a result of lagged responses or colonization delays, all of which act as barriers to recovery (Uezu and Metzger, 2016; Watts et al., 2020; Metzger et al., 2009).

The primary goal of this study was to characterize the temporal dynamics of boreal forest bird communities in response to disturbance and/or reclamation histories. Specifically, we assessed whether communities at 34 monitoring stations with varied land use and management legacies demonstrate temporal changes consistent with stable, directional, or convergent assembly dynamics. By comparing temporal community dynamics among sites with different disturbance or management histories, we aimed to reveal general relationships between community dynamics and specific footprint conditions or management practices. Establishing these patterns is important for informing restoration, especially when disturbances are complex and interact across space and time (Buma, 2015). Our long-term monitoring stations have been exposed to energy-sector disturbances to varying degrees, and some have experienced subsequent natural disturbances (e.g., wildfire) and footprint reclamation (*hereafter* successive events). Thus, we clustered our stations into different disturbance and reclamation scenarios (Table 1) to evaluate relationships between temporal community dynamics and specific disturbance and reclamation legacies. Finally, to quantify the drivers of the observed temporal dynamics, we evaluated how the intensity of original energy-sector footprints and changes in vegetation altered bird community dynamics. We hypothesized that, at the local scale, landbird community composition would diverge over time at a faster rate in areas that are associated with higher footprint intensity and recent successive events that drive substantial and rapid changes in vegetation. In addition, our study provides a conceptual framework for similar landscapes to assess temporal dynamics to understand how communities respond to industrial disturbances that intersect with varying levels of successive disturbances and human interventions, and to better evaluate the benefits of habitat restoration and

Table 1
Classification of MAPS stations into disturbance and reclamation scenarios. Scenarios include no successive events (NSE), young reclaimed, old reclaimed and wildfire. VWET and SNDR experienced other types of successive disturbances and were not assigned to these scenarios. Stations were further categorized into footprint intensity terciles.

Station	Footprint intensity	Disturbance and reclamation scenarios
RUSL	Low	No successive events
CSTU	Low	No successive events
HNGS	Low	No successive events
MAKR	Low	No successive events
CRSL	Low	No successive events
SNDR	Low	New linear disturbances (2012-2016)
ODYS	Low	No successive events
GRGR	Low	High intensity wildfire (2016)
ELBS	Low	No successive events
MNDY	Low	No successive events
BPND	Low	No successive events
SNDY	Low	No successive events
ELBN	Moderate	No successive events
HFSH	Moderate	Young reclaimed (2011)
WPCK	Moderate	No successive events
MUSR	Moderate	No successive events
HNGN	Moderate	High intensity wildfire (2016)
HNGW	Moderate	High intensity wildfire (2016)
ENGS	Moderate	No successive events
THEY	Moderate	No successive events
PRES	Moderate	High intensity wildfire (2016)
VWET	Moderate	Flooding (2013)
POPC	Moderate	No successive events
HBVR	High	No successive events
CREB	High	No successive events
HSHO	High	No successive events
CRCL	High	Old reclaimed (1983)
BCDS	High	No successive events
DEMP	High	Old reclaimed (1995)
CRLK	High	Old reclaimed (~1985)
GWAY	High	Old reclaimed (1983)
BISN	High	Young reclaimed (2003)
SFEN	High	Young reclaimed (2012)
BMLN	High	Young reclaimed (2009)

management in energy-sector footprints.

2. Methods

2.1. Study area and field data collection

We used bird community data from 34 Monitoring Avian Productivity and Survivorship (MAPS) stations located in the Athabasca Oil Sands Region of Alberta (AOSR), Canada (Appendices A and B). These sites operated between 2011 and 2024 (Tables 1 and 2; Foster et al., 2017). Stations were located in predominantly upland mixedwood or deciduous-dominated forests and varied with respect to human footprint extent and activity, post-disturbance vegetation recovery, and the timing and degree to which they have experienced disturbances related to fire and energy-sector development. All stations were operated for five to 14 years. Stations that had experienced recent disturbances encompassed varying amounts of early seral habitats.

Bird monitoring followed the MAPS protocol, which consists of constant-effort mist-netting and bird banding during the breeding season (DeSante et al., 2004). Sampling at each station was conducted on single days spaced approximately 10 days apart between early June and early August in each year of operation, covering the breeding period of migratory songbirds in the region. Each station contained 8–10 fixed mist nets that sampled an area of ~8 ha. Nets were typically operated for 6 h per banding day, beginning at local sunrise. With few exceptions, each bird was aged as either an adult or juvenile (Pyle, 1997) and banded with a uniquely numbered aluminum leg band issued by the Canadian Wildlife Service.

Table 2

Model outputs of time lag analysis. TLA slope indicates the direction and magnitude of temporal community dynamics. Significant positive slopes suggest directional change; negative slopes indicate convergent dynamics; non-significant or near-zero slopes indicate community stability or stochastic fluctuations without a clear temporal trend. Mean Hellinger distance at lag-1 represents the average community dissimilarity between consecutive years. Sites marked with † are best supported by quadratic models. See appendix A for additional site information and results.

Station	TLA slope	R^2	Mean Hellinger distance at lag 1	P value
SFEN	0.3031	0.4149	0.4406	<0.05
BMLN	0.2181	0.4643	0.2797	<0.05
HNGW†	0.1980	0.6760	0.5014	<0.05
SNDR	0.1843	0.4744	0.6412	<0.05
BISN†	0.1508	0.7885	0.4651	<0.05
GRGR	0.1426	0.1322	0.7332	0.054
HNGN	0.1311	0.2370	0.5841	<0.05
CRLK	0.1190	0.3318	0.5703	<0.05
HNGS	0.1143	0.4473	0.5811	<0.05
CREB	0.1085	0.1936	0.5724	<0.05
THEY	0.0908	0.2333	0.5722	<0.05
ENGS	0.0878	0.3167	0.5011	<0.05
PRES	0.0773	0.3092	0.4953	<0.05
CRSL	0.0737	0.1571	0.6794	<0.05
POPC	0.0701	0.2851	0.4721	<0.05
HFSH	0.0686	0.1757	0.4639	0.141
HSHO	0.0647	0.3168	0.4686	<0.05
DEMP	0.0613	0.0769	0.5078	0.108
HBVR	0.0578	0.1077	0.5041	0.175
MUSR	0.0489	0.1594	0.5636	<0.05
RUSL	0.0476	0.1236	0.4769	0.060
CSTU	0.0446	0.0921	0.5215	0.091
ELBN†	0.0445	0.2176	0.5256	<0.05
CRCL	0.0433	0.0983	0.4897	<0.05
BPND	0.0391	0.1471	0.5322	<0.05
VWET	0.0288	0.1097	0.5216	<0.05
GWAY	0.0227	0.0418	0.5296	0.069
WPCK†	0.0199	0.3138	0.6722	0.363
ELBS	0.0136	0.0117	0.4991	0.193
BCDS	0.0078	0.0049	0.5088	0.347
MAKR	0.0062	0.0056	0.5199	0.251
SNDY	−0.0154	0.0067	0.7056	0.751
ODYS	−0.0204	0.0188	0.5788	0.715
MNDY	−0.0355	0.0311	0.7340	0.815

2.2. Analytical framework

Our study consisted of multiple approaches chosen to be consistent with TLA-based studies and to hierarchically disentangle how bird community trajectories are influenced by environmental change, particularly energy-sector footprints (Fig. 1). First, we performed TLA, which provides a quantitative measure of temporal community dynamics summarized as station-specific TLA slopes (Section 2.3). Relating TLA slopes to site characteristics or disturbance legacies provides general insights into how trajectories are influenced by the environment, which is the commonly reported approach. We further used TLA metrics to (Section 2.4–2.5): (1) compare TLA slopes among disturbance and reclamation scenarios to assess whether stations belonging to different scenarios had distinct community trajectories and (2) investigate which specific deterministic environmental drivers contribute to community trajectories and to what degree. To achieve this, we adopted analytical approaches established in TLA-based studies. These included bivariate comparisons to provide exploratory inferences of the correlations between TLA slopes and specific environmental variables (Pereira e Silva et al., 2012) and secondary regressions to further evaluate cumulative effects of multiple environmental variables and complex responses of community trajectories (Spotswood et al., 2015).

