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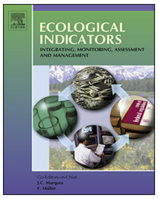

Original Articles

How do ecological resilience metrics relate to community stability and collapse?

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ABSTRACT

The concept of ecological resilience (the amount of disturbance a system can absorb before collapsing and reorganizing) holds potential for predicting community change and collapse—increasingly common issues in the Anthropocene. Yet neither the predictions nor metrics of resilience have received rigorous testing. The cross-scale resilience model, a leading operationalization of resilience, proposes resilience can be quantified by the combination of diversity and redundancy of functions performed by species operating at different scales. Here, we use 48 years of sub-continental avian community data aggregated at multiple spatial scales to calculate resilience metrics derived from the cross-scale resilience model (i.e., cross-scale diversity, cross-scale redundancy, within-scale redundancy, and number of body mass aggregations) and test core predictions inherent to community persistence and change. Specifically, we ask how cross-scale resilience metrics relate community stability and collapse. We found low mean cross-correlation between species richness and cross-scale resilience metrics. Resilience metrics constrained the magnitude of community fluctuations over time (mean species turnover), but resilience metrics but did not influence variability of community fluctuations (variance in turnover). We show shifts in resilience metrics closely predict community collapse: shifts in cross-scale redundancy preceded abrupt changes in community composition, and shifts in cross-scale diversity synchronized with abrupt changes in community composition. However, we found resilience metrics only weakly relate to maintenance of particular species assemblages over time. Our results distinguish ecological resilience from ecological stability and allied concepts such as elasticity and resistance: we show communities may fluctuate widely yet still be resilient. Our findings also differentiate the roles of functional redundancy and diversity as metrics of resilience and reemphasize the importance of considering resilience metrics from a multivariate perspective. Finally, we support the contention that ecological stability is nested within ecological resilience: stability predicts the behavior of systems within an ecological regime, and resilience predicts the maintenance of regimes and behavior of systems collapsing into alternative regimes.

1. Introduction

> "If there is a worthwhile distinction between resilience and stability it is important that both be measurable."
>
> C. S. Holling, 1973

As the Anthropocene progresses, community change and collapse are increasingly common (Folke et al., 2004; Steffen et al., 2015). The concept of ecological resilience, defined by Holling (1973) as the amount of disturbance a system can absorb before collapsing into an alternative regime, holds potential for predicting community change and collapse (Angeler and Allen, 2016). Quantifying ecological resilience has been a long-term pursuit in ecology (Carpenter et al., 2005; Cumming et al., 2005; Standish et al., 2014), ecological resilience has been applied internationally in management frameworks (Briske et al., 2008; Bestelmeyer et al., 2017; Seidl et al., 2016), and multiple ecological resilience metrics have been proposed (Allen et al., 2005; Baho et al., 2017). Yet neither the core predictions nor metrics of ecological resilience theory have received rigorous testing (Angeler and Allen, 2016; Sundstrom et al., 2018).

Ecological resilience theory makes key predictions concerning complex, nonlinear, and abruptly shifting system behavior, making it uniquely applicable to Anthropocene issues (Gunderson, 2000). Ecological resilience is related to, but distinct from, ecological stability (the

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ability of a system to return to an equilibrium state post-disturbance—also known as “engineering resilience,” “bounce-back time,” “resistance,”, and “elasticity”; Holling, 1973; Hillebrand et al., 2018; Pimm, 1984). This is a crucial distinction because while ecological resilience makes predictions concerning abrupt regime shifts into alternative states, ecological stability only makes predictions concerning a single regime (Angeler and Allen, 2016). Ecological resilience theory predicts that a system may fluctuate greatly (have low stability and exhibit non-equilibrium behavior) and yet have high ecological resilience or conversely fluctuate little and have low ecological resilience (Angeler and Allen, 2016; Holling, 1973). That is, a resilient system will constrain the magnitude of fluctuations so that the system stays within a given regime, but the same resilient system may exhibit high instability within the regime (Gunderson et al., 2012). By definition, loss of ecological resilience increases the likelihood of system collapse and regime shifts due to loss of structures, functions, and feedbacks that maintain the current regime (Allen et al., 2005). Thus, ecological resilience should be both quantifiably distinct from stability and clearly correspond with community change and collapse (Holling, 1973; Standish et al., 2014).

The cross-scale resilience model, a leading model for operationalizing and quantifying ecological resilience (hereafter referred to simply as “resilience”), provides the opportunity to test these core predictions of resilience theory (Peterson et al., 1998; Sundstrom et al., 2018). The cross-scale resilience model establishes that redundancy and diversity of organism functions across discontinuous scale domains of resource use in a system confer resilience (Holling, 1992; Peterson et al., 1998; Fig. 1). Quantifying redundancy and diversity of functions across these discontinuous scale domains can produce metrics to estimate the relative resilience of systems (Bouska, 2018, Sundstrom et al., 2018; Angeler et al., 2019a). For example, Allen et al. (2005) proposed several cross-scale resilience metrics such as within-scale redundancy, cross-scale redundancy, cross-scale diversity, and number of scale domains.

Here, we use a half-century of sub-continental avian community data to calculate cross-scale resilience metrics and test how resilience relates to community stability and collapse. We do this by testing two core resilience theory predictions concerning its relationship with stability and two concerning its relationship with community change and collapse. The first resilience-stability relationship prediction is that resilience is distinct from stability: we test this by quantifying the degree of correlation between species richness and cross-scale resilience metrics. Although species richness is not a direct metric of stability, it is correlated with stability and influences the ability of a system to “bounce back” from disturbances (Hautier et al., 2015; Ives and Carpenter, 2007; McCann, 2000; Mougi and Kondoh, 2012; Tilman and Downing, 1994). The second resilience-stability relationship prediction is that resilience will constrain the magnitude of system fluctuations but not their variability: we test this by determining the relationship between cross-scale resilience metrics and the mean and variance of annual species turnover. In this case, cross-scale diversity is expected to reduce mean turnover the most, and all resilience metrics should have little influence on turnover variance (Allen et al., 2005; Angeler et al., 2019a). The first resilience-collapse relationship prediction is that changes in cross-scale resilience metrics will predict community collapse: we test this by determining if changes in cross-scale resilience metrics synchronize with abrupt shifts in community composition. Within-scale redundancy, cross-scale redundancy, and number of scale domains are expected to most strongly predict community collapse (Nash et al., 2016; Roberts et al., 2019; Spanbauer et al., 2016). Finally, the second resilience-collapse prediction is cross-scale resilience metrics will only weakly predict maintenance of specific species assemblages: we test this by determining how cross-scale resilience metrics relate to changes in community similarity over time (Gunderson, 2000; Angeler et al., 2019b).

