

Shifting macroecological patterns and static theory failure in a stressed alpine plant community

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Abstract. Accumulating evidence suggests that ecological communities undergoing change in response to either anthropogenic or natural disturbances exhibit macroecological patterns that differ from those observed in similar types of communities in relatively undisturbed sites. In contrast to such cross-site comparisons, however, there are few empirical studies of shifts over time in the shapes of macroecological patterns. Here, we provide a dramatic example of a plant community in which the species–area relationship and the species–abundance distribution change markedly over a period of six years. These patterns increasingly deviate from the predictions of the maximum entropy theory of ecology (METE), which successfully predicts macroecological patterns in relatively static systems. The error in the species–area relationship prediction additionally correlates over time with increased stress measured as mortality minus recruitment, providing a link between demography and the failure of macroecological theory. Information on the dynamic state of an ecosystem inferred from snapshot measurements of macroecological community structure can potentially assist in identifying causes and consequences of disturbance and extending the domain of current theories and models to disturbed ecosystems.

Key words: alpine vegetation; demographic decline; disturbance ecology; drought; ecological theory; maximum entropy; species–abundance distribution; species–area relationship.

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INTRODUCTION

Macroecological models and theories that attempt to predict patterns in the abundance, distribution, and energetics of species often implicitly or explicitly assume that the ecosystem under study is static (Fisher et al. 2010) and thus exhibits patterns that are unchanged from year to year. However, most real ecosystems are not

static in time and disturbance is pervasive (Sousa 1984, Wu and Loucks 1995). It is possible that community-level properties are resistant to disturbance (Supp and Ernest 2014); however, there is a significant amount of evidence from multi-site comparisons that ecosystems undergoing change in response to either anthropogenic or natural disturbance regimes do exhibit macroecological patterns that differ from those observed

in relatively undisturbed sites in similar types of ecosystems (Kempton and Taylor 1974, Carey et al. 2006, Dornelas et al. 2009, Harte 2011, Supp et al. 2012, Mayor et al. 2015, Rominger et al. 2015, Newman et al. 2020). Additionally, the patterns observed at these disturbed sites differ from one another, which could indicate that different types of disturbance produce different deviation patterns. Therefore, understanding how macroecological patterns change over time in response to disturbance can provide useful information for improving models, identifying the drivers of change and relevant mechanistic processes, and forecasting the future state of the system, including identifying warning signs for large-scale ecosystem change (Hill and Hamer 1998, Gaston and Blackburn 2000, Fisher et al. 2010, Turner 2010, Newman 2019).

The maximum entropy theory of ecology (METE) is one such theory that works well for static ecosystems but fails for disturbed ecosystems (Harte 2011). METE is based on an inference procedure derived from information theory and predicts patterns of distribution, abundance, and energetics using instantaneous values of a community's state variables: total area, total abundance, total species richness, and total system metabolism. Numerous examples exist of the success of METE for systems in which the state variables are relatively static, as well as its failures in ecosystems in which state variables are changing in response to disturbance (Harte et al. 2008, 2009, 2013, 2017, Harte 2011, White et al. 2012, Xiao et al. 2015, Newman et al. 2020).

Despite these cross-site comparisons demonstrating METE's failure for disturbed ecosystems, the effect on theory performance of cumulative stress over time at a single site has not been documented. Here, we describe shifting macroecological patterns in an alpine plant community in western Colorado over a study period from 2014 to 2019. In southwestern North America, a region that includes our study site, the period 2000–2018 was the second driest 19-yr period in the past 1200 yr (Williams et al. 2020). This has led to an increase in the frequency of hotter, drier years with low winter snowpack and earlier snowmelt over the last decade (refer to *Discussion* for local estimates). Demographically, the site has had a 10% loss of species, increasing mortality, and declining recruitment rates (see

Results) during the study period, as well as extremely limited soil development, strongly suggesting that this community is stressed and experiencing demographic decline. Together, these site characteristics provide an excellent opportunity to determine how macroecological patterns shift in response to disturbance, link these shifts to demographic change, and document how well METE describes these patterns over time.

MATERIALS AND METHODS

Site and census design

We examine six years of census data from a site on a southeast facing ridgeline with $\sim 20^\circ$ slope, on Mount Baldy, in the Gunnison National Forest of western Colorado (Blonder et al. 2018; Fig. 1). The site contains a sparsely populated alpine plant community with a total of eighteen species in its most species-rich year. In the year with greatest abundance, there was an average of only nine individuals per square meter. For a more complete site description, a species list, and an analysis of the relationships among species traits, individual survival, fecundity, recruitment, and abiotic microenvironmental factors, see Blonder et al. (2018).