2.3. Time lag analysis (TLA)

We performed time lag analysis (*hereafter* TLA) to assess patterns of temporal dynamics in bird communities (Collins et al., 2000, 2015; Kampichler and van der Jeugd, 2013). TLA is a distance-based approach that quantifies both the rate of community change over time and the directional versus non-directional characteristics of community dynamics by regressing community dissimilarity against increasing time lags (e.g., 1-year lags, 2-year lags, etc.).

First, we transformed abundance data of adult birds, calculated as the number of unique individuals per species, using the Hellinger transformation, which makes abundance data suitable for Euclidean-based analysis by preserving relative abundance relationships and minimizing the influence of highly abundant and rare species. This transformation also addresses the double-zero problem, common in raw community data where shared absences can distort ecological distances when using Euclidean distances alone (Legendre and Gallagher, 2001). Subsequently, we calculated Euclidean distances of Hellinger-transformed data (*hereafter* Hellinger distance) across different time lags. We chose Hellinger distance because it ignores fluctuations in absolute abundance when relative abundance patterns remain unchanged, thereby separating compositional changes from numerical variations. This also enables assemblages to be compared directly regardless of their species richness and abundances, and controls for sampling variability across studies (Kampichler and van der Jeugd, 2013; Kampichler et al., 2014). To avoid bias from smaller sample sizes at longer time lags, we followed Collins et al. (2000) and applied square root transformation to the time lags before fitting linear regression models between Hellinger distances and time lags. We also fitted quadratic polynomial models to detect any nonlinear temporal dynamics. To compare community dynamics across stations and for subsequent analyses that required a single station-level estimate of temporal dynamics, we used the linear TLA slopes for all stations.

We compared the fit of nested linear and quadratic models using AIC (Akaike Information Criterion) and a nested ANOVA F-test. The quadratic model was retained to indicate nonlinear responses when it improved fit ($P < 0.05$ or lower AIC). To assess the statistical significance of the observed TLA slopes, we conducted a Monte Carlo permutation test with 10,000 iterations following Thibault et al. (2004) and Kampichler et al. (2014). In each iteration, we randomly shuffled species

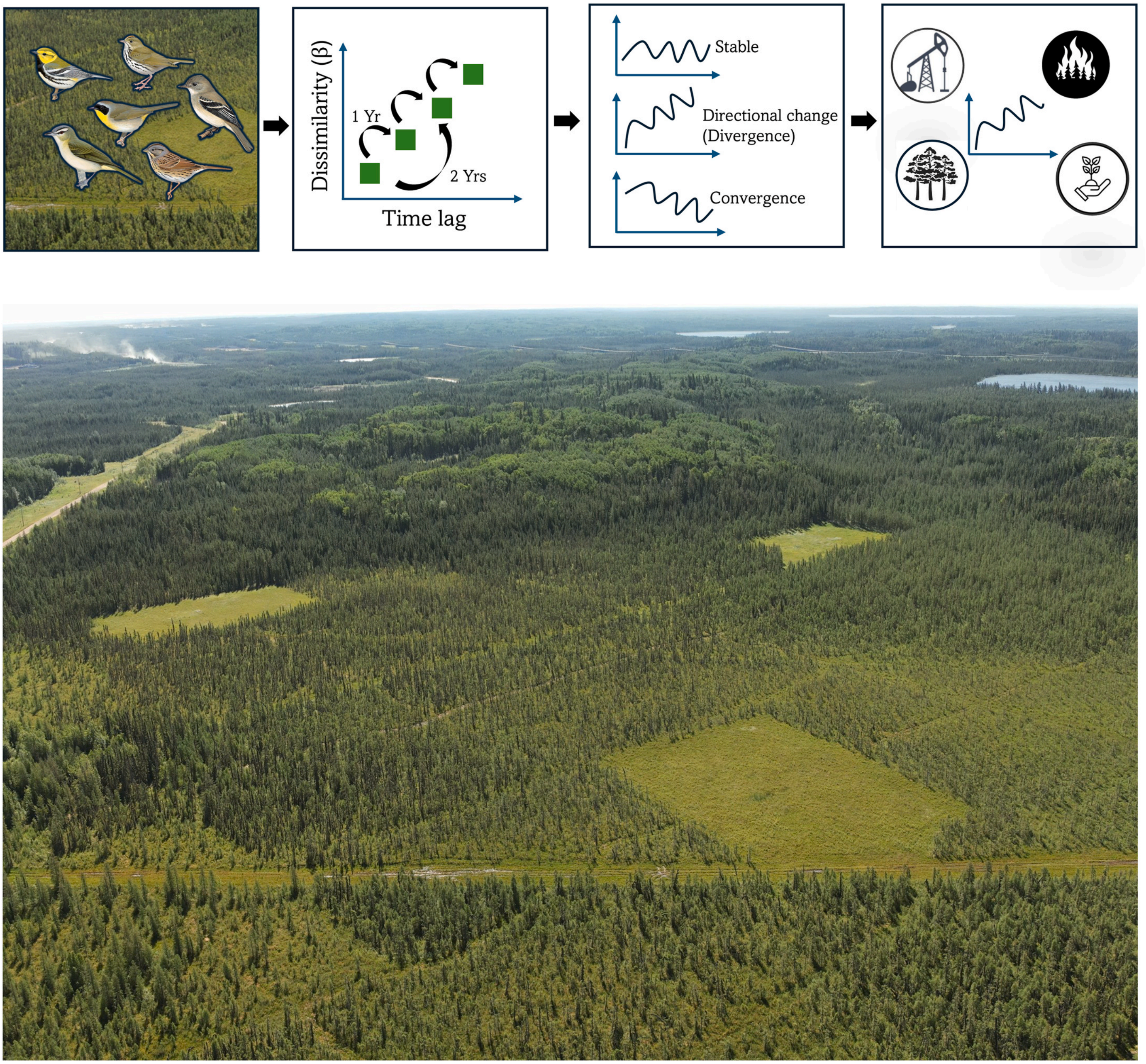

Fig. 1. Conceptual framework for determining temporal dynamics of bird communities associated with energy-sector footprints. The process begins with monitoring bird communities annually along a gradient of footprint intensity and across stations exposed to successive events, including wildfire and reclamation. We then quantify changes in community composition across increasing time lags (temporal β-diversity) to estimate the direction and rate of temporal community trajectories. Finally, we evaluate how environmental changes influence and relate to these dynamics (Top). Aerial photograph showing the abandoned energy-sector footprints in the boreal forest of Alberta, Canada (Bottom).

abundance values across years and recalculated the slope to generate null distributions. We then calculated the *p*-value as the proportion of randomized slopes that exceeded or equaled the observed slope.

Significant positive TLA slopes indicate directional change (divergence), meaning that species composition becomes increasingly different from its initial state as time progresses. This divergence may be driven by internal or external factors or by autocorrelated stochastic variability where past states influence present species composition. Significant negative TLA slopes show convergent dynamics, where the community returns toward a previous state observed earlier in the time series. This may result from perturbations or processes such as recovery. Non-significant or near-zero TLA slopes suggest an absence of directional change and can result from either community stability, where species composition remains relatively constant, or random fluctuations in species abundances without a clear temporal pattern. In the latter case, such patterns reflect high stochasticity, resembling a white noise process where the abundance of a species at a given time is substantially independent of the previous state (Collins et al., 2000; Kampichler and van der Jeugd, 2013; García-Navas et al., 2021). In TLA, the combination of slope and R^2 provides insights into temporal community dynamics. Steeper slopes and higher R^2 values indicate strong directional change with limited stochastic variation, leading to greater temporal divergence. In contrast, shallower slopes and lower R^2 values suggest weak directional trends and a higher degree of stochasticity in community change. However, slope and R^2 alone may not fully disentangle deterministic environmental drivers from autocorrelated stochastic processes (e.g., first-order Markov processes), which may also contribute to significant positive slopes. Evaluating TLA metrics against environmental predictors (e.g., human disturbances and changes in vegetation) helps assess whether temporal trajectories reflect the influence of deterministic forces rather than pure autocorrelated stochastic processes (sections 2.4–2.5).