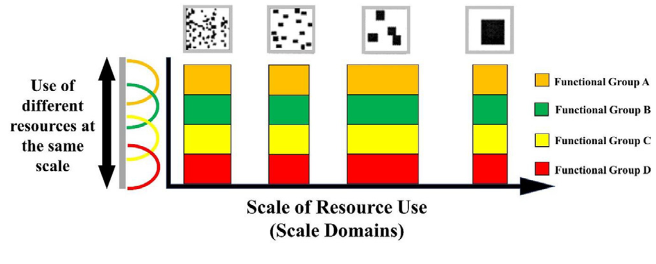

Fig. 1. The hypothesized relationship between the scale of a species’ interaction with their environment (as assayed by their body size) and their membership in a functional group—modified from Peterson et al. (1998). Differently-sized species use resources at different spatial and temporal scales. Species in the same functional group use similar resources, but those that operate at larger scales require those resources to be more aggregated in space than do species that operate at smaller scales. Within scales, a diversity of functional groups provides robust ecological functioning, whereas replication of function across scales reinforces ecological function. Ecological resilience emerges from diversity of ecological function at specific scales and the replication of function across a diversity of scales.

2. Methods

2.1. *Calculating cross-scale resilience metrics*

Cross-scale resilience metrics are calculated by first identifying a biotic community within a system (e.g., an avian forest community) and acquiring census presence/absence data from the biotic community (Allen et al., 2005), identifying the discontinuous scale domains at which functions are performed by each species in the biotic community (Nash et al., 2014a,b), and finally using functional traits of species across scale domains to estimate functional redundancy and diversity within and across scale domains (Fischer et al., 2007).

2.1.1. *Identifying biotic communities*

For biotic community data, we used the North American Breeding Bird Survey (BBS) which estimates bird community composition via yearly roadside avian point-count surveys (Sauer et al., 2017). Begun in 1966, the BBS is conducted along a series of > 2500 permanent, randomly-distributed routes during the breeding season (Sauer et al., 2017). We analyzed BBS route data from 1967 − 2014.

We defined avian communities by spatially binning BBS routes according to US Environmental Protection Agency (EPA) ecoregions (Omernik and Griffith, 2014; Fig. 2). These ecoregions are spatially hierarchical, meaning that finer-scaled ecoregions are bounded by and nested within larger-scaled ecoregions. Because smaller-scale EPA ecoregion boundaries are bounded by US political boundaries, we only consider BBS routes within the continental United States. We considered avian communities at the three progressively smaller spatial scales (EPA ecoregion levels II, III, IV; Fig. 2). If binned BBS data within an ecoregion did not extend for ≥ 24 years (i.e., ≥ 50% of the study period), we excluded that ecoregion from analysis (Table S1; see supplementary computer code for further details).

2.1.2. *Identifying discontinuous scale domains*

We performed discontinuity analysis on binned BBS data for each ecoregion at each scale using the “discontinuity detector” method (Barichievy et al., 2018) based on the Gap Rarity Index which identifies scale domains by detecting discontinuities in log-ranked organism body masses (Restrepo et al., 1997). For taxa with determinant growth, mean body mass reliably differentiates size aggregations and is strongly allometric to the scale domains at which functions are carried out by organisms (Allen et al., 2006; Holling, 1992; Nash et al., 2014b). Because of known negative observation biases for waterfowl and allied families and because water-dwelling avian families’ follow different body masses patterns than terrestrial avian families, we removed all

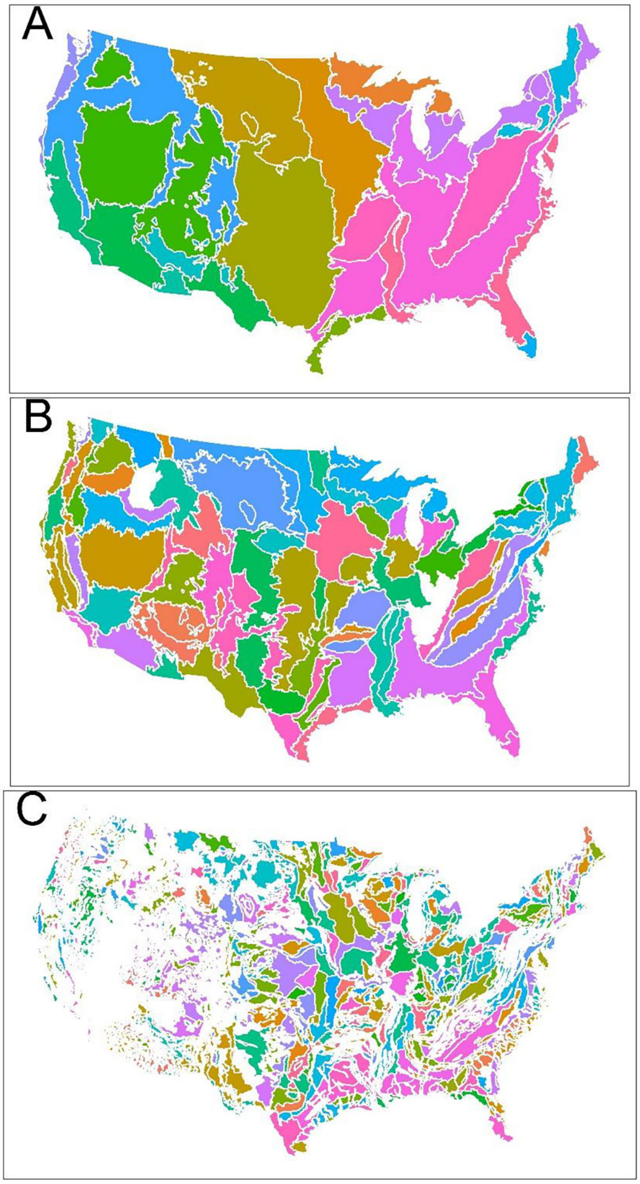

Fig. 2. Maps of US Environmental Protection Agency ecoregions corresponding with level 2 (A), level 3 (B), and level 4 (C). Missing (white-out) ecoregions did not contain sufficiently long time series of North American Breeding Bird Survey data (≥ 24 years). White lines indicate ecoregion boundaries.

species from the Anseriformes, Gaviiformes, Gruiformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes, and Suliformes families from the analysis (Holling, 1992; Sundstrom et al., 2012). We obtained mean body mass estimates for all remaining species from the CRC Handbook of Avian Body Masses (Dunning, 2007). Because Gap Rarity Index tends to overestimate discontinuities in species-poor samples, we removed any route with < 40 species observed (Barichievy et al., 2018; Stow et al., 2007). We simply counted the number of body mass aggregations to obtain that metric.

2.1.3. *Estimating within- and cross-scale functional redundancy, cross-scale diversity*

We assigned functional types to each species according to diet and foraging strategies (Ehrlich et al., 1988). We broke diets into carnivore, herbivore, and omnivore groups, where omnivores are defined as species with approximately even proportions of plant and animal intake (Bouska, 2018). We divided foraging strategies into five groups: water, ground, foliage, bark, and air (Sundstrom et al., 2012). Thus, functional groups represented combinations of diet and foraging strategies (e.g., water carnivore, ground herbivore, etc.).