The relative sparseness of the vegetation, compared to other alpine plant communities with short growing seasons, is largely due to the substrate, which is composed of exposed and undeveloped rock strata, comprising Mancos Shale (Upper Cretaceous) downslope and quartz



Fig. 1. Study site located on Mount Baldy in the Gunnison National Forest of western Colorado.

monzonite porphyry (Upper Eocene) upslope. Soil across the site consists primarily of ~5–10 cm of fine weathered black scree over bedrock. Snowfall usually begins in October with snow-melt completed in June or July.

The data set used here comprises six years from 2014 to 2019 and derives from a complete annual vegetation census. All individuals including seedlings were recorded and located to the nearest centimeter. The site is partitioned by two-meter-wide corridors into a 5×10 grid with 50 plots, each with dimension two meters by two meters (Appendix S1: Fig. S1). Data are collected annually during peak flowering season in late July or early August of each year. Individuals are considered dead and removed from the census in subsequent years if no above-ground growth was recorded for more than two years or if they germinated and died within the same year. Data and field methods are originally published for 2014–2017 in Blonder et al. (2018) and updated for 2014–2019 in Blonder et al. (2021).

Species–area relationship (SAR)

The SAR describes the dependence of species richness on censused area. A complete nested SAR design is derived by dividing the entire community into disjoint equal-area quadrats and averaging the number of species over all quadrats of equal area. To construct species–area curves, we ignored the corridors between the 50 plots and combined the data into one continuous plot (see *Discussion* for justification). We then resectioned the data into a 32×64 grid, in order to have a sufficient number of either square quadrats or $2^n \times 2^{n-1}$ rectangular quadrats. Both horizontal and vertical orientations were considered for rectangular quadrats by averaging over equal areas (see Data S1).

This design allowed us to study areas of relative size: 32, 64, 128, 256, 512, 1024, and 2048 (32×64), where the smallest scale was set by the requirement that we have at least six species on average at that scale. The criterion of at least six species is based on a necessary requirement for the validity of METE: $\exp(-S) \ll 1$ (Harte 2011). This requirement is also why we were not able to construct 50 separate SARs each year using each of the 50 plots as a study system; the species richness would have been too low within the plots to

be able to examine the SAR across a wide range of spatial scales.

METE predicts that the slope of the species–area curve at a given scale is a function of the ratio of the number of individuals, N , to the number of species, S , at that scale. Hence, if data are plotted as local slope, z , at a given scale vs. the ratio, or log of the ratio, of N to S at that scale, then all SARs are predicted to collapse onto a universal curve (Harte et al. 2009). Thus, we express the SAR by plotting z , the local slope of the species–area curve expressed as $\log(S)$ vs. $\log(A)$, against $\log(N/S)$, where N and S are measured at the same spatial scale at which z is calculated.

To an excellent approximation, METE predicts that the area-dependent slope, $z(A)$, as a function of $N(A)$ and $S(A)$ is given by

$$z(A) \cong \left[\log(2) \log \left(\frac{1}{1 - e^{-\beta(N(A), S(S))}} \right) \right]^{-1} \quad (1)$$

where β is given by the solution to

$$\frac{N(A)}{S(A)} = \frac{\sum_{n=1}^{N(A)} e^{-\beta n}}{\sum_{n=1}^{N(A)} \frac{e^{-\beta n}}{n}} \quad (2)$$

and natural logarithms are used. A more exact form for the METE-predicted slope $z(A)$ in Eq. 1 is given in Harte (2011). Because our average values of N at each scale can be non-integer, β is calculated using linear interpolation between two adjacent integer values.

To calculate the observed slopes of the species–area curve at each area, we used the slope of the straight line connecting the adjacent points on either side, that is, the points corresponding to the next lowest and next highest area in the species–area curve. This is consistent with the way in which Eq. 1 above was derived. This meant we could not calculate observed slopes at the endpoints of our species–area curve, leaving a total of six slopes.

To quantify the change in prediction performance over the years, we compared the mean squared error between the observed and predicted slopes for each year.

$$\text{error} = \frac{1}{K} \sum_{i=1}^K (\text{observed slope}_i - \text{predicted slope}_i)^2 \quad (3)$$

where K , the number of spatial scales where we could predict the slope, is six.

Species-abundance distribution (SAD)

The SAD, $\Phi(n|S, N)$, is the probability that a species has n individuals given that the community has S species and N individuals. The empirical SAD for any community is sparse because a sample will not give data for every abundance ranging from 1 to N . We instead plot rank vs. log(N) distributions, with abundances of each species ranked by decreasing abundance (see Data S1).