2.4. *Environmental predictors, disturbance and reclamation scenarios*

The MAPS stations used in this study were established along a gradient in the intensity of energy-sector footprints. We treated energy-sector forest clearings (footprints) as the initial and primary disturbance, and subsequent wildfire and active vegetation restoration (reclamation) as successive events. To evaluate the effects of changes in the environment on temporal dynamics of bird communities, we used two sets of environmental variables: (1) footprint intensity (quantified as footprint amount) and (2) post-disturbance vegetation conditions, which are influenced by footprints and subsequent disturbances or reclamation activities at each station.

We characterized vegetation at each station following the habitat structure assessment protocol of Nott (2003). At each station, vertical vegetation structure was measured as percent area cover in different strata: understorey (height 0.5–5 m), midstorey (height 5–15 m), and canopy (height $>$15 m). For each stratum, we calculated station-level cover as an area-weighted mean across habitat types. We then combined the station-level understorey, midstorey and canopy estimates into a single vertical cover index (*hereafter* cumulative vertical cover). Ground vegetation (*hereafter* ground cover; height $<$0.5 m, e.g., graminoids and forbs) was retained as a separate variable.

Vegetation metrics derived from station-level surveys included the temporal mean of cumulative vertical cover (averaged across all survey years for each station) and the coefficient of variation (CV) of ground cover (SD/Mean × 100), which measured temporal variability across those same survey years (*hereafter* ground cover CV). To test whether unequal survey years across stations influenced CV values, we tested the correlation between the number of years surveyed and the CV (Pearson correlation, $r = -0.09$, $P = 0.63$). This non-significant relationship confirmed that CV was not confounded by sampling effort. Footprint data were obtained from the ABMI human footprint spatial data sources (ABMI, 2017). Footprint variables included the baseline footprint amount (2010) within a 5–km buffer, comprising energy-sector and oil sands mining footprints (*hereafter* baseline footprint), and Δ footprint, calculated as the change in footprint amounts between the baseline year (2010) and a later survey year (2018) (Saracco et al., 2022). When we incorporated multiple explanatory variables in the same analysis, we tested for multicollinearity among variables using variance inflation factor (VIF), and all predictors had VIF $<$2, indicating minimal collinearity.

To understand the relationship between temporal community dynamics and energy-sector footprints and subsequent disturbance or reclamation events and to describe community trajectories in a way that can inform footprint management and reclamation practices, we classified MAPS stations into four disturbance and reclamation scenarios (Table 1): (1) no successive events (NSE), where station history was primarily characterized by initial energy-sector footprints only with no subsequent disturbances (e.g., wildfire) or active vegetation restoration; (2) young reclaimed, defined as $<$ 10 years since reclamation; (3) old reclaimed, defined as $\geq$ 18 years since reclamation; and (4) wildfire (Table 1). Years since reclamation were considered relative to the first year of bird monitoring at each station. Two stations (VWET and SNDR) were not assigned to any of these scenarios because they experienced other types of successive disturbances (Table 1) and were excluded only from analyses that compared the four scenarios. Additionally, we classified stations into three terciles (low, moderate and high) based on baseline footprints. Terciles were determined by ranking stations by footprint amount and subsetting them into three equal-frequency bins (Table 1). Because footprints were also evaluated as a continuous predictor in complementary analyses, concerns about the arbitrariness of the tercile boundaries were minimized.

2.5. *Influence of environmental variables on temporal dynamics*

We used non-parametric Kruskal-Wallis test to quantify whether temporal community trajectories indicated by TLA slopes varied among the four scenarios, given the small sample sizes in some groups ($n_i < 5$). First, we compared the four primary scenarios (Table 1) and next subdivided NSE stations by baseline footprint terciles to assess whether initial footprint level influenced community trajectories independent of successive events.

Next, we evaluated the influence of footprint amount and vegetation on TLA slopes across all stations. We first examined bivariate relationships between TLA slopes and each predictor (cumulative vertical cover, square-root transformed CV ground cover, baseline footprint and Δ footprint) using simple linear regressions (ordinary least squares). Subsequently, to assess the combined influence of all environmental predictors on TLA slopes, we performed multiple linear regression using information-theoretic approach (Burnham and Anderson, 2002). We constructed six candidate models (Table 3), including the same four environmental variables representing the effects of footprints *per se* and subsequent changes in local vegetation. We considered models with linear and quadratic terms to detect potential nonlinear responses. Candidate models were limited to linear and quadratic terms to avoid overfitting from higher-order polynomial functions and excessive parameters (Wenger and Olden, 2012). We calculated AIC corrected for small sample size (AICc), ΔAICc relative to the best model and Akaike weights (w_i) for each candidate model. The best-supported model was selected based on the lowest AICc, corresponding to the highest w_i, where the latter quantifies the probability that a given model is best among the candidate models.

Model assumptions for all linear regression models were evaluated using DHARMa residual diagnostics (Hartig, 2024), which assess uniformity, dispersion and outliers of residuals.

Table 3

Model selection results for six candidate models relating temporal bird community trajectories (TLA slopes) to local environmental predictors. Shown are the log-likelihood (logLik), number of estimated parameters (*K*), AIC corrected for small sample size (AICc), ΔAICc (relative to the best model) and Akaike weights (w_i). The best-supported model is shown in bold.

Candidate model	logLik	*K*	AICc	ΔAICc	w_i
BaseFP + ΔFP + poly(VCov, 2) + GCov	**52.33**	**7**	**−86.34**	**0.00**	**0.729**
BaseFP + ΔFP + VCov + GCov	49.07	6	−83.03	3.31	0.139
poly(BaseFP, 2) + ΔFP + VCov + GCov	50	7	−81.69	4.65	0.071
BaseFP + poly(ΔFP, 2) + VCov + GCov	49.13	7	−79.95	6.40	0.030
BaseFP + ΔFP + VCov + poly(GCov, 2)	49.08	7	−79.84	6.50	0.028
poly(BaseFP, 2) + poly(ΔFP, 2) + poly(VCov, 2) + poly(GCov, 2)	52.49	10	−75.42	10.93	0.003

BaseFP = baseline footprint; ΔFP = change in footprint, VCov = cumulative vertical cover; GCov = coefficient of variation of ground cover. *K* includes the intercept and residual variance estimate. poly(x, 2) indicates a second-order polynomial including both linear and quadratic terms.

3. Results

3.1. Direction and rate of temporal dynamics

Boreal landbird assemblages in the Athabasca oil sands region showed three main patterns of temporal community trajectories: directional change, stochastic fluctuations or stable dynamics, and signs of convergent dynamics. The pattern and the magnitude of each type of dynamic are attributable to site-specific disturbance or reclamation legacies (Figs. 2 and 3 and Appendix C).

Among the 34 MAPS stations, compositional change in bird assemblages across different time lags at HNGW, BISN, ELBN, and WPCK was best supported by quadratic models. In contrast, other stations showed linear relationships (Table 2, Fig. 2). Overall, 31 MAPS stations demonstrated positive TLA slopes, and 20 of these slopes were statistically significant ($P < 0.05$). These significant positive slopes suggest the continuous accumulation of dissimilarity in species composition over time or directional changes, analogous to divergence in community