We then used functional groups along with body mass aggregations to calculate cross-scale redundancy (average number of aggregations for which each functional group has at least one representative), within-scale redundancy (the average number of representatives from each functional group within each aggregation), and cross-scale diversity (the average diversity of functional groups across aggregations) metrics for each ecoregion within each of the three spatial scales (Fig. 2). The equations for these are as follows:

$$Cross-scale\ \ Redundancy = \frac{1}{a}\sum_{i=1}^{a}(\varphi)_i$$

$$Within-scale\ \ Redundancy = \frac{1}{a}\sum_{i=1}^{a}\left(\frac{1}{f}\sum_{j=1}^{f}f_j\right)_i$$

$$Cross-scale\ \ Diversity = \frac{1}{a}\sum_{i=1}^{a}\left(-\sum_{j\ =1}^{f}p_j\ln p_j\right)_i$$

where a is the i^{th} number of body mass aggregations, φ is the number of functional groups with at least one representative in an aggregation, f is the j^{th} functional group in the i^{th} body mass aggregation, and p is the j^{th} species in each aggregation.

2.2. *Resilience-stability test 1: relationship between cross-scale resilience and richness*

We used cross-correlation to compare species richness with each cross-scale resilience metric (number of body mass aggregations, cross-scale redundancy, within-scale redundancy, cross-scale diversity) for each ecoregion across −5 to 5 lags. That is, we used cross-correlation to quantify temporal covariance of richness and resilience metrics, determining if patterns of resilience metrics preceded (back to 5 time steps before) or followed (forward to 5 time steps after) patterns of richness. For each lag, we calculated the mean and 85% confidence intervals of the absolute values of correlation coefficients across ecoregions.

2.3. *Resilience-stability test 2: relationship between cross-scale resilience and turnover*

Second, we determined the relationship between cross-scale resilience metrics and species turnover. We calculated relative species turnover (the proportion of the species pool that turns over annually) using the following equation (Diamond, 1969; Wonkka et al., 2017):

$$Turnover_{t+1} = (U_t + U_{t+1})/(S_t + S_{t+1})$$

where U_t is the number of species present in the ecoregion at year t that were not present in year $t + 1$; U_{t+1} is the number of species present in the ecoregion at year $t + 1$ that were not present in year t; S_t is the total number of species present in the ecoregion at year t; and S_{t+1} is the total number of species present in the ecoregion at year $t + 1$.

We then developed two linear mixed models: 1) to determine if resilience metrics influenced the magnitude of species turnover, we used the mean of the absolute value of species turnover over time as the response variable, and 2) to determine if resilience metrics influenced the variability of species turnover, we used the standard deviation of species turnover over time as the response variable. For both models, we set mean resilience metrics over time as the predictor variables. We allowed intercepts to vary by hierarchically nested EPA ecoregions (e.g., for level III ecoregions, random effect in R package “lme4” syntax was “(1|Level I/Level II)”). To minimize collinearity, we calculated variance inflation factors and sequentially removed predictor variables (resilience metrics) with the highest variance inflation factor until

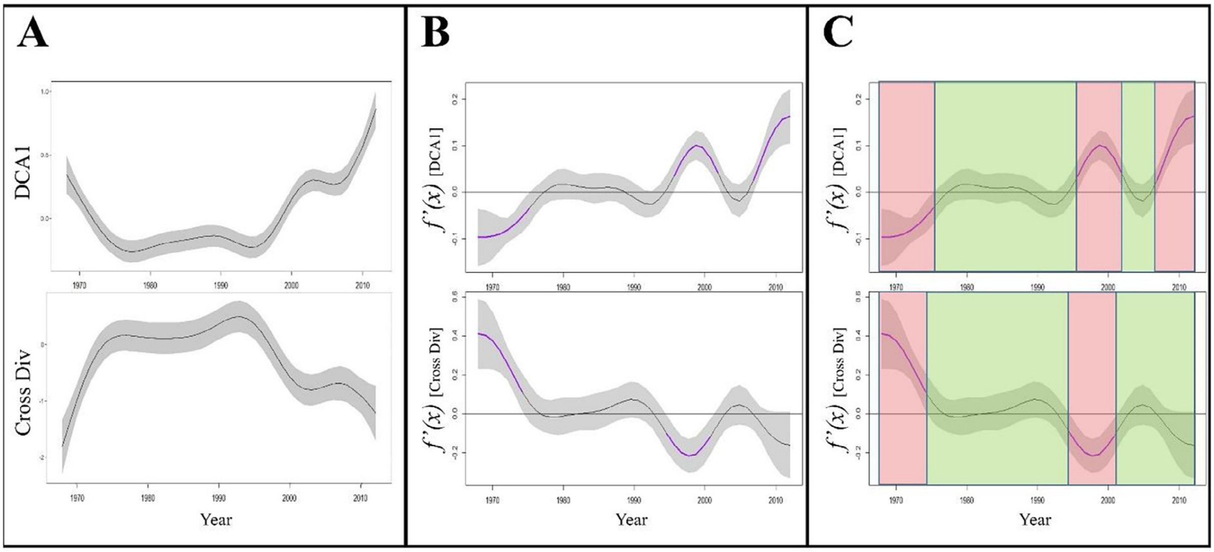

Fig. 3. Visual depiction of methods for detecting synchrony/asynchrony in abrupt shifts in community composition (DCA1) and in resilience metrics (e.g., cross-scale diversity [Cross Div]). Panel A shows an example of predicted DCA1 and Cross Div values derived from generalized additive models. Panel B shows approximate derivatives of predicted DCA1 and Cross Div values. Panel C shows the binary test for synchrony/asynchrony, where red bars (abrupt shifts) and green bars (no abrupt shift detected) aligning indicate synchrony and lack of alignment indicates asynchrony.

variance inflation factor values for all variables were ≤3.

2.4. *Resilience-collapse test 1: relationship between cross-scale resilience and abrupt shifts*

We determined whether significant temporal shifts in cross-scale resilience metrics synchronized with abrupt shifts in community composition. To identify abrupt shifts in community composition, we 1) performed detrended correspondence analysis (DCA; “decorana” function from the vegan package in R) on Hellinger-transformed relative abundances of species in each ecoregion over time, 2) extracted values of the first DCA axis (DCA1) for each year, 3) used generalized additive models (GAMs) to model changes in DCA1 over time (with year as the smoothed predictor) for each ecoregion, 4) extracted predicted DCA1 response values from GAMs for each ecoregion (Fig. 3a), and 5) determined where community structure significantly changed by first calculating derivatives and 85% confidence limits around the derivatives from the GAM predictions and then locating ranges in the time series where derivative confidence limits did not encompass zero (Simpson, 2018; Fig. 3b). We located shifts in cross-scale resilience metrics in a similar fashion–by extracting GAM predictions, calculating derivatives and confidence intervals, and locating ranges where confidence limits did not encompass zero (Fig. 3b). To test for synchrony between cross-scale resilience metrics and structural community change, we encoded DCA1 and resilience metric time series as binary variables, where either a significant shift (85% confidence limit of derivative did not encompass zero) occurred or did not for each time step (i.e., each year of BBS data; Fig. 3c). We aggregated significant increases and decreases into an absolute value because both significant increases and decreases in ordinated values (e.g., DCA) or resilience metrics, regardless of directionality, could signal regime shifts. We set the binary DCA1 variable as the response and binary resilience metrics predictors in a binomial generalized linear mixed model. We checked for collinearity with variance inflation factors.