METE predicts that the SAD is a log-series distribution given by

$$\Phi(n|S, N) = \frac{e^{-\beta n}}{n \log\left(\frac{1}{1-e^{-\beta}}\right)} \quad (4)$$

where β is given by Eq. 2.

We construct a predicted rank abundance curve from Eq. 4 by computing cumulative probabilities for each n value from the predicted SAD. To assess the fit of predictions, we compute the mean squared error between the predicted and observed rank abundance curves for each of the years. There is a small uncertainty in the way we calculate the predicted rank abundance curve as it could be shifted up or down by half of a rank. Thus, for each S and N value in the data set, we drew 1000 samples from the predicted SAD and rank-ordered each sample to determine how likely the observed rank abundance curve was.

Stress factors

We examined mortality and recruitment to potentially quantify stress over time (see Data S1). Mortality is defined as the number of individuals who died in each year. Mortality data are not available in 2014 and 2019 because the study did not include individuals who died in 2014 and data from 2020 are required to determine which individuals died in 2019. Recruitment, defined as the number of seedlings in each year, was measured in all six years. By fitting linear models to the data, we derived correlations between SAR and SAD error metrics with mortality, recruitment, net loss (the difference between mortality and recruitment), number of individuals, and species richness, and thereby

determined which if any of these metrics might quantify the stress driving changes in the SAR and SAD.

All code was written in Python using standard libraries such as numpy and scipy for analysis and matplotlib for graphs.

RESULTS

SAR

The observed SAR in each of the census years is shown in a graph of local slope, z , vs. $\log(N/S)$ (Fig. 2), where number of individuals, N , and number of species, S , are measured at the same spatial scale at which z is calculated (Eq. 1). On each graph, the METE scale-collapse prediction is shown as well. Note that, because N scales linearly with area in a complete nested design, while S increases less rapidly than linearly with area, larger values of $\log(N/S)$ correspond to larger areas. Appendix S1: Fig. S2 shows the observed species-area curves used to calculate the observed slopes.

In 2014, there is good agreement between theory and observation. In the subsequent years, the slope, z , declines faster than predicted as N/S increases. The deviation between theory and observation is larger at larger area.

The deviation of the observed slope from the METE prediction (Eq. 3) for each year is shown in Fig. 3a. From 2014 to 2018, there is a monotonic increase in that deviation, with a small decrease appearing in 2019.

SAD

The SAD in each of the census years is shown in a graph of $\log(n)$ vs. the rank order of the species (Fig. 4). The rank-ordered observed abundances are shown as dots, and the predicted rank abundance curve is shown as a thick line. The rank-ordered results of 1000 samples from the predicted SAD are shown as thin lines.

As with the SAR findings, agreement between the observed and predicted SADs is best in 2014 (Fig. 3b). In this case, however, we see constant, rather than increasing, disagreement in years 2015–2019.

Stress factor trends

We examined the correlation between our SAR and SAD errors with recruitment, mortality, net

