esa ECOSPHERE

MACROSYSTEMS ECOLOGY

Disturbance macroecology: a comparative study of community structure metrics in a high-severity disturbance regime

ERICA A. NEWMAN,[1,2,]† MARK Q. WILBER,[3] KAREN E. KOPPER,[4] MAX A. MORITZ,[5,6]
DONALD A. FALK,[2] DON MCKENZIE,[7] AND JOHN HARTE[8,9]

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA*
[2]*School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA*
[3]*Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, California 93106 USA*
[4]*North Cascades National Park, 7280 Ranger Station Road, Marblemount, Washington 98267 USA*
[5]*Agriculture and Natural Resources Division, University of California Cooperative Extension, Santa Barbara, California, USA*
[6]*Bren School of Environmental Science and Management, University of California at Santa Barbara, Santa Barbara, California 93106 USA*
[7]*School of Environmental and Forest Sciences, University of Washington, Anderson Hall, Seattle, Washington 98195 USA*
[8]*Department of Environmental Science, Policy, and Management, University of California at Berkeley, 130 Mulford Hall, Berkeley, California 94720 USA*
[9]*Energy and Resources Group, University of California at Berkeley, 310 Barrows Hall, Berkeley, California 94720 USA*

Citation: Newman, E. A., M. Q. Wilber, K. E. Kopper, M. A. Moritz, D. A. Falk, D. McKenzie, and J. Harte. 2020. Disturbance macroecology: a comparative study of community structure metrics in a high-severity disturbance regime. Ecosphere 11(1):e03022. 10.1002/ecs2.3022

Abstract. Macroecological studies have established widespread patterns of species diversity and abundance in ecosystems but have generally restricted their scope to relatively steady-state systems. As a result, how macroecological metrics are expected to scale in ecosystems that experience natural disturbance regimes is unknown. We examine macroecological patterns in a fire-dependent forest of Bishop pine (*Pinus muricata*). We target two different-aged stands in a stand-replacing fire regime: a mature stand with a diverse understory and with no history of major disturbance for at least 40 yr, and one disturbed by a stand-replacing fire 17 yr prior to measurement. We compare properties of these stands with macroecological predictions from the Maximum Entropy Theory of Ecology (METE), an information entropy-based theory that has proven highly successful in predicting macroecological metrics in multiple ecosystems and taxa. Ecological patterns in the mature stand more closely match METE predictions than do data from the more recently disturbed, mid-seral stage stand. This suggests METE's predictions are more robust in late-successional, slowly changing, or steady-state systems than those in rapid flux with respect to species composition, abundances, and organisms' sizes. Our findings highlight the need for a macroecological theory that incorporates natural disturbance, perturbations, and ecological dynamics into its predictive capabilities, because most natural systems are not in a steady state.

Key words: Bishop pine (*Pinus muricata;*) California Floristic Province; closed-cone pine forest; macroecology; Maximum Entropy Theory of Ecology (METE); natural disturbance; species abundance distribution; species–area relationship; wildfire.

Received 20 March 2019; revised 7 October 2019; accepted 16 October 2019. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** newmane@berkeley.edu

INTRODUCTION

Disturbance is pervasive in ecosystems, and it influences patterns of species diversity, abundance, and community membership over space and through time (Turner 1989, Wu and Loucks 1995). However, macroecology, the discipline concerned with large-scale patterns of diversity, has generally avoided studies of disturbed systems for two reasons: First, disturbed systems are perceived as being in transition and unlikely to produce replicable, generalizable results, and second, assumptions of steady-state, equilibrium and stabilizing mechanisms in macroecological theory are common and often required in order to solve equations (Hubbell 2001). Macroecology has instead focused primarily on ecosystems that are perceived to be relatively stable (Fisher et al. 2010), in that they exhibit low variance in community structure through time (Turner et al. 1993). Disturbed ecosystems—and patches within ecosystems—are often in flux with respect to species composition and richness, species–area relationships (SARs), distribution of abundances across species, and body sizes, and intraspecific spatial distributions of individuals. This is true of ecosystems that have recently undergone, or are continuing to undergo, natural disturbances (those that are part of a repeating disturbance regime, sensu Turner 2010), anthropogenic changes, and other ecological disruptions. Although ecosystems in steady-state, even at the local scale, are relatively rare (Sousa 1984, Wu and Loucks 1995), standard macroecological study systems are often chosen specifically because they are in or near steady states (*e.g.*, most of the Center for Tropical Forest Science plots represent late-successional, primary forest; Condit 1998, : Chapter 1) and therefore do not consider the dynamics of disturbed sites or entire disturbance regimes. Natural disturbances have both large- and small-scale structuring effects in all ecosystems (Turner 1989, Hamer and Hill 2000), but we are not aware of any macroecological study that has addressed how metrics of biodiversity and abundance scale in disturbance-dependent ecosystems.