2.5. *Resilience-collapse test 2: relationship between cross-scale resilience and community similarity*

We determined the relationship between cross-scale resilience metrics and patterns of community similarity over time. We estimated community similarity over time via the Jaccard index. That is, we calculated Jaccard similarity between each year of BBS data for each ecoregion and then used linear regression to estimate change in community identity over time (i.e., slope; *sensu* Dornelas et al., 2014). Because the Jaccard index ranges from 0 (complete dissimilarity in species) to 1 (complete similarity in species), a slope of zero indicates no change in community composition over time, and a slope of −1 indicates a complete change in species pool. We then developed linear mixed models, setting the slope of the Jaccard index as the response variable. For predictor variables, we used initial resilience metric values (the chronologically first value for each resilience metric for each ecoregion) and mean resilience metric values (the average of each resilience metric value across the time series for each ecoregion). To account for variance in certainty of Jaccard slope fits, we used 1/standard error of each Jaccard slope fit as prior weights for linear mixed models. We used the methods from Test 2 for minimizing collinearity as above (i.e., sequential removal of predictor variables via variance inflation factors).

3. Results

3.1. *Resilience-stability test 1: relationship between cross-scale resilience and richness*

Mean cross-correlation between richness and resilience metrics was low across scales and individual metrics, ranging from r = 0.16 ± 0.01 (cross-scale redundancy at lag −5 at the finest scale) to r = 0.63 ± 0.02 (cross-scale diversity at lag 0 at the finest scale; Fig. 4). Patterns were consistent across scales: the strongest correlation between richness and all metrics at all scales occurred at lag zero (annually) after which correlations decreased sharply (Fig. 4). At the broadest scale (level II), confidence limits show little difference between individual metrics’ correlations with richness (Fig. 4). At the finer scales (levels III, IV), cross-scale diversity correlated most strongly with richness (Fig. 4). Within-scale redundancy showed the second greatest correlation with richness (max r = 0.50 ± 0.02 at level IV, lag 0; Fig. 4). Cross-scale redundancy (r = 0.34 ± 0.02 at lag 0) and number of aggregations (0.29 ± 0.02 at lag 0) displayed the weakest correlation with richness at finer scales (Fig. 4).

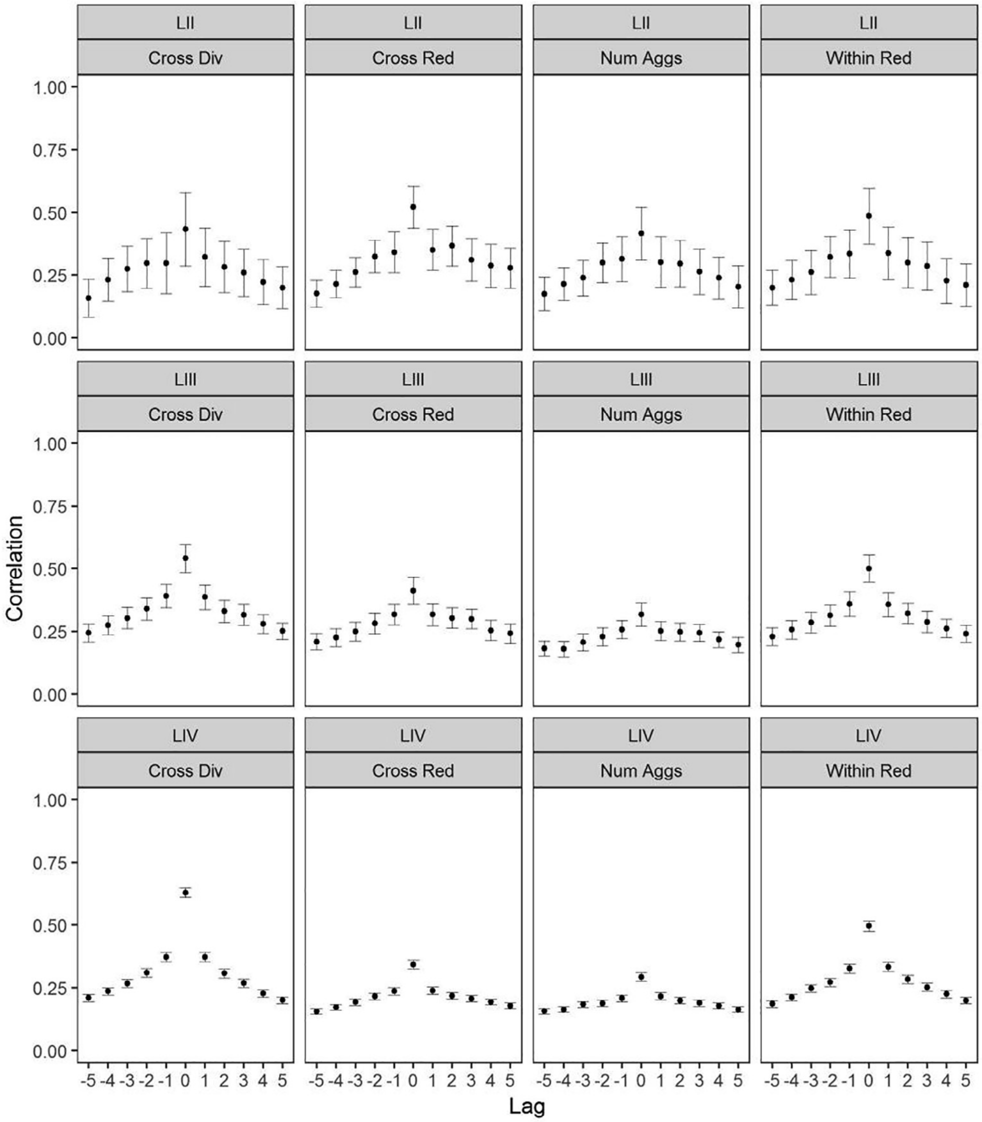

Fig. 4. Mean cross-correlation estimates and 85% confidence limits between species richness and cross-scale resilience metrics at multiple hierarchical scales. Y-axis indicates degree of correlation (r), and x-axis indicates lags ranging from −5 to 5, where lag 0 indicates annual correlation. Richness and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1967 – 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). *Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.*

3.2. Resilience-stability test 2: relationship between cross-scale resilience and turnover

Resilience metrics had significantly negative relationships with mean annual species turnover at all scales, but resilience metrics showed little or no association with standard deviation of annual species turnover (Fig. 5; Table S1). Cross-scale diversity was a significant predictor of mean species turnover at the broadest scale and the strongest predictor at the finest scale (−0.027 ± 0.001 and −0.034 ± 0.002 at levels II and IV respectively), and cross-scale diversity was a significant negative predictor of standard deviation in species turnover at the finest scale (−0.004 ± 0.002). Cross-scale redundancy was a significant predictor at all scales, although its strength decreased at finer scales until it was the weakest predictor at the finest scale (−0.018 ± 0.011, −0.015 ± 0.001, and −0.0059 ± 0.004 at ecoregion levels II, III, and IV respectively). Cross-scale redundancy also significantly negatively predicted standard deviation in species turnover at the finest scale (−0.005 ± 0.003). Within-scale redundancy was a significant predictor at the middle scale (−0.017 ± 0.006), and number of aggregations was a significant predictor of middling strength at the finest scale (−0.018 ± 0.004) (Fig. 5).