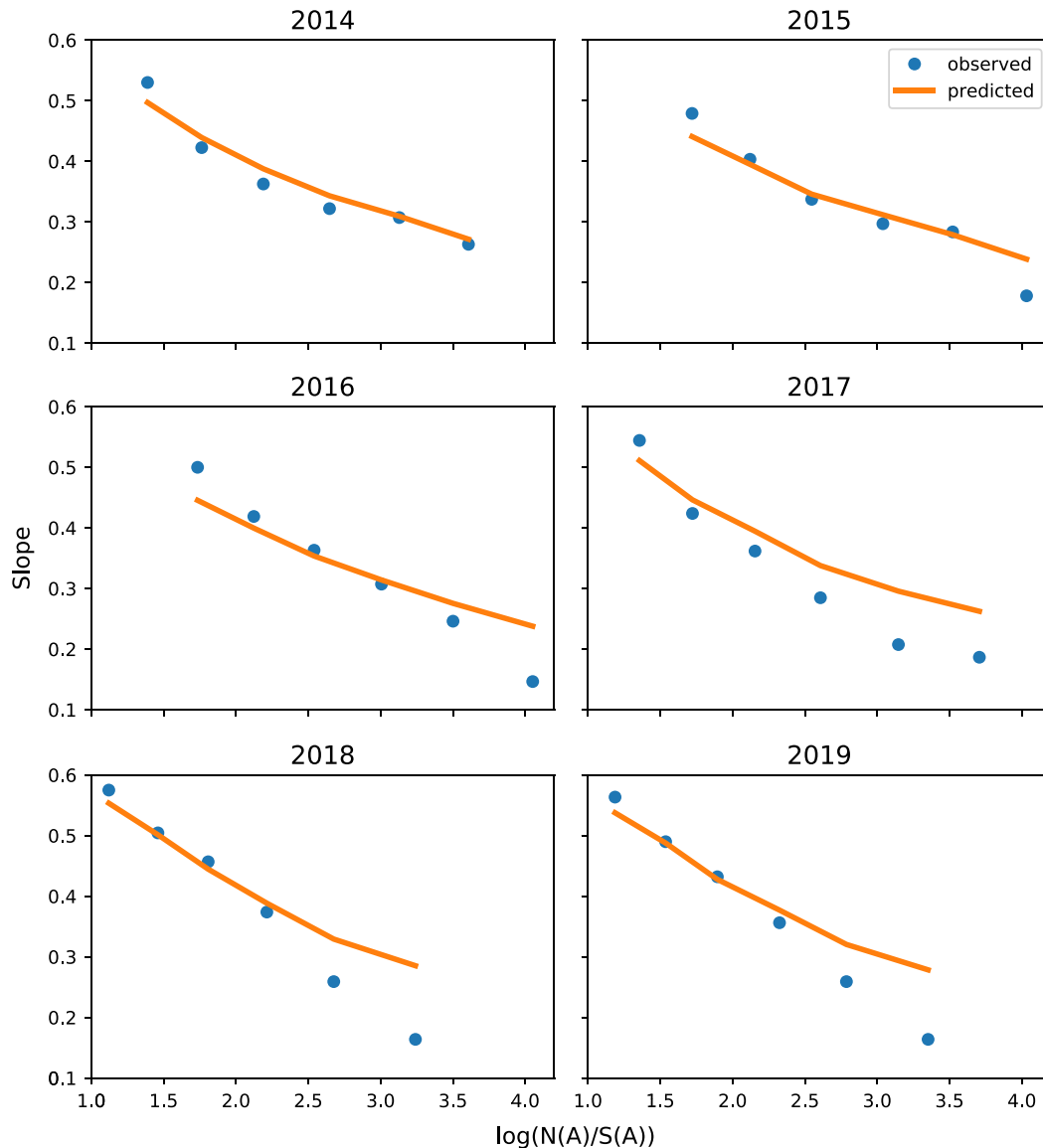


Fig. 2. Comparison of slopes of the observed species–area curves and METE scale-collapse predictions in each of the six years.

loss, number of individuals, and species richness (Fig. 5) over time and report the correlation coefficients of linear fits in Table 1. Appendix S1: Fig. S3 shows the graphs of each of the error stress metric pairs along with their regression lines. The SAR error and net loss appeared to have the strongest relationship (Fig. 6). The SAR error and mortality had a moderately strong relationship, but no other even moderate correlations

were found for the SAR error and none were found for the SAD error.

DISCUSSION

Our analysis showed that the species–area relationship and the species-abundance distribution increasingly deviated from the predictions of METE over a period of six years from 2014 to

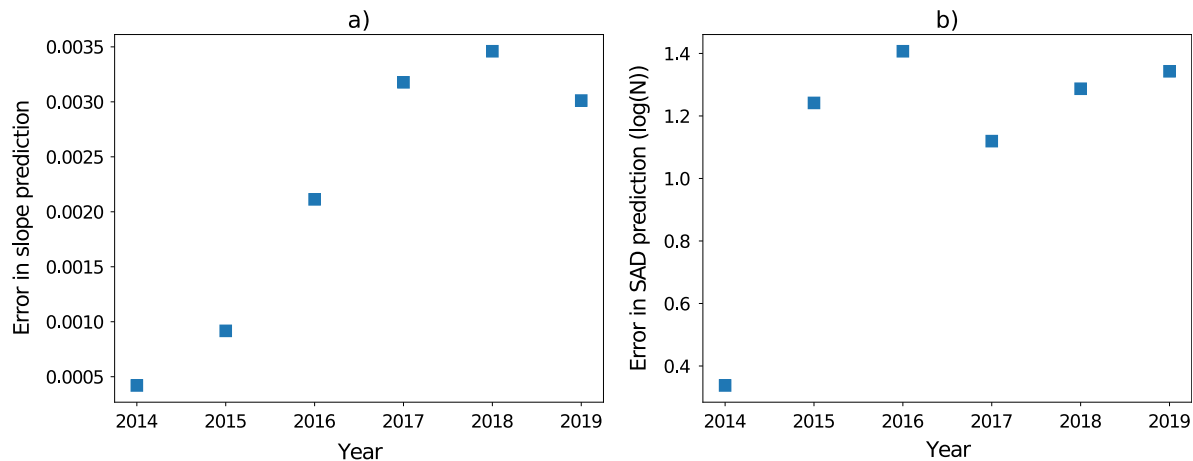


Fig. 3. (a) Mean squared error between the observed and predicted slopes. Initial agreement with METE in 2014 decreases in subsequent years as depicted by the increasing errors. (b) Mean squared error between the observed and predicted rank abundance curves. Agreement with METE in 2014 is followed by consistent disagreement.