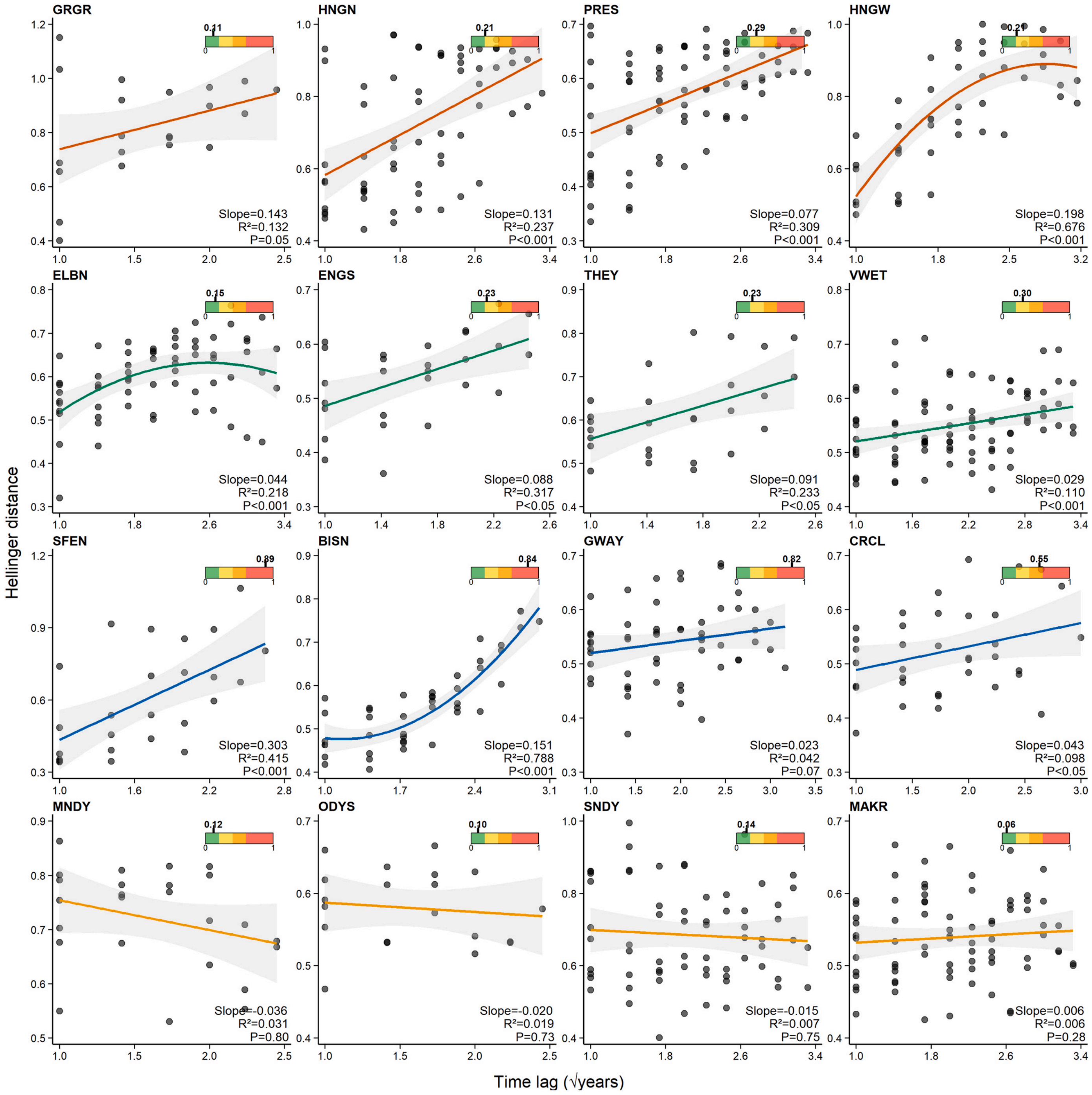

Fig. 2. Examples of bird communities showing varying temporal dynamics identified by time-lag analysis for 16 MAPS stations in the AOSR. Heat map bars indicate baseline footprint intensity within a 5 km buffer. Stations are ordered in rows to emphasize their disturbance and reclamation legacies. First row: stations affected by wildfire; second row: stations associated with moderate footprint and no successive events, except VWET which was exposed to flooding for one year. Third row: stations reclaimed at different times (SFEN and BISN = young reclaimed, and GWAY and CRCL = old reclaimed); fourth row: stations considered natural sites, representing relatively undisturbed, low energy footprint and no successive events. Statistical parameters displayed are TLA slope, R^2 and significance at $\alpha = 0.05$.

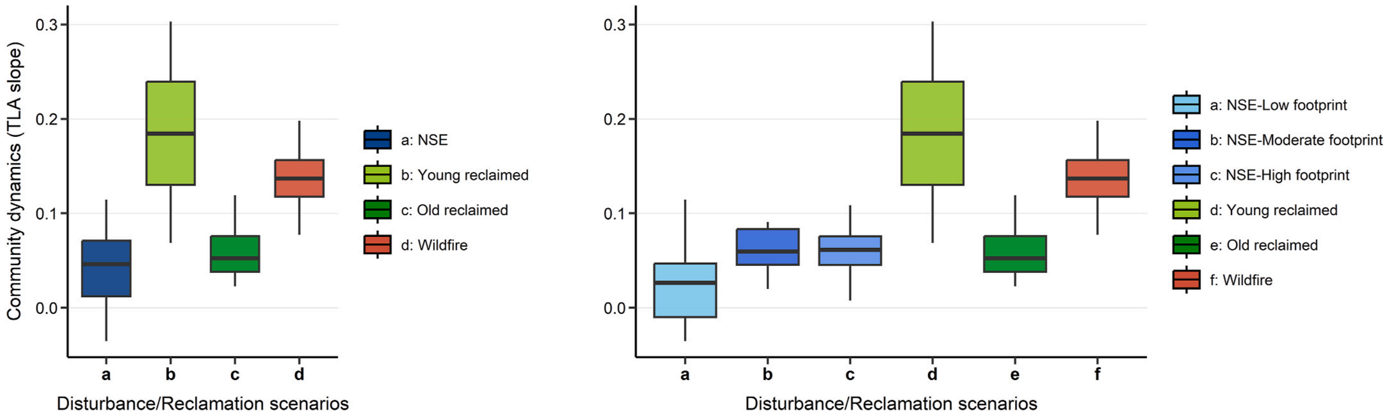

Fig. 3. Differences in TLA slopes across disturbance and reclamation scenarios. Left panel: Stations grouped as (a) no successive events (NSE), (b) young reclaimed, (c) old reclaimed, and (d) stations exposed to wildfire. Right panel: NSE stations further subdivided by baseline footprint intensity into (a) low, (b) moderate and (c) high, and compared with (d) young reclaimed, (e) old reclaimed, and (f) wildfire. Boxplots show medians (horizontal lines) and interquartile range (boxes). Kruskal-Wallis test indicated significant differences in TLA slopes ($P < 0.05$) across scenarios.

trajectories. Notably, all stations classified as wildfire-exposed and young-reclaimed, whose footprint intensity was moderate to high (Table 1), showed a significant directional change over time. Ten MAPS stations, including HFSH, DEMP, HBVR, RUSL, CSTU, GWAY, WPCK, ELBS, BCDS, and MAKR, yielded non-significant or near-zero positive TLA slopes implying stochastic variations in community composition which likely reflect stable communities consisting of higher proportions of species with constant mean abundances over time. Of these 10 stations, all except HFSH fell into the no successive events or old reclaimed scenarios. SNDY, ODYS, and MNDY had negative TLA slopes, indicating convergent dynamics. All three stations were characterized by relatively undisturbed forest conditions at local scale and were classified in the no successive events scenario and low footprint intensity tercile (Tables 1 and 2, Fig. 2).

Stations with significant positive TLA slopes ($n = 20$) generally demonstrated steeper slope values (ranging from 0.0288 to 0.3031), indicating relatively faster directional dynamics across time lags. In contrast, stations that produced non-significant positive TLA slopes ($n = 10$) yielded relatively shallower slopes (ranging from 0.0062 to 0.0686). GRGR was an exception; although it produced a relatively high TLA slope (0.1426), the p value was not significant ($P = 0.054$) (Table 2, Fig. 2).

Mean Hellinger distance at lag-1, which represents year-to-year compositional dissimilarity (beta diversity), varied substantially among MAPS stations (Table 2). There was no apparent association between the four scenarios and Hellinger distance at lag-1, except that the four stations in the young-reclaimed scenario had the lowest mean lag-1 Hellinger distance values compared to other stations, despite three of them (BISN, SFEN, BMLN) ranking among the highest TLA slopes indicating rapid directional change with low year-to-year changes in community composition.

3.2. Variation in temporal dynamics among disturbance and reclamation scenarios

TLA slopes differed significantly among the four disturbance and reclamation scenarios (Table 1): no successive events (NSE), young reclaimed, old reclaimed, and wildfire (Kruskal-Wallis test: $P = 0.0035$; Fig. 3, left panel). The results were consistent when the NSE scenario was further subdivided into low, moderate and high footprint intensity terciles (Kruskal-Wallis test: $P = 0.0074$; Fig. 3, right panel).