3.3. Resilience-collapse test 1: relationship between cross-scale resilience and abrupt shifts

At all scales, resilience metrics synchronized significantly with abrupt community shifts (Figs. 6 and 7; Table S2). At the broadest scale (level II), cross-scale diversity (1.0 ± 0.53) and cross-scale redundancy (0.67 ± 0.55) synchronized with community change (Figs. 4, 6 and 7). At the middle scale (level III), number of aggregations (0.21 ± 0.20) and within-scale redundancy (0.62 ± 0.20) exhibited synchrony with community change (Figs. 6 and 7), but cross-scale redundancy exhibited asynchrony (i.e., a negative model coefficient; −0.3 ± 0.19) with community change (Figs. 6 and 7). And at the finest scale (level IV), all resilience metrics synchronized with abrupt community shifts: cross-scale diversity showed the strongest synchrony (0.58 ± 0.08; Figs. 3, 6 and 7), and number of aggregations showed the weakest synchrony (0.11 ± 0.09).

3.4. Resilience-collapse test 2: relationship between cross-scale resilience and community similarity

At the broadest and middle scales (levels II, III), neither initial nor mean resilience metric values significantly predicted changes in community similarity over time (Table S3). But at the finest scale (level IV),

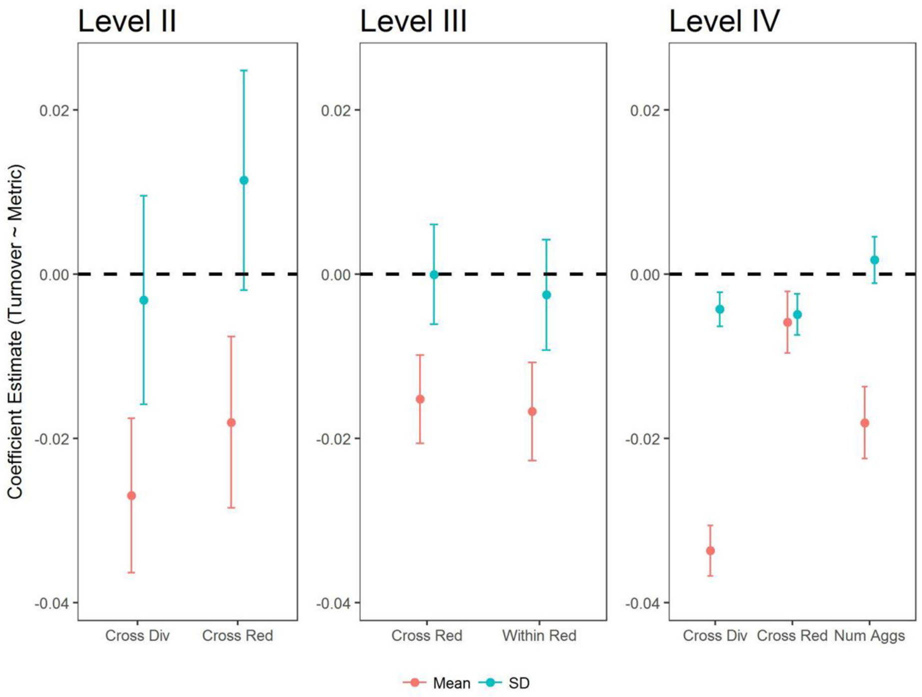

Fig. 5. Coefficient estimates and 85% confidence limits from linear mixed models testing the relationship between mean annual species turnover and mean resilience metrics (red dots) and the standard deviation (SD) of annual species turnover and mean resilience metrics (blue dots) at multiple hierarchical scales. Species turnover and resilience metrics were calculated from avian community data recorded at North American Breeding Bird Survey routes from 1967 − 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). *Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.*

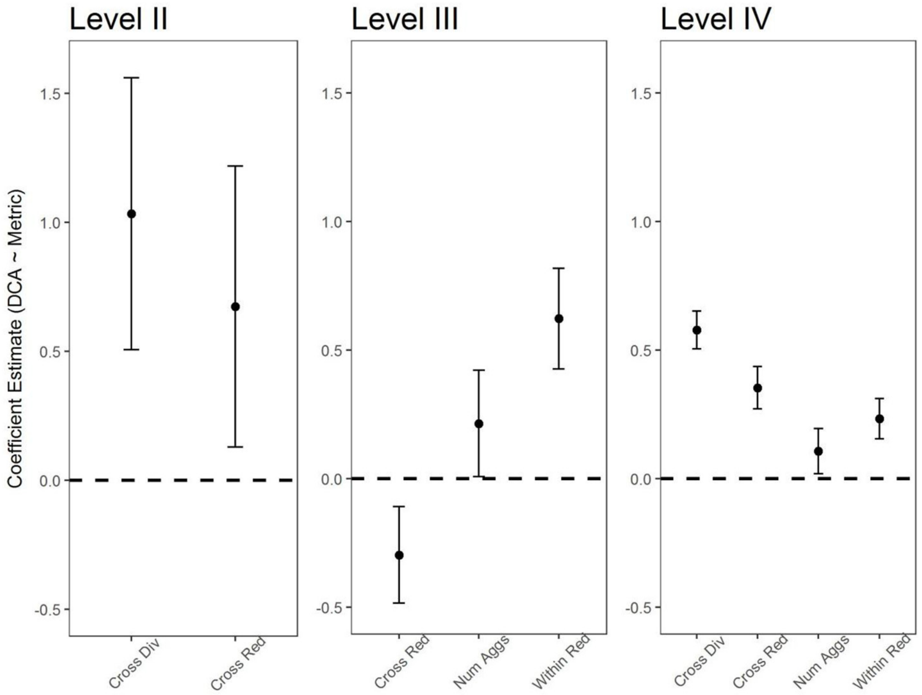

Fig. 6. Coefficient estimates and 85% confidence limits from binomial generalized linear mixed models testing synchrony between abrupt community shifts and resilience metrics at multiple hierarchical scales. Synchrony is defined as simultaneous occurrence of regime shifts (i.e., significant change in first axis of Detrended Correspondence Analysis) and significant shifts in resilience metrics. Abrupt community shifts and resilience metrics were derived from avian community data recorded at North American Breeding Bird Survey routes from 1967 − 2014 aggregated by US Environmental Protection Agency ecoregions. Ecoregions range from broad (Level II) to fine (Level IV). *Note: DCA = first axis of detrended correspondence analysis; Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy; Num Aggs = number of body mass aggregations; Within Red = within-scale redundancy.*

initial values of cross-scale diversity (0.0002 ± 0.0001) and number of aggregations (0.0002 ± 0.0001) significantly, albeit weakly, predicted reduced community change (i.e., pushed Jaccard slopes closer to zero–no net community change; Table S3).