2019, in conformity with previous speculation (Harte 2011, Harte and Newman 2014, Newman et al. 2020) that increasing theory failure over time will be observed in ecosystems undergoing change. Our results suggest that the goodness of fit of ecological models may contain useful information on the state of the system that can be applied to forecasting and generalizing ecological models to more dynamic systems.

SAR and SAD results

Over a six-year period, both the observed SAR and the SAD at the field site exhibit a departure over time from METE predictions. The METE-predicted SAR is not a power law; rather, the predicted slope decreases with area. As is evident in Fig. 2, the general pattern of deviation from METE in this study is in the direction of even further deviation from power law behavior, with the slope decreasing more rapidly with scale than METE predicts. This is in contrast with results from another study (Newman et al. 2020) that compared the SAR in two nearby bishop pine forests: one that had recently burned and was undergoing post-fire succession and a mature forest that had not burned in many decades. The mature forest SAR was accurately predicted by Eq. 1, whereas the SAR in the recently burned forest was more consistent with a power law. This informs us that we cannot expect any

simple universality in the pattern of deviation from the static prediction when systems are subject to different types of disturbance regimes. Note that although deviations of predicted from observed SAR slopes by the amounts shown in Fig. 2 are only on the order of 0.1, they are comparable to the discrepancy seen by Newman et al. (2020) in the post-burn bishop pine forest and larger than the averaged discrepancies seen in undisturbed sites (Harte 2011).

The change over time in the SAD, and its pattern of deviation from the METE prediction, is also illuminating. We observed agreement with METE in 2014 followed by poor performance in the following years. On the one hand, a decrease in the number of species with very few individuals was observed. Whereas there were, for example, four species with either one or two individuals in 2014, there was an average of 1.2 such species over the years from 2015 to 2018. Less anticipated was the decrease in abundances of the most abundant species, resulting in a SAD that is not described by the METE-predicted log-series distribution nor by a lognormal distribution. This explains the flatter appearance of the SADs in Fig. 4; on a log abundance vs. rank graph, a flatter curve corresponds to more evenness in the SAD, or in other words, more species having similar abundance and fewer species with extremely high or low