3.3. Drivers of temporal community dynamics: footprints and vegetation

In simple linear regression models, temporal variability in ground cover was positively related to TLA slopes ($\beta = 0.0322$, $R^2 = 0.18$, $P = 0.012$) (Fig. 4a), meaning that bird communities in stations with greater variation in ground cover over time experienced faster and more pronounced directional changes. Baseline footprint amount was positively associated with TLA slopes ($\beta = 0.107$, $R^2 = 0.17$, $P = 0.015$) (Fig. 4b),

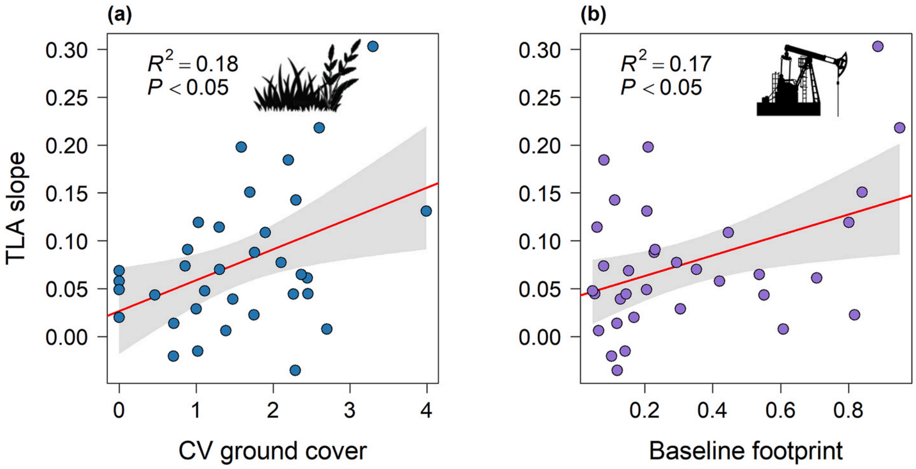

Fig. 4. Relationship between temporal bird community dynamics (TLA slopes) and environmental predictors. Simple linear regression plots display TLA slopes relative to (a) coefficient of variation (CV) of ground cover (square-root transformed) and (b) baseline energy-sector footprint.

indicating that bird communities in stations with higher levels of baseline footprint had rapid and directional changes in community composition (Fig. 2). Cumulative vertical cover and baseline footprint showed a negative correlation; stations with higher baseline footprint were associated with lower vertical cover ($\beta = -39.47$, $R^2 = 0.22$, $P = 0.0048$). Stations with higher cumulative vertical cover generated lower TLA slopes ($\beta = -0.0014$, $R^2 = 0.21$, $P = 0.006$), indicating relatively greater temporal stability in bird communities at stations with consistently higher vertical vegetation. The effect of Δ footprint on TLA slopes was not significant ($P = 0.095$).

The relationship between TLA slope and environmental predictors, evaluated through multimodel inference, was best supported by the model including a nonlinear function of cumulative vertical cover (AICc $= -86.34$, $w_i = 0.729$). The overall model explained considerable variation in TLA slope (adjusted $R^2 = 0.38$, $F_{5,28} = 5.06$, $P = 0.002$. Cumulative vertical cover was significantly associated with TLA slope (quadratic term: $\beta = 0.144$, SE $= 0.059$, $P = 0.022$; linear term: $\beta = -0.110$, SE $= 0.067$, $P = 0.112$) (Fig. 5), whereas other predictor variables were not strongly supported.

Regression model residuals did not indicate any violations of model assumptions across all models, showing uniform distribution of residuals and no deviations in dispersion or outlier tests (Appendix D).

4. Discussion

In dynamic forest landscapes, recovery of wildlife communities can be challenging because our understanding of how communities respond to changes that follow initial disturbances remains limited; yet this knowledge is key for planning and implementing restoration. By evaluating station-level temporal community dynamics, relating them to disturbance and management legacies, and identifying drivers of these dynamics, we provide insights into the community trajectories expected under different disturbance or reclamation scenarios, informing management decisions for footprint restoration in the boreal forest.

4.1. Patterns of temporal community dynamics

Arrested succession or ecological time lags may hinder community recovery, as reported in abandoned energy-sector footprints in the boreal forest of Alberta for plants (Sutheimer et al., 2025) and for birds in other ecosystems (Uezu and Metzger, 2016; Watts et al., 2020). Overall, none of the stations in our study that experienced disturbances demonstrated stalled community trajectories within the time periods examined. This study draws on an ongoing monitoring program in which the first set of stations was established in 2011. Although our study did not include long-term monitoring beyond 14 years, which might be necessary to capture lag or arrested responses, the stations and years incorporated represented a wide range of disturbance legacies, times since disturbance, and footprint restoration histories. This variation provides a reasonable opportunity to identify such non-dynamic responses had they been present. Nevertheless, there are many nuances in defining what “long-term” means in ecological studies, and definitions vary across the literature, from at least 10 years (Lindenmayer and Likens, 2010) to many decades or more (Magnuson, 1990). We acknowledge that the community trajectories reported in our study could reflect only a phase of a dynamic trajectory or may appear differently when assessed over longer temporal scales.

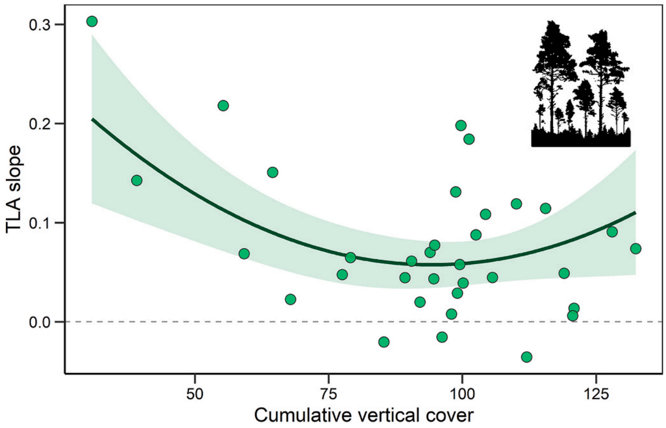

Fig. 5. Relationship between cumulative vertical vegetation cover and temporal bird community dynamics (TLA slopes) from the best-supported model. The shaded band indicates 95% confidence intervals and points represent observed station-specific TLA slopes. The partial effect of cumulative vertical cover was nonlinear and significant ($P = 0.022$).

Overall, temporal changes in boreal bird communities across our stations encompassed all three trajectory types: directional change, convergent, and stable or stochastic dynamics. Importantly, in most cases these dynamics were strongly linked to station-specific disturbance and subsequent reclamation legacies. In addition, TLA slopes varied significantly among disturbance and reclamation scenarios, suggesting that temporal community dynamics are influenced by local disturbance and management legacies (Figs. 2 and 3). Stations such as CSTU, ELBS, MAKR, RUSL, and WPCK had non-significant, low or near-zero TLA slopes, characteristic of stable communities. None of them had experienced successive events. The majority of these stations were less disturbed at the local scale, having been exposed to minimal to no past energy-sector disturbances or the nearest footprints were limited to old or revegetated linear features, which have been reported to be less influential for boreal bird communities than other energy-sector footprints (Lankau et al., 2025; Kalukapuge et al., 2024). This provides further support for the interpretation that these communities showed stable temporal dynamics. Non-significant or shallow TLA slopes may suggest two mechanisms: 1) communities composed of species with stable abundances, or mixtures of stable and dynamic species with low temporal fluctuations (Kampichler and van der Jeugd, 2013) or 2) low densities of species where stochastic colonization and extinction facilitate erratic dynamics without a defined direction, as observed in some ecosystems (e.g., alpine bird communities; García-Navas et al., 2021). Our results are supported by multiple empirical studies (Korňan and Svitok, 2025; Wesołowski et al., 2022; Kampichler et al., 2014) and simulated data (Kampichler and van der Jeugd, 2013), showing that bird communities inhabiting relatively undisturbed forests demonstrate temporal stability in species composition reflected by small or non-significant TLA slopes. Some stations such as BPND, ELBN, and MUSR also had moderate to low footprint intensity and no successive events but showed statistically significant TLA slopes ranging between 0.0391 and 0.0489. While we categorized all statistically significant positive slopes as indicating directional change, the magnitude of these slopes is important for interpretation. Kampichler and van der Jeugd, 2013 reported that the TLA slope is the most important indicator of community dynamics and simulated that assemblages with low temporal variability rarely exceed a TLA of 0.05. This supports our interpretation that these stations experienced low temporal variability in community composition despite generating statistically significant slopes.