4. Discussion

Using a half-century of subcontinental community data, we provide quantitative support for core predictions of ecological resilience theory regarding how ecological resilience relates to ecological stability and collapse. Per Holling's call in his seminal manuscript on resilience theory (Holling, 1973), we found resilience is related to but distinct from stability. Importantly, our results distinguish ecological resilience from concepts allied with stability such as engineering resilience, "bounce-back" time to equilibrium, resistance, and elasticity (Gunderson, 2000; Pimm, 1984; Standish et al., 2014). We also show that shifts in cross-scale resilience metrics clearly predict and coincide with abrupt community shifts, but at the same time, resilience is weakly related to community change in terms of maintenance of a particular species assemblages over time. We also provide interpretability for cross-scale resilience metrics: we distinguish the roles of functional redundancy and diversity metrics of community collapse and community similarity, respectively (Peterson et al., 1998; Walker et al., 1999), and we show number of aggregations (i.e., scale domains) may be an

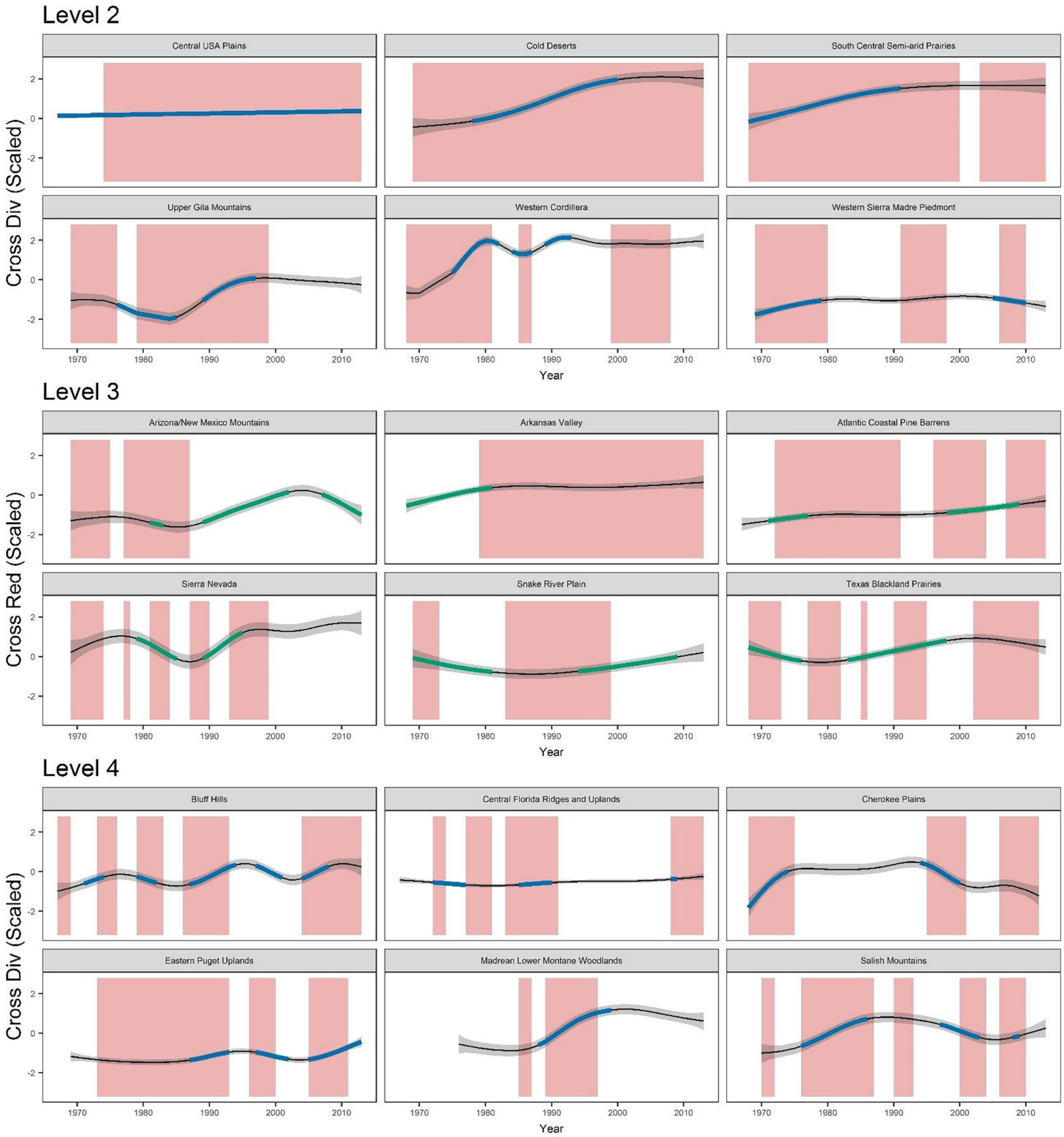

Fig. 7. Comparison of synchrony/asynchrony between periods of significant avian abrupt community shifts (red blocks) and periods of significant changes in cross-scale resilience metrics across a sample of Environmental Protection Agency Levels 2, 3, and 4 ecoregions from 1967 − 2014. Black lines (y-axis) indicate predicted values from GAMs of resilience metrics, grey shading indicates pointwise 85% confidence limits around predictions, and colored sections indicate regions of significant change in time series (where simulated confidence limits of derivatives from GAMs did not encompass zero). *Note: Cross Div = cross-scale diversity; Cross Red = cross-scale redundancy.*

unresponsive metric if systems reorganize around similar numbers of scale domains during and post-collapse, meaning this metric may only detect extreme collapse events (Angeler et al., 2019b; Roberts et al., 2019).

Our results reaffirm the importance of avoiding the conflation of ecological resilience and ecological stability. Stability theory predicts a particular community composition (e.g., higher species richness) will reduce variance in system functionality but makes no assertions concerning alternative states (Allan et al., 2011; Cardinale et al., 2013; Tilman, 1996; Wagg et al., 2018). Additionally, stability typically does not consider ecological complexity features, such as spatial and temporal scaling structures or thresholds (Baho et al., 2017; Hillebrand et al., 2018). In contrast, resilience theory predicts resilient systems may exhibit wide ranges of variance, community composition will be dynamic and adaptive, and scaling patterns of functional redundancy and diversity within communities (instead of particular community compositions) will determine the ability of a system to remain within one of multiple alternative regimes (Allen et al., 2014; Angeler et al., 2019a; Chillo et al., 2011; Sundstrom et al., 2018). Our results support these differences between stability and resilience: resilience metrics had low degrees of correlation with species richness, a metric that is closely correlated to stability and the ability of a system to "bounce back" from disturbances (Hautier et al., 2015; Ives and Carpenter, 2007; McCann, 2000; Mougi and Kondoh, 2012; Tilman and Downing, 1994). That is, greater richness did not necessarily beget greater resilience. This finding contrasts with a pervasive conflation of richness and resilience

(Bellwood and Hughes, 2001; Fischer et al., 2007; Oliver et al., 2015; Standish et al., 2014). As expected, cross-scale diversity exhibited the highest correlation with richness, although its correlation was much less than typical cutoffs for collinearity. Cross-scale resilience metrics also did not predict variability in community composition (standard deviation in species turnover) except weakly at the finest scale. This supports the resilience theory prediction that systems may have low stability (high variance in species turnover) but high resilience (Holling, 1973). Our results also support the contention that the concept of ecological stability is nested within ecological resilience: resilience metrics constrained the magnitude of temporal community fluctuations (mean species turnover) but only weakly predicted variability in community fluctuations—which is the purview of stability theory (Angeler and Allen, 2016; Hautier et al., 2015; Mougi and Kondoh, 2012).