Macroecologists have invoked disturbance broadly (including human activities, environmental variability, invasive species, and so on) as a factor responsible for deviations from theoretical predictions or expected patterns (Dornelas 2010), but it remains unclear whether macroecological patterns reported across ecosystems are properties of all ecological systems, or only of undisturbed, steady-state communities. Because non-steady-state systems are so pervasive and widespread (Sousa 1984, Wu and Loucks 1995), the failure to incorporate disturbance into macroecology poses a major challenge to the utility of this field in understanding ecological dynamics as well as global change. Synthesizing a "macroecology of disturbance" that incorporates quantitative macroecological metrics could have considerable benefits for conservation efforts, given that many ecosystems with active disturbance regimes (and the species that have evolved in them) rank among the most globally endangered (Noss et al. 1995, Turner 2010, Schlossberg and King 2015). Distinguishing the effects of natural disturbances from those of anthropogenic changes is also important for predicting future states of ecosystems.

Here, we will restrict the use of the term disturbance to refer to natural disturbances, which satisfy the following four characteristics: (1) They cause mortality of individual organisms in a community; (2) however, they do not cause mortality of all individuals in the community or metacommunity and therefore do not result exclusively in primary succession; (3) they are part of a historical and repeating disturbance regime (Turner 2010) with well-defined characteristics (Pickett and White 1985, Turner et al. 1998, Turner 2010); and (4) the disturbance is absolute rather than relative (Pickett and White 1985) in that each disturbance event is "a relatively discrete event in time that disrupts the ecosystem, community or population structure and changes the resources, substrate availability or physical environment" (Pickett and White 1985, White and Jentsch 2001). This strict operational definition of disturbance as synonymous with natural disturbance is consistent with its usage in several influential reviews of disturbance ecology (Pickett and White 1985, White and Jentsch 2001, Turner 2010). We differentiate (natural) disturbances from ecological perturbations and disruptions, which will refer to other processes that restructure an ecological community, including events that are natural in origin but are not part of historical, repeating disturbance regimes (*e.g.*, landslides, extremely rare weather events), and those that are novel and may be anthropogenic in origin (*e.g.*, human impacts). A lava flow or landslide that kills or physically removes all plant individuals in the community and results in primary succession would therefore not be a disturbance, but rather a perturbation, disruption, or catastrophe under our definition (criterion 2). We note that properties (1) and (2) are scale-dependent.

Past macroecological work that incorporates ecological disturbances of any type focused predominantly on their effects on the shape of the species abundance distribution (SAD; see Appendix S1 for acronyms used in this paper). Although the SAD is well studied (reviewed in McGill et al. 2007, White et al. 2012, Baldridge et al. 2016), the underlying shape of a natural or generic SAD is debated (see for example Hill et al. 1995, Hill and Hamer 1998, Nummelin 1998, Ulrich et al. 2010), and various distributions have been proposed, with mixed empirical support for each. For the rank-abundance form of the SAD, a lognormal distribution is reported from many steady-state systems (Whittaker 1965, May 1975, Gray 1981, Ulrich et al. 2010), whereas other studies (Kempton and Taylor 1974, Dennis and Patil 1979), including big data approaches, suggest that the log-series distribution may be the most common across systems and taxa (White et al. 2012, Baldridge et al. 2016), and one study suggests the prevalence of the double geometric distribution (Alroy 2015). One-time ecological perturbations are often invoked as responsible for a lognormal SAD (Kempton and Taylor 1974, Bazzaz 1975, Death 1996, Hill and Hamer 1998, Newman et al. 2014). Work focusing on succession suggests a transition in the shape of the SAD from geometric in early successional stages to lognormal and subsequently log series in later stages (Bazzaz 1975, Whittaker 1975). Kempton and Taylor (1974) show in a comparative study that moth communities in undisturbed plots sites in the Rothamsted Insect Survey in England are best modeled by log-series SADs, and plots recovering from agricultural activity have lognormal SADs. Certain ecological factors, sampling methods (Ulrich et al. 2010), detection issues (Tokeshi 1993), and mathematical processes (based on the central limit theorem) may also produce the lognormal (Tokeshi 1993). Other macroecological metrics are less well studied in the context of ecological disturbance or disruption, although the SAR has been examined experimentally with removal of seed predators (Supp et al. 2012), and the effects of ecological perturbations are beginning to be investigated in an increasingly macroecological framework (Supp and Ernest 2014, Mayor et al. 2015).

The Maximum Information Entropy Theory of Ecology (METE) is a macroecological theory (described in Harte et al. 2008, 2009, Harte 2011, Harte and Newman 2014, Brummer and Newman 2019) that provides a statistical framework for linking related metrics (McGill 2010) that are often otherwise considered in isolation: the SAR, the SAD, the species-level spatial abundance distributions (SSADs; a metric quantifying the spatial distribution or clumping of individuals in a species over a given area), and the z-D universal scale collapse relationship, which relates the local slope of the SAR to the ratio of abundance to species richness at that scale (Wilber et al. 2015). Maximum Entropy Theory of Ecology relies on maximum information entropy inference (MaxEnt) to predict least-biased probability distributions, given empirical constraints (Jaynes 1982), but invokes no explicit physical or ecological mechanisms (Harte 2011, Harte and Newman 2014). An application of the MaxEnt procedure, the ASNE version of METE (Harte and Newman 2014), uses only the relationships between four non-adjustable state variables that take on values from the system being measured: A_0 (total area under consideration), S_0 (total species), N_0 (total abundance), and E_0 (total metabolic energy). The state variables are static, not dynamic in this formulation, and there are no adjustable parameters characterizing the scaling of species diversity, abundances, and energetics in a system. Mathematical forms of empirical constraints arise from ratios of the state variables.