Our study did not include true reference sites, which would be characterized by forests that are both locally and regionally undisturbed for birds. Ideally, such sites would occur within the same region as the monitoring stations, avoid any disturbance, and be located within the same forest type; these criteria are difficult to achieve in the Athabasca oil sands region. Instead, we included stations such as MNDY, ODYS, and SNDY to represent relatively undisturbed stations, providing the closest representation of reference conditions within the disturbance gradient captured across the 34 monitoring stations in this study. Although negative TLA slopes have not been commonly reported, stations in our study such as MNDY, ODYS, and SNDY were characterized by negative TLA slopes, indicating signs of convergent dynamics. All three stations were relatively undisturbed at the station level and were classified in the no successive events scenario. Apparent stability or convergent dynamics over a given period can reflect both the current behavior of communities and their potential in achieving these dynamics but do not necessarily indicate long-term resilience or community recovery to the pre-disturbance or reference community composition. Thus, inferences about resilience and recovery require careful consideration of the time frame evaluated, concurrent environmental changes, and the choice of ecologically relevant reference states.

4.2. *Environmental drivers of temporal community dynamics*

TLA quantifies the strength of community trajectories through the direction and steepness of the slope combined with the R^2 value. While empirical and simulated studies demonstrate that significant positive slopes and high R^2 values indicate strong directional change rather than white-noise stochasticity (Angeler et al., 2009; Collins and Xia, 2015), these metrics alone may not completely separate the influence of deterministic environmental drivers from autocorrelated stochastic processes (e.g., first-order Markov processes), which may also contribute to positive TLA slopes (Kampichler and van der Jeugd, 2013). To disentangle these components, temporal community changes can be evaluated against external environmental variation. In our study, we addressed this by relating station-level TLA slopes to categorical disturbance legacies and modeling with static and temporally measured environmental variables. Because significant positive TLA slopes were commonly found in stations with high disturbance intensity and subsequent events and were strongly associated with both human footprints and changes in local vegetation, our findings are more consistent with directional trajectories driven by deterministic processes rather than purely autocorrelated stochastic dynamics.

4.2.1. *Influence of energy-sector footprints*

As we hypothesized, human footprint intensity had a significant positive influence on temporal dynamics. Bird communities in stations with greater footprint amounts showed stronger directional change over time (Table 2; Figs. 2 and 4b.). Most stations with disturbance legacies are linked to substantial energy-sector disturbances, whether subsequently reclaimed (e.g., SFEN, BISN), or unreclaimed, and still associated with moderate to high footprint intensity (e.g., CREB, ENGS), followed directional changes in species composition that diverged over time, albeit at varying rates. Saracco et al. (2022) provide complementary evidence from demographic perspectives at the same monitoring stations, reporting declines in adult captures, productivity and residency probability across species in response to increasing energy-sector disturbances. Our results also showed that even among stations experiencing directional dynamics, the rate of compositional change declined with the decreasing footprint intensity and the absence of successive events (Fig. 2). This gradient suggests that the initial footprint amount creates an environment for faster directional change, which is then further altered by subsequent disturbance or reclamation events.

4.2.2. *Role of subsequent disturbances and reclamation*

Successive events such as wildfire or restoration activities appeared to cause dominant, additive or interactive effects on temporal community trajectories. Community dynamics at reclaimed stations varied with both time since reclamation and the intensity of associated energy-sector footprints. SFEN, BMLN, and BISN had the highest baseline footprint amounts among all stations. They also had the most amount of vegetation reclamation in recent years (2012, 2009 and 2003, respectively), creating early successional habitat and bird communities that were characterized by rapid temporal divergence (Table 2, Fig. 2). The influence of anthropogenic forest clearings can persist for decades after the initial disturbance, particularly for birds associated with mature or old-growth forests (Hart et al., 2025, Leston et al., 2018). Thus, it is unlikely that stable communities will be observed in recently reclaimed landscapes with some mature remnant forest. Young-reclaimed energy footprints such as wellsites are typically characterized by early successional vegetation (Azeria et al., 2020), which has been observed to support transitional early-seral and open habitat birds (linear features: Kalukapuge et al., 2024; wellsites: Wilson and Bayne, 2019) that are likely to generate directional community dynamics.

In contrast, at old-reclaimed stations where forest restoration extends back ≥18 years, 28 years for GWAY and CRCL and 18 years for DEMP; specifically, GWAY and DEMP yielded non-significant TLA slopes, and CRCL had a low slope (0.0433). This pattern suggests that bird communities at older reclamation sites have achieved relatively stable communities composed of higher proportions of constant species with minimal erratic fluctuations and overall slow temporal variability. The number of years since reclamation in energy-sector footprints such as wellsites can have a strong influence on on-footprint vegetation and associated bird communities. Older reclaimed sites differ considerably from younger sites and are characterized by increased canopy cover and a gradual transition away from early successional vegetation (Azeria et al., 2020). Consequently, the wildlife communities, including birds, in reclaimed areas may become increasingly similar to those of mature forests over time, although complete convergence is not likely to be achieved until the restored area and the adjacent forest become equivalent in age or structure which may require a wildfire to reset successional dynamics (Hawkes and Gerwing, 2019; Wilson and Bayne, 2019). In the specific case of the station CRLK, which is situated in an area with high baseline footprint but reclaimed approximately 25 years ago, the site showed substantial temporal divergence and is generally considered an older reclaimed site. This may be due to legacy effects of the initial disturbance where historical land use continues to influence biological communities (Cuddington, 2011), which can lead to colonization credit, meaning delayed colonization of some species (Haddou et al., 2022) or long-term lag responses in species recovery (Uezu and Metzger, 2016). All four stations in the young-reclaimed scenario had the lowest year-to-year community dissimilarity, suggesting that stations undergoing rapid unidirectional change can still show low variability in annual fluctuations in community composition. This indicates that annual temporal beta diversity can be uncorrelated with community trajectories assessed across multiple time lags and may be insufficient to capture the directionality of overall temporal community trajectories.

GRGR, HNGN, HNGW, and PRES were exposed to the 2016 Fort McMurray wildfire, yet their overall baseline footprint intensity falls within the low to moderate range compared to other stations. In the boreal forest, wildfire has been shown to override the effects of energy footprints by promoting vegetation regeneration and recruitment, and in some cases early successional dynamics may persist for ~10 to 20 years after fire (Sutheimer and Nielsen, 2025). In the boreal forest of western North America, bird communities immediately following fire are well documented to be dominated by post-fire habitat specialists such as woodpeckers, and after a few years the encroachment of shrubs and young trees, attract species that nest and forage in shrubs and open areas, resulting in marked shifts in species composition (Hobson and Schieck, 1999; Schieck and Song, 2006). Such post-fire habitat conditions and vegetation dynamics appear to place these four MAPS stations among those that continue to accumulate compositional changes over time, as revealed by their high and significantly positive TLA slopes. This pattern is consistent with Jones et al. (2017), who reported positive TLA slope (~0.1) in mesic grassland breeding bird communities in management areas subjected to annual and quadrennial prescribed burning.

4.2.3. *Influence of vegetation dynamics*

Overall, stations that experienced events resulting in substantial changes in vegetation, characterized by reduced or highly dynamic vegetation strata, showed pronounced and rapid directional change in bird community composition over time (Figs. 2, 4a and 5). In addition, higher baseline footprint amount was associated with lower vegetation cover, indicating that stations wth greater footprint intensity have reduced vertical vegetation. Conversely, higher temporal variability in ground cover and the baseline footprint amount promoted directional change (Fig. 4). Although only cumulative vertical cover was statistically significant ($P < 0.05$) in the multiple regression, where partial regression coefficients isolate the unique contribution of each predictor after accounting for others, the bivariate models still yielded significant and ecologically meaningful relationships between TLA slopes and environmental variables. This difference is expected when predictors share variance. Graham (2003) notes that even weak multicollinearity can cause important variables to appear non-significant in multivariable models. Accordingly, we reported findings from both approaches, which collectively suggest that the disturbance effects of footprints on temporal community dynamics of boreal birds are largely mediated by changes in local vegetation.

5. Conclusions and management implications

Policies for management and reclamation of forest landscapes often do not require active restoration of wildlife *per se*; instead, recovery of wildlife communities is expected to continue passively following vegetation succession. However, community trajectories can vary depending on how dynamic post-disturbance environments are, and understanding these patterns is important for effective footprint restoration. Using boreal bird communities in the AOSR, we demonstrated the variability of community trajectories and their relationships with specific disturbance or reclamation scenarios.