Similarly, resilience theory predicts systems with higher resilience will be more likely to retain similar structures and functions over time, but unlike stability, resilience theory makes few predictions on the maintenance of a particular species assemblage (Allen and Holling, 2010; Bellwood and Hughes, 2001; Gunderson, 2000). Our results support this premise. Cross-scale resilience metrics were not strongly associated with maintenance of a particular group of species. Instead, resilience metrics predicted maintenance of overall community structure per their synchrony with abrupt community shifts across scales. That is, resilience metrics predict significant abrupt community shifts but not community similarity over time (Angeler et al., 2019b). However, higher resilience metrics did weakly predict maintenance of community composition over time as well as constraining mean species turnover which still supports a connection between species composition and resilience.

The cross-scale resilience model differentiates the roles of functional redundancy and functional diversity, and we corroborate this (Bellwood and Hughes, 2001; Elmqvist et al., 2003; Nash et al., 2016; Peterson et al., 1998). For instance, the model predicts losses in critical functions across scaling domains will increase the propensity for ecological regime shifts; but more specifically, redundancy is expected to confer resilience via response diversity (Elmqvist et al., 2003; Walker et al., 1999), while diversity confers resilience via the ability to produce and adapt to novelty (Allen and Holling, 2010; Gunderson and Holling, 2002). And indeed, we show shifts in functional redundancy across scales (cross-scale redundancy) were asynchronous with community-level change, whereas shifts in functional diversity across scales (cross-scale diversity) were synchronous with abrupt community shifts. Thus, tracking changes in functional redundancy could determine system propensity for regime shifts, and tracking functional diversity could identify periods of reorganization during a disturbance that could result in a regime shift. Importantly, the distinction between functional diversity and redundancy manifested in one of the three scales we analyzed. The reason for this is unclear, but because resilience is a scale-dependent property of ecological systems, the scale-dependent behavior of functional redundancy is not unexpected (Gunderson and Holling, 2002; Allen et al., 2005; Allen et al., 2014). Current research on identifying ecologically meaningful scales (e.g., Angeler et al., 2015) and identifying the spatial boundaries of ecological regimes (i.e., spatial regimes; Allen et al., 2016) stand to clarify the scale-specific behaviors of functional redundancy in reflecting resilience.

Because resilience is an emergent property of complex systems, no single metric can encapsulate it (Angeler and Allen, 2016). The peril of developing resilience metrics is reliance on one or a few to measure a given property of interest. For example, within the stability literature, the diversity-stability debate has long been buffeted by waves of interest in one metric (e.g., species richness) or another (functional diversity, phylogenetic diversity, evenness, etc.) as well as conflicting results from the same metric (Hillebrand et al., 2018; Ives and Carpenter, 2007; McCann, 2000). Likewise, within resilience literature, this has played out in the search for univariate generic early warning signals of regime shifts (Burthe et al., 2016; Clements et al., 2015; Van Nes and Scheffer, 2007) and specific distance-to-thresholds for a specified context (i.e. the resilience of what to what) (Carpenter et al., 2001; Groffman et al., 2006). In contrast, the cross-scale resilience model and its metrics require and assume simultaneous consideration of multiple metrics to quantify resilience (Allen et al., 2005; Angeler and Allen, 2016; Sundstrom and Allen, 2014; Sundstrom et al., 2018). We show that individual resilience metrics varied in their relationships with stability and abrupt community shift metrics, meaning each metric reflects unique aspects of system resilience. Thus, our results support considering metrics of resilience from a multivariate perspective.

For resilience theory to progress, it must have measurable and interpretable characteristics (Carpenter et al., 2005; Cumming et al., 2005; Baho et al., 2017). Although we demonstrate the ability of resilience metrics to compare changes in a system's resilience over time, how to compare relative resilience between systems remains unclear. It is not obvious that a system with more body mass aggregations is more resilient than a system with fewer (Allen et al., 2005). Likewise, it is not clear that when resilience erodes and regime shifts occur that the number of body mass aggregations will change; they may simply reorganize around a similar number of scale domains (Angeler et al., 2019b; Gunderson et al., 2012). Also, it is unclear what increases versus decreases in resilience metrics mean for propensity toward regime shifts (Allen et al., 2005; Fischer et al., 2007). This may be a result of the present "relative" nature of resilience metric units. However, the clarity of signal in resilience metrics that we demonstrate (with noisy data spanning half a century and much of a continent) suggest comparable patterns exist, and comparisons can improve if measurements over time provide refined pictures of system resilience (Angeler and Allen, 2016; Baho et al., 2017). This bodes well for the usefulness of resilience metrics in the Anthropocene, where the need for understanding system resilience to change and collapse is only increasing.

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Data availability

The data we used is freely available via the U.S. Geological Survey's North American Breeding Bird Survey and the U.S. Environmental Protection Agency's ecoregion database.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105552.

References

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., Hillebrand, H., 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proc. Natl. Acad. Sci. 108 (41), 17034–17039.

Allen, C.R., Holling, C., 2010. Novelty, adaptive capacity, and resilience. Ecol. Soc. 15 (3).

Allen, C.R., Angeler, D.G., Garmestani, A.S., Gunderson, L.H., Holling, C.S., 2014. Panarchy: Theory and application. Ecosystems 17 (4), 578–589.

Allen, C.R., Garmestani, A., Havlicek, T., Marquet, P.A., Peterson, G., Restrepo, C., Weeks, B., 2006. Patterns in body mass distributions: Sifting among alternative hypotheses. Ecol. Lett. 9 (5), 630–643.

Allen, C.R., Gunderson, L., Johnson, A., 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8 (8), 958.

Allen, C.R., Angeler, D.G., Cumming, G.S., Folke, C., Twidwell, D., Uden, D.R., 2016. Quantifying spatial resilience. J. Appl. Ecol. 53 (3), 625–635.

Angeler, D.G., Allen, C.R., Uden, D.R., Johnson, R.K., 2015. Spatial patterns and functional redundancies in a changing boreal lake landscape. Ecosystems 18 (5), 889–902.

Angeler, D.G., Allen, C.R., 2016. Quantifying resilience. J. Appl. Ecol. 53 (3), 617–624.

Angeler, D.G., Fried-Petersen, H.B., Allen, C.R., Garmestani, A., Twidwell, D., Chuang, W., Wonkka, C.L., 2019a. Adaptive capacity in ecosystems. Resilience Complex Socioecol. Syst. 60, 1.

Angeler, D., Allen, C., Twidwell, D., Winder, M., 2019b. Discontinuity analysis reveals alternative community regimes during phytoplankton succession. Front. Ecol. Evolut. 7, 139.

Baho, D.L., Allen, C.R., Garmestani, A., Fried-Petersen, H., Renes, S.E., Gunderson, L., Angeler, D.G., 2017. A quantitative framework for assessing ecological resilience. Ecol. Soc. 22 (3).

Barichievy, C., Angeler, D.G., Eason, T., Garmestani, A.S., Nash, K.L., Stow, C.A., Allen, C.R., 2018. A method to detect discontinuities in census data. Ecol. Evol. 8 (19), 9614–9623.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292 (5521), 1532–1535.