Empirical tests of METE strongly support its core predictions, including the SAR and SAD (Harte et al. 2008, 2009, White et al. 2012, McGlinn et al. 2013), SSADs (Harte 2011), and certain metabolic predictions (Newman et al. 2014, Xiao et al. 2015), but some spatial distribution and metabolic predictions are not supported (see McGlinn et al. 2015, Newman et al. 2014, Xiao et al. 2015). METE has accurately predicted the SAR, SAD, and SSAD for a range of natural communities spanning different taxa and biomes, including herbaceous plants, trees, vertebrates, and invertebrates, and in temperate, tropical, and montane environments, as well as isolated island communities (Harte et al. 2008, 2009, Harte 2011, Rominger et al. 2016). Maximum Entropy Theory of Ecology also applies in communities where not all of the biodiversity has been sampled and only a focal community is modeled (Harte et al. 2013; Appendix S2). This study represents the first assessment of these common macroecological metrics for a plant community in a high-severity natural disturbance regime.

Applying METE to ecosystems in transition

In this study, we apply METE to an episodically disturbed ecosystem to test how well various macroecological metrics describe community structure at the stand level (specifically the SAR and the related z-D curve, SAD, and SSADs), whether or not there are departures from theoretical predictions, and whether those departures are systematic with disturbance. We compare a forest stand that has undergone a major disturbance (stand-replacing wildfire 17 yr previously) in Bishop pine forests and for a nearby, mature stand in the same disturbance regime (Brown et al. 1999) at Point Reyes National Seashore (PRNS) in California, USA. We hypothesize that the METE will predict these community structure metrics more accurately in the more mature plot (Mount Vision) because it has had a longer time since disturbance to reach steady-state dynamics, and METE's predictions will be less accurate for the more recently disturbed, mid-seral stage plot (Bayview). While the mid-seral stage plot is past the early successional stage of high and rapidly changing diversity (Ornduff and Norris 1997, Ornduff 1998), it remains an unusual example of forest structure and dynamics because of its dense, uniform size structure and arrangement of trees, which undergo density-dependent mortality (Harvey and Holzman 2014). These factors affect macroecological state variables and their ratios in a predictable manner. If departures of data from theory appear to be coherent in the mid-seral stage plot, it may be possible to identify the influence of disturbance on macroecological patterns, and we may extend these analyses to a broad range of ecosystem types in future work.

As applied here, METE might accurately capture snapshots of rapidly changing ecosystems at an instant in time, and the predictions of the ASNE version of METE are static and instantaneous. Here, we used separate plots with differing disturbance histories to capture the macroecological patterns that characterize live, aboveground plant communities within separate patches in a disturbed landscape. We hypothesize that any of METE's individual predictions might not work for one or both of the different-aged plots, which would mean that the theory's four state variables do not contain adequate information to constrain the predicted distribution in question to the empirical distribution. A signature of disturbance may emerge in the SAR, z-D relationship, SAD, or SSADs if any of these metrics fail individually, or fail in some combination consistently across other disturbed ecosystems. We expect that if SADs are more uneven and there is increased variation in aggregation measured by SSADs across species, we can also expect approximate power law behavior in the SAR (Wilber et al. 2015). More specifically, with a lognormal SAD and a Poisson distribution for the SSAD, Preston's analysis (1948) indicates that we would see a power law SAR in the mid-seral stage plot.

Because METE is constrained to predict the maximum information entropy distributions only, the functional forms are fixed after the state variables are specified. Failures of METE to predict ecological metrics accurately in rapidly changing ecosystems would indicate the need to modify the theory to information that captures specific ecological processes. Alternately, if an information entropy-based theory of macroecology (METE) performs equally well for both the mature and disturbed plots, we would have supporting evidence that the information contained in the four state variables that constrain the predicted distributions is sufficient to describe general patterns in ecosystems, regardless of their disturbance status. This would suggest that METE's successes are independent of the disturbance history of an ecosystem, and its predictions may be generalizable across ecosystems in any successional state.

Materials and Methods

Bishop pines: a forest type that experiences natural disturbance

This study focuses on Bishop pine (*Pinus muricata* D. Don) forest stands and their associated plant communities, which exhibit an unusual natural history of disturbance-mediated stand replacement. Bishop pine is endemic to the California Floristic Province in North America and has a patchy distribution along the coast of California, USA, and Baja California, Mexico, including the California Channel Islands (Millar 1983, 1986, Little 1971, Stephens and Libby 2006; Fig. 1). Mature stands (~40–120 yr old) may have individuals that are widely spaced and a moderately diverse understory of forbs and shrubs. The species produces serotinous cones that remain on