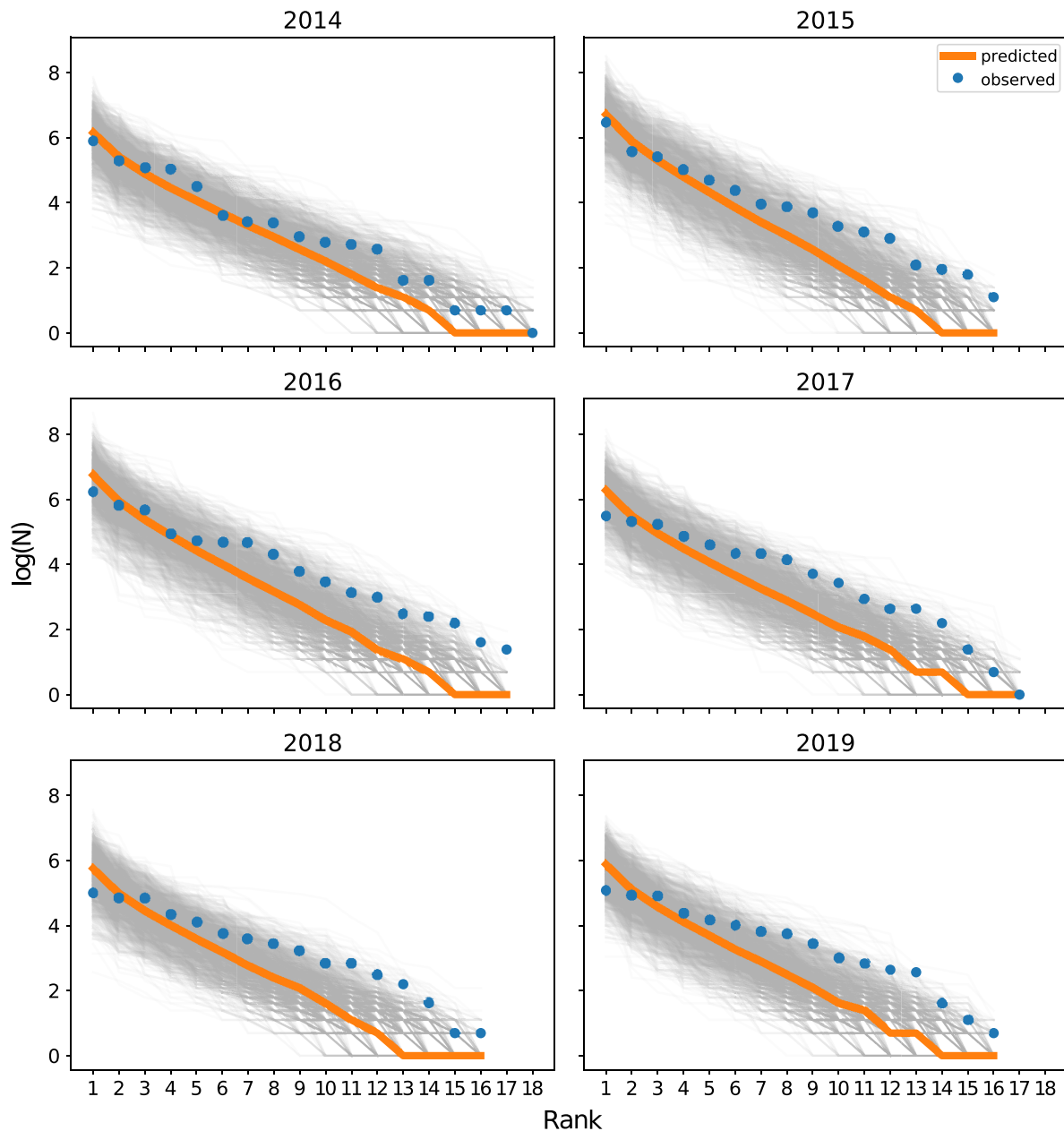


Fig. 4. Comparison of observed and METE-predicted SAD through rank-ordered graphs in each of the six years. The cloud of thin lines represents 1000 rank-ordered random draws from the predicted SAD.

abundance. This appearance of the SADs is more characteristic of an exponential distribution which contrasts with evidence from another study suggesting that disturbance results in a lognormal distribution (Kempton and Taylor 1974). It also contrasts with evidence from the bishop pine study (Newman et al. 2020), which

shows a rank-log(abundance) curve that bows in the opposite direction (i.e., a concave curve) from the SADs in Fig. 4.

Thus, both the SAD and the SAR findings reported here suggest that disturbance can exert different effects on macroecological patterns in different systems. In order to attribute and