Bird communities showed directional change, stable and convergence dynamics that were strongly related to local scale energy-sector footprints and successive events. Spatio-temporal monitoring of community composition across multiple sites with varied disturbance histories enabled understanding both the direction and rate of trajectories more explicitly than a simpler space-for-time substitution approach. Thus, we strongly recommend long-term monitoring of species composition at sites spanning gradients of disturbance scenarios to evaluate footprint recovery from wildlife perspectives more reliably. Original footprint intensity often triggered community divergence, but trajectories were highly influenced by successive disturbances and reclamation. This indicates the cumulative effects of interacting events that should be considered in reclamation planning rather than relying on initial disturbance conditions alone. Mechanisms of community trajectories cannot be understood without accounting changes in vegetation dynamics which could be driven by both the footprint and the successive events. Footprint reclamation generated mixed trajectories depending on time since reclamation. Older reclaimed sites, in the absence of successive disturbances, supported relatively stable communities, suggesting the need for realistic recovery timelines and controls on interference to achieve desired outcomes. Finally, even in a regionally disturbed landscape, stations with low footprint intensity and minimal successive events, were associated with stable communities. Accordingly, we suggest that temporally stable communities may serve as a reliable indicator of how intact a landscape remains from a bird community perspective. Limiting both initial and subsequent disturbances that alter local vegetation attributes may increase the potential for stable species composition and recovery in bird communities.

CRediT authorship contribution statement

Tharindu Kalukapuge: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Christine M. Godwin:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Kenneth R. Foster:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **James F. Saracco:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Erin Bayne:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding sources

Funding in support of this project has been provided by Syncrude Canada Ltd., Hammerstone Infrastructure Materials Ltd., Canadian Natural Resources Limited, Cenovus Energy, ConocoPhillips Canada Resources Corp., Devon Energy, Husky Oil Operations Ltd., Imperial Oil Ltd., Suncor Energy Inc., TOTAL E&P Canada, CNOOC International, the Oil Sands Developers Group, Mitacs Accelerate and the Oil Sands Monitoring Program.

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript, and the analyses and conclusions presented are independent of the position of any of the funders, and of the Oil Sands Monitoring (OSM) Program.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christine M. Godwin, Kenneth R. Foster reports financial support was provided by Oil Sands Monitoring Program. Tharindu Kalukapuge reports financial support was provided by Owl Moon Environmental Inc. (OMEI) and Mitacs Accelerate Research grant. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We are greatly indebted to the many banders who collected the field data used in this study, and to The Institute for Bird Populations biologists who supported the field and data management programs. All birds were captured and banded following protocols and permits issued by the Canadian Wildlife Service Bird Banding Office (Master Permit 10858) and Alberta Environment and Protected Areas. We thank Xue Yan Chan for the aerial photograph used in Fig. 1, Apoorv Saini for assistance with the study area map, and Colleen Sutheimer and BERA project for providing geospatial data layers used in the map. We especially thank researchers in the Bayne Lab, University of Alberta, for their insightful discussions and constructive comments and suggestions that helped improve this work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2026.129622.

Data availability

Data will be made available on request.

References

ABMI, 2017. The Status of Human Footprint in Alberta (Preliminary Report. Version 1999-2015.

Angeler, D.G., Viedma, O., Moreno, J., 2009. Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. Ecology 90, 3245–3257. https://doi.org/10.1890/07-0391.1.

Azeria, E.T., Santala, K., McIntosh, A.C., Aubin, I., 2020. Plant traits as indicators of recovery of reclaimed wellsites in forested areas: slow but directional succession trajectory. For. Ecol. Manag. 468, 118180. https://doi.org/10.1016/j.foreco.2020.118180.

Bagchi, S., Singh, N.J., Briske, D.D., Bestelmeyer, B.T., McClaran, M.P., Murthy, K., 2017. Quantifying long-term plant community dynamics with movement models:

implications for ecological resilience. Ecol. Appl. 27, 1514–1528. https://doi.org/10.1002/eap.1544.

Ball, J.R., Bayne, E.M., Machtans, C.S., 2009. Energy sector edge effects on songbird nest fate and nest productivity in the boreal forest of Western Canada: a preliminary analysis. In: Fourth International Partners in Flight Conference: Tundra to Tropics: Connecting Birds, Habitats, and People, pp. 37–44.

Bayne, E.M., Boutin, S., Tracz, B., Charest, K., 2005a. Functional and numerical responses of ovenbirds (*Seiurus aurocapilla*) to changing seismic exploration practices in Alberta's boreal forest. Ecoscience 12 (2), 216–222. https://doi.org/10.2980/i1195-6860-12-2-216.1.

Bayne, E.M., Wilgenburg, S.L., Boutin, S., Hobson, K.A., 2005b. Modeling and field-testing of ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landsc. Ecol. 20, 203–216. https://doi.org/10.1007/s10980-004-2265-9.

Buckley, H.L., Day, N.J., Case, B.S., Lear, G., Ellison, A.M., 2018. Multivariate methods for testing hypotheses of temporal community dynamics. bioRxiv, 362822. https://doi.org/10.1101/362822.

Buckley, H.L., Day, N.J., Lear, G., Case, B.S., 2021. Changes in the analysis of temporal community dynamics data: a 29-year literature review. PeerJ 9, 11250. https://doi.org/10.7717/peerj.11250.

Buma, B., 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6, 1–15. https://doi.org/10.1890/ES15-00058.1.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical information-theoretic Approach. Springer, New York.

Collins, S.L., 2000. Disturbance frequency and community stability in native tallgrass prairie. Am. Nat. 155, 311–325. https://doi.org/10.1086/303326.

Collins, S.L., Micheli, F., Hartt, L., 2000. A method to determine rates and patterns of variability in ecological communities. Oikos 91, 285–293. https://doi.org/10.1034/j.1600-0706.2000.910209.x.

Collins, S.L., Xia, Y., 2015. Long-term dynamics and hotspots of change in a desert grassland plant community. Am. Nat. 185, E30–E43. https://doi.org/10.1086/679315.

Crosby, A.D., Leston, L., Bayne, E.M., Sólymos, P., Mahon, C.L., Toms, J.D., Song, S.J., 2023. Domains of scale in cumulative effects of energy sector development on boreal birds. Landsc. Ecol. 38, 3173–3188. https://doi.org/10.1007/s10980-023-01779-8.

Cuddington, K., 2011. Legacy effects: the persistent impact of ecological interactions. Biological Theory 6, 203–210. https://doi.org/10.1007/s13752-012-0027-5.

Damgaard, C., 2019. A critique of the space-for-time substitution practice in community ecology. Trends Ecol. Evol. 34, 416–421. https://doi.org/10.1016/j.tree.2019.01.013.

DeSante, D.F., Saracco, J.F., O'Grady, D.R., Burton, K.M., Walker, B.L., 2004. Methodological considerations of the monitoring Avian productivity and survivorship (MAPS) program. Stud. Avian Biol. 29, 28–45.

Enemar, A., Cavallin, B., Nyholm, E., Rudebeck, I., Thorner, A.M., 1994. Dynamics of a passerine bird community in a small deciduous wood, S Sweden, during 40 years. Ornis Svec. 4, 65–104. https://doi.org/10.34080/os.v4.23023.

Fleming, W.D., 2001. Effects of Pipeline rights-of-way on Forest Birds in the Boreal Forest of Alberta (Thesis.). University of Alberta, Edmonton, Alberta, Canada.

Foster, K.R., Godwin, C.M., Pyle, P., Saracco, J.F., 2017. Reclamation and habitat-disturbance effects on landbird abundance and productivity indices in the oil sands region of northeastern Alberta, Canada. Restor. Ecol. 25, 532–538. https://doi.org/10.1111/rec.12478.

García-Navas, V., Sattler, T., Schmid, H., Ozgul, A., 2021. Spatial heterogeneity in temporal dynamics of Alpine bird communities along an elevational gradient. J. Biogeogr. 48, 886–902. https://doi.org/10.1111/jbi.14045.

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815. https://doi.org/10.1890/02-3114.

Haddou, Y., Mancy, R., Matthiopoulos, J., Spatharis, S., Dominoni, D.M., 2022. Widespread extinction debts and colonization credits in United States breeding bird communities. Nat. Ecol. Evol. 6, 324–331. https://doi.org/10.1038/s41559-021-01653-3.