Bestelmeyer, B.T., Ash, A., Brown, J.R., Densambuu, B., Fernández-Giménez, M., Johanson, J., Shaver, P., 2017. State and transition models: theory, applications, and challenges. In: Rangeland Systems. Springer, Cham, pp. 303–345.

Bouska, K.L., 2018. Discontinuities and functional resilience of large river fish assemblages. Ecosphere 9 (7), e02351.

Briske, D.D., Bestelmeyer, B.T., Stringham, T.K., Shaver, P.L., 2008. Recommendations for development of resilience-based state-and-transition models. Rangeland Ecol. Manage. 61 (4), 359–367.

Burthe, S.J., Henrys, P.A., Mackay, E.B., Spears, B.M., Campbell, R., Carvalho, L., et al., 2016. Do early warning indicators consistently predict nonlinear change in long-term ecological data? J. Appl. Ecol. 53 (3), 666–676.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Wilsey, B.J., 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. Ecology 94 (8), 1697–1707.

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4 (8), 765–781.

Carpenter, S.R., Westley, F., Turner, M.G., 2005. Surrogates for resilience of social–ecological systems. Ecosystems 8 (8), 941–944.

Chillo, V., Anand, M., Ojeda, R.A., 2011. Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. Ecosystems 14 (7), 1168–1177.

Clements, C.F., Drake, J.M., Griffiths, J.I., Ozgul, A., 2015. Factors influencing the detectability of early warning signals of population collapse. Am. Nat. 186 (1), 50–58.

Cumming, G.S., Barnes, G., Perz, S., Schmink, M., Sieving, K.E., Southworth, J., Van Holt, T., 2005. An exploratory framework for the empirical measurement of resilience. Ecosystems 8 (8), 975–987.

Diamond, J.M., 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Natl. Acad. Sci. 64 (1), 57–63.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science 344 (6181), 296–299.

Dunning Jr, J.B., 2007. CRC Handbook of Avian Body Masses. CRC Press.

Ehrlich, P., Dobkin, D.S., Wheye, D., 1988. Birder's Handbook. Schuster, Simon.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. Front. Ecol. Environ. 1 (9), 488–494.

Fischer, J., Lindenmayer, D., Blomberg, S.P., Montague-Drake, R., Felton, A., Stein, J., 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. Ecosystems 10 (6), 964–974.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., et al., 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9 (1), 1–13.

Gunderson, L.H., 2000. Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. 31 (1), 425–439.

Gunderson, L.H., Holling, C.S., 2002. Panarchy: Understanding Transformations in Systems of Humans and Nature. Island Press, Washington, DC.

Gunderson, L.H., Allen, C.R., Holling, C.S., 2012. Foundations of ecological resilience. Island Press.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348 (6232), 336–340.

Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., Striebel, M., 2018. Decomposing multiple dimensions of stability in global change experiments. Ecol. Lett. 21 (1), 21–30.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4 (1), 1–23.

Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. 62 (4), 447–502.

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. Science 317 (5834), 58–62.

McCann, K.S., 2000. The diversity–stability debate. Nature 405 (6783), 228.

Mougi, A., Kondoh, M., 2012. Diversity of interaction types and ecological community stability. Science 337 (6092), 349–351.

Nash, K.L., Allen, C.R., Angeler, D.G., Barichievy, C., Eason, T., Garmestani, A.S., et al., 2014a. Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology 95 (3), 654–667.

Nash, K.L., Allen, C.R., Barichievy, C., Nyström, M., Sundstrom, S., Graham, N.A., 2014b. Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. Oikos 123 (8), 971–983.

Nash, K.L., Graham, N.A., Jennings, S., Wilson, S.K., Bellwood, D.R., 2016. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. J. Appl. Ecol. 53 (3), 646–655.

Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., et al., 2015. Biodiversity and resilience of ecosystem functions. Trends Ecol. Evol. 30 (11), 673–684.

Omernik, J.M., Griffith, G.E., 2014. Ecoregions of the conterminous united states: Evolution of a hierarchical spatial framework. Environ. Manage. 54 (6), 1249–1266.

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1 (1), 6–18.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307 (5949), 321.

Restrepo, C., Renjifo, L.M., Marples, P., 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern and body mass distribution. Trop. Forest Remnants: Ecol., Manage. Conserv. Fragment. Commun. 171–189.

Roberts, C.P., Allen, C.R., Angeler, D.G., Twidwell, D., 2019. Shifting avian spatial regimes in a changing climate. Nat. Clim. Change 9 (7), 562. https://doi.org/10.1038/s41558-019-0517-6.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53 (1), 120–129.

Simpson, G.L., 2018. Modeling palaeoecological time series using generalized additive models. bioRxiv, 322248.

Spanbauer, T.L., Allen, C.R., Angeler, D.G., Eason, T., Fritz, S.C., Garmestani, A.S., Sundstrom, S.M., 2016. Body size distributions signal a regime shift in a lake ecosystem. Proc. R. Soc. B: Biol. Sci. 283 (1833), 20160249.

Standish, R.J., Hobbs, R.J., Mayfield, M.M., Bestelmeyer, B.T., Suding, K.N., Battaglia, L.L., et al., 2014. Resilience in ecology: Abstraction, distraction, or where the action is? Biol. Conserv. 177, 43–51.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Folke, C., 2015. Planetary boundaries: Guiding human development on a changing planet. Science 347 (6223), 1259855.

Stow, C., Allen, C.R., Garmestani, A.S., 2007. Evaluating discontinuities in complex systems: Toward quantitative measures of resilience. Ecol. Soc. 12 (1).

Sundstrom, S.M., Allen, C.R., 2014. Complexity versus certainty in understanding species' declines. Divers. Distrib. 20 (3), 344–355.

Sundstrom, S.M., Allen, C.R., Barichievy, C., 2012. Species, functional groups, and thresholds in ecological resilience. Conserv. Biol. 26 (2), 305–314.

Sundstrom, S.M., Angeler, D.G., Barichievy, C., Eason, T., Garmestani, A., Gunderson, L., et al., 2018. The distribution and role of functional abundance in cross-scale resilience. Ecology 99 (11), 2421–2432.

Tilman, D., 1996. Biodiversity: Population versus ecosystem stability. Ecology 77 (2), 350–363.

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367 (6461), 363.

Van Nes, E.H., Scheffer, M., 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. Am. Nat. 169 (6), 738–747.

Wagg, C., Dudenhöffer, J.-H., Widmer, F., van der Heijden, M.G., 2018. Linking diversity, synchrony and stability in soil microbial communities. Funct. Ecol. 32 (5), 1280–1292.

Walker, B., Kinzig, A., Langridge, J., 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2 (2), 95–113.

Wonkka, C.L., West, J.B., Twidwell, D., Rogers, W.E., 2017. Grass mortality and turnover following core rangeland restoration practices. Rangeland Ecol. Manage. 70 (3), 290–300.

Sauer, J.R., Niven, D.K., Hines, J.E., Ziolkowski, D.J., Pardieck, K.L., Fallon, J.E., Link, W. A., 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD. Retrieved from {https://www.pwrc.usgs.gov/bbs/}.