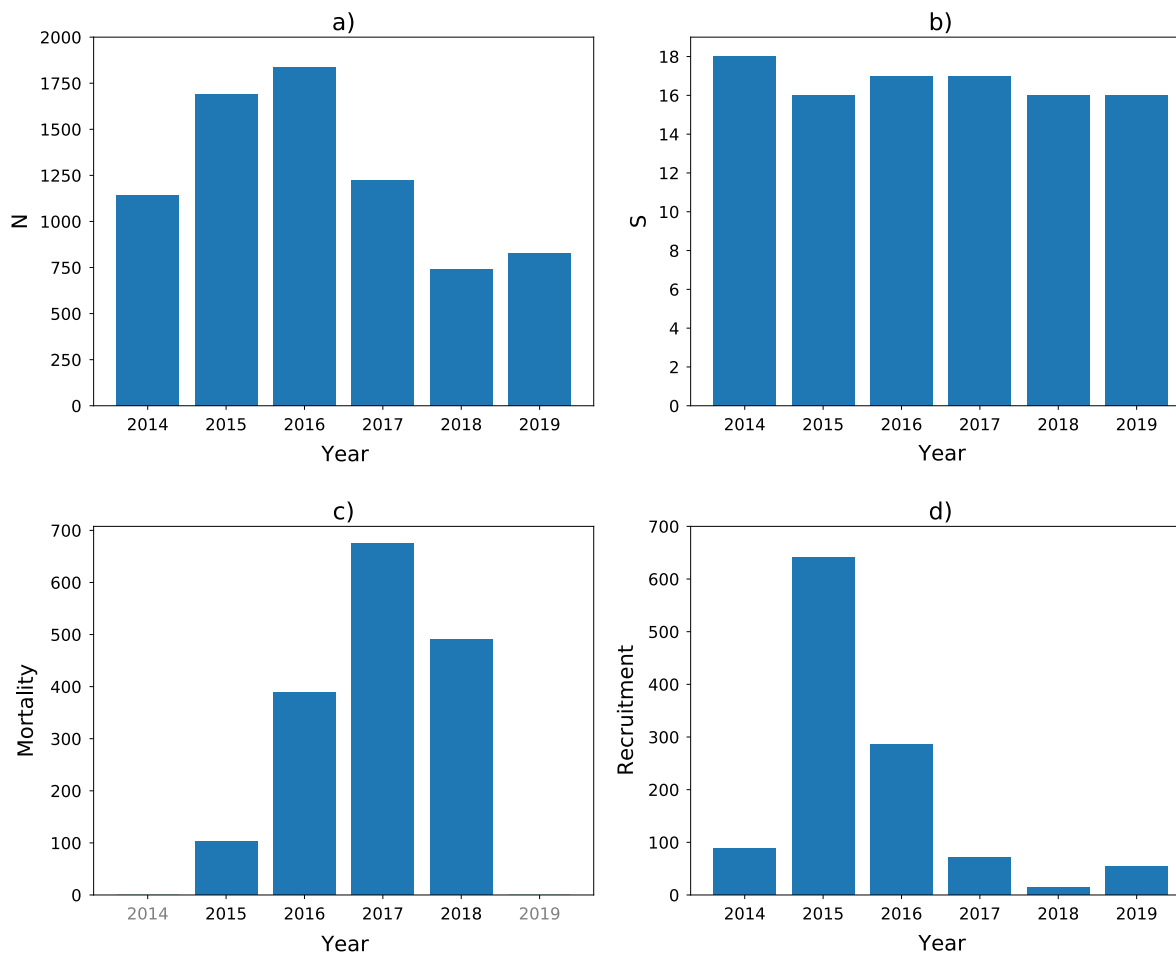


Fig. 5. Abundance, species richness, mortality, and recruitment over time.

Table 1. Correlation coefficients of linear fits on SAR and SAD error vs. abundance, species richness, mortality, and recruitment.

Factor	Correlation	
	With SAR error	With SAD error
Total abundance	−0.51	0.14
Total no. species	−0.50	−0.80
Mortality	0.91	−0.38
Recruitment	−0.56	0.22
Net loss†	0.97	−0.27

† Net loss = mortality – recruitment.

catalog the various patterns that macroecological metrics exhibit under different types of disturbance, further studies comparing the effects of different stressors on similar systems will be required. This would also help develop a more

dynamic theory that can predict such a variety of patterns. While White et al. (2012) looked at the SAD in 15,848 plant, mammal, arthropod, and bird communities and concluded that the log-series outperformed the lognormal, no comprehensive analysis of the relationship between the shape of the SAD, the SAR, and the disturbance level or degree of departure of the ecosystem state variables from steady state has been carried out.

Compressed SAR

In our analysis, we made the choice to ignore the corridors between the 50 plots and compress them into one continuous plot that we then sectioned into quadrats more finely. Consider the difference between what we observed and what would be observed if we had a full data set that

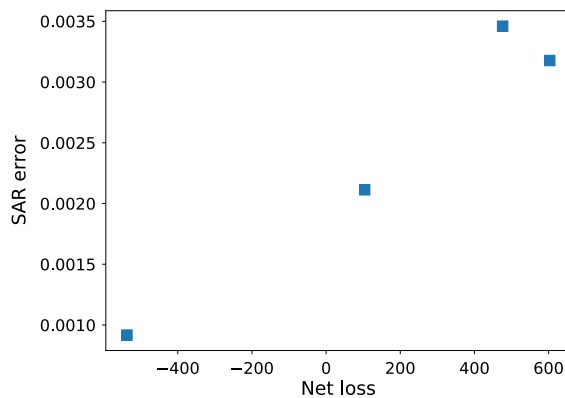


Fig. 6. Plot of SAR error vs. net loss.

included individuals present within the corridors. When we compress the plots as we did, individuals in different plots are brought closer together than they really are in the full data set. Generally, as a consequence of species turnover, the number of species in common between plots decreases as the distance between them increases. Thus, within areas of the same size in the compressed and full data set, we would expect there to be more species in the compressed area since it spans a larger distance. In other words, the observed slopes computed from the compressed data will be higher than in a full data set at corresponding areas. This might appear to introduce an artifact, but in the MaxEnt procedure that METE uses, this will not matter. In particular, MaxEnt predicts the shape of the SAR from the values of state variables (number of species and number of individuals) that impose constraints on information entropy maximization. At the same spatial scale, these state variables will differ between the compressed and full data sets, with number of individuals independent of the compression and number of species increased, at fixed scale, in the compressed data. Because the predicted slopes depend upon the state variables, both they and the observed slopes are changed as a consequence of compression.