Hart, T., Crosby, A., Leston, L., Schmiegelow, F., Bayne, E., 2025. Edge effects reduce persistence but not colonization in a declining Setophaga virens (*Black-throated Green Warbler*) population in Alberta's boreal forest. Ornithological Applications duaf068. https://doi.org/10.1093/ornithapp/duaf068.

Hartig, F., 2024. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Contributed Packages. CRAN. https://doi.org/10.32614/cran.package.dharma.

Hawkes, V.C., Gerwing, T.G., 2019. Wildlife usage indicates increased similarity between reclaimed upland habitat and mature boreal forest in the Athabasca oil Sands region of Alberta, Canada. PLoS One 14, 0217556. https://doi.org/10.1371/journal.pone.0217556.

Hobson, K.A., Schieck, J., 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. 9, 849–863. https://doi.org/10.2307/2641334.

Jones, S.K., Ripplinger, J., Collins, S.L., 2017. Species reordering, not changes in richness, drives long-term dynamics in grassland communities. Ecol. Lett. 20, 1556–1565. https://doi.org/10.1111/ele.12864.

Kalukapuge, T., Leston, L.F., Martínez-Lanfranco, J.A., Bayne, E., 2024. Response of boreal songbird communities to the width of linear features created by the energy sector in Alberta, Canada. Avian Conserv. Ecol. 19. https://doi.org/10.5751/ACE-02730-190214.

Kampichler, C., Angeler, D.G., Holmes, R.T., Leito, A., Svensson, S., Jeugd, H.P., Wesołowski, T., 2014. Temporal dynamics of bird community composition: an analysis of baseline conditions from long-term data. Oecologia 175, 1301–1313. https://doi.org/10.1007/s00442-014-2979-6.

Kampichler, C., Turnhout, C.A., Devictor, V., Jeugd, H.P., 2012. Large-scale changes in community composition: determining land use and climate change signals. PLoS One 7, 35272. https://doi.org/10.1371/journal.pone.0035272.

Kampichler, C., van der Jeugd, H.P., 2013. Determining patterns of variability in ecological communities: time lag analysis revisited. Environ. Ecol. Stat. 20 (2), 271–284. https://doi.org/10.1007/s10651-012-0219-y.

Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164. https://doi.org/10.2307/3235676.

Korňan, M., Svitok, M., 2025. Species reordering and turnover shape long-term dynamics of a primeval temperate forest breeding bird assemblage. Community Ecol. 1–16. https://doi.org/10.1007/s42974-025-00279-w.

Lankau, H.E., Leston, L.F., Bayne, E.M., 2025. Boreal songbird response to variation in natural seismic line vegetation recovery. Avian Conserv. Ecol. 20. https://doi.org/10.5751/ACE-02904-200205.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. https://doi.org/10.1007/s004420100716.

Leston, L., Bayne, E., Schmiegelow, F., 2018. Long-term changes in boreal forest occupancy within regenerating harvest units. For. Ecol. Manag. 421, 40–53. https://doi.org/10.1016/j.foreco.2018.02.029.

Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. Biol. Conserv. 143, 1317–1328. https://doi.org/10.1016/j.biocon.2010.02.013.

Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E., Wardle, G.M., 2012. Value of long-term ecological studies. Austral Ecol. 37, 745–757. https://doi.org/10.1111/j.1442-9993.2011.02351.x.

Magalhães, M.F., Beja, P., Schlosser, I.J., Collares-Pereira, M.J., 2007. Effects of multi-year droughts on fish assemblages of seasonally drying mediterranean streams. Freshw. Biol. 52, 1494–1510. https://doi.org/10.1111/j.1365-2427.2007.01781.x.

Magnuson, J.J., 1990. Long-term ecological research and the invisible present. Bioscience 40, 495–501. https://doi.org/10.2307/1311317.

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Watt, A. D., 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol. Evol. 25, 574–582. https://doi.org/10.1016/j.tree.2010.06.016.

Mahon, C.L., Holloway, G.L., Bayne, E.M., Toms, J.D., 2019. Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. Ecol. Appl. 29, 01895. https://doi.org/10.1002/eap.1895.

Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G., Pardini, R., 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biol. Conserv. 142, 1166–1177. https://doi.org/10.1016/j.biocon.2009.01.033.

Nott, P., 2003. Monitoring Avian Productivity and Survivorship (MAPS) Habitat Structure Assessment (HSA) Protocol: Describing Vertical and Horizontal Spatial Habitat Patterns at MAPS Stations. Institute for Bird Populations.

Palmer, M.A., Ambrose, R.F., Poff, N.L., 1997. Ecological theory and community restoration ecology. Restor. Ecol. 5, 291–300. https://doi.org/10.1046/j.1526-100X.1997.00543.x.

Pereira e Silva, M.C., Dias, A.C.F., van Elsas, J.D., Salles, J.F., 2012. Spatial and temporal variation of archaeal, bacterial and fungal communities in agricultural soils. PLoS One 7, e51554. https://doi.org/10.1371/journal.pone.0051554.

Pyle, P., 1997. Identification Guide to North American Birds, Part 1. Slate Creek Press, Bolinas, California.

Saracco, J.F., Pyle, P., Kaschube, D.R., Kohler, M., Godwin, C.M., Foster, K.R., 2022. Demographic declines over time and variable responses of breeding bird populations to human footprint in the Athabasca oil sands region, Alberta, Canada. Ornithological Applications 124. https://doi.org/10.1093/ornithapp/duac037.

Schieck, J., Song, S.J., 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of Western North America: literature review and meta-analyses. Can. J. For. Res. 36, 1299–1318. https://doi.org/10.1139/x06-017.

Spotswood, E.N., Bartolome, J.W., Allen-Diaz, B., 2015. Hotspots of community change: temporal dynamics are spatially variable in understory plant composition of a California oak woodland. PLoS ONE 10, e0133501. https://doi.org/10.1371/journal.pone.0133501.

Sutheimer, C.M., Filicetti, A.T., Viliani, L., Nielsen, S.E., 2025. Regeneration lags and growth trajectories influence passive seismic line recovery in Western North American boreal forests. Restor. Ecol. 33, 14353. https://doi.org/10.1111/rec.14353.

Sutheimer, C.M., Nielsen, S.E., 2025. Early succession across boreal forest transitions after linear disturbance and wildfire. Forests 16, 1333. https://doi.org/10.3390/f16081333.

Thibault, K.M., White, E.P., Ernest, S.M., 2004. Temporal dynamics in the structure and composition of a desert rodent community. Ecology 85, 2649–2655. https://doi.org/10.1890/04-0321.

Uezu, A., Metzger, J.P., 2016. Time-lag in responses of birds to Atlantic forest fragmentation: restoration opportunity and urgency. PLoS One 11, 0147909. https://doi.org/10.1371/journal.pone.0147909.

Vellend, M., 2016. The Theory of Ecological Communities. Princeton University Press.

Watts, K., Whytock, R.C., Park, K.J., Fuentes-Montemayor, E., Macgregor, N.A., Duffield, S., McGowan, P.J., 2020. Ecological time lags and the journey towards conservation success. Nat. Ecol. Evol. 4, 304–311. https://doi.org/10.1038/s41559-019-1087-8.

Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods Ecol. Evol. 3, 260–267. https://doi.org/10.1111/j.2041-210X.2011.00170.x.

Wesołowski, T., Czeszczewik, D., Hebda, G., Maziarz, M., Mitrus, C., Rowiński, P., Neubauer, G., 2022. Long-term changes in breeding bird community of a primeval temperate forest: 45 years of censuses in the Białowieża National Park (Poland. Acta Ornithol. (Warszaw) 57, 71–100. https://doi.org/10.3161/00016454AO2022.57.1.005.

Wesołowski, T., Mitrus, C., Czeszczewik, D., Rowiński, P., 2010. Breeding bird dynamics in a primeval temperate forest over thirty-five years: variation and stability in the changing world. Acta Ornithol. (Warszaw) 45, 209–232. https://doi.org/10.3161/000164510X551354.

Wilson, S.J., Bayne, E.M., 2019. Songbird community response to regeneration of reclaimed wellsites in the boreal forest of Alberta. Journal of Ecoacoustics 3, 1–11. https://doi.org/10.22261/JEA.I4B2LF.