If our goal was to predict the slopes for the uncompressed data, this would pose a problem; however, our goal is to study the errors between the METE-predicted slopes and observed slopes over the years. The errors should follow the same trend for the full and compressed data set,

because in the compressed data set, the observed and predicted slopes have both simply been shifted upward and to the left on the plot of $\log(N/S)$ vs. slope, since both slope and S at each scale have increased.

Predicted rank abundance curves

In our analysis, we generated and ranked 1000 samples from the predicted SAD and observed that our predicted rank abundance curve falls roughly in the middle of the samples (Fig. 4). This shows that the method we used to calculate the predicted rank abundance curve from the predicted SAD is reasonable and an appropriate measure to use when computing the errors for the SAD. The samples additionally provide a visualization of how far from METE's prediction the observed data are as many of the points fall outside the range of the samples in every year but 2014.

Demographic evidence for stress

In Rocky Mountain subalpine meadow plant communities, date of snowmelt has been shown to be a useful quantitative measure of drought that is particularly relevant to plant productivity (Harte 2019) and plant flowering phenology (Dunne et al. 2002). Although we lack snowmelt data from our study site, there are multi-decadal melt date data from the Rocky Mountain Biological Laboratory (RMBL) approximately 10 km to the SE (Harte 2019). During the periods 2005–2019, average melt date was 127.7; in 2014, it was calendar day 137.4, which also ranked as the 8th latest melt date in a 29-yr record (Harte 2019). In the four years following 2014, melt date averaged calendar day 122.0. Thus, indirect evidence suggests that in the region, 2014 was a relatively favorable snow year, which would result in less stress from drought than subsequent years during our study period, perhaps explaining the better performance by METE in fitting the SAD and SAR in 2014. However, to identify any trends between stress and the SAD and SAR errors in METE predictions, we represent stress by combinations of mortality and recruitment, as they can serve as more direct evidence of stress on a system.

The stress factors offer insight into the SAR error, but less so into the SAD error (Table 1). In terms of the signs of the correlation coefficients,

we expected recruitment, number of individuals, and species richness to negatively correlate with error because these values tend to be lower in stressed and disturbed systems. Conversely, we expected mortality and net loss to positively correlate with error because these values tend to be higher in stressed and disturbed systems. The signs on the SAR error correlations with recruitment, abundance, and species richness are as expected (-0.56 , -0.51 , and -0.50 , respectively) and similarly for mortality and net loss ($+0.91$ and $+0.97$, respectively). The only even moderately explanatory factor for the SAD error, species richness ($r = -0.80$), also has the expected negative sign. It is interesting to note that the SAR can be derived from the SAD and a spatial function describing species-level aggregation (Harte 2011). Because net loss does not have the expected sign or a strong correlation with the SAD error, either net loss is impacting intraspecific spatial structure or other unidentified stresses are affecting the SAR. In stressful environments, there is evidence that facilitation reduces mortality for clustered individuals (Brooker et al. 2008, Jia et al. 2011), which would lead to a disproportionate number of deaths for unclustered individuals and an increase in overall aggregation. Further work is required to understand how mortality and recruitment affect spatial patterning at this site.

Our findings point to the importance of extending the static MaxEnt-based macroecological theory to the dynamic regime. Under disturbance, individuals of certain species may have different demographic responses, which could shift macroecological patterns away from predictions based purely on information-theoretic ecological theory. Within the framework of METE, disturbances are signaled by time-varying state variables, but it is not yet apparent whether the relationship between shifting state variables and theory failure is the same for natural disturbance regimes and anthropogenic disturbance, even when they both exert an influence on the same demographic variable such as say mortality. By combining the MaxEnt inference procedure with mechanism-based drivers of disturbance, it might be possible to understand how disturbance alters macroecological patterns and conversely how altered patterns allow attribution of stress factors.

CONCLUSION

Observed deviations from static theory predictions in the shapes of macroecological metrics such as the SAD and the SAR have the potential to identify causes of disturbance and to help generalize current static macroecological theories to more dynamic regimes. It remains to be seen whether insight into ecosystem response to disturbance is more readily obtainable from analysis of macroecological metrics or if it is necessary to make more traditional repeated observations on very fine scale, in which the taxonomic identity, location, and traits of the individuals in a plant community, along with local variability in abiotic conditions, are recorded. Based on the clear trends observed in our analysis of the Mt. Baldy data, and the evidence herein that such trends are at least partially specific to different types of disturbance, we conclude that further investigation into shifting macroecological patterns could expedite the effort to better predict ecosystem responses in the Anthropocene.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1000/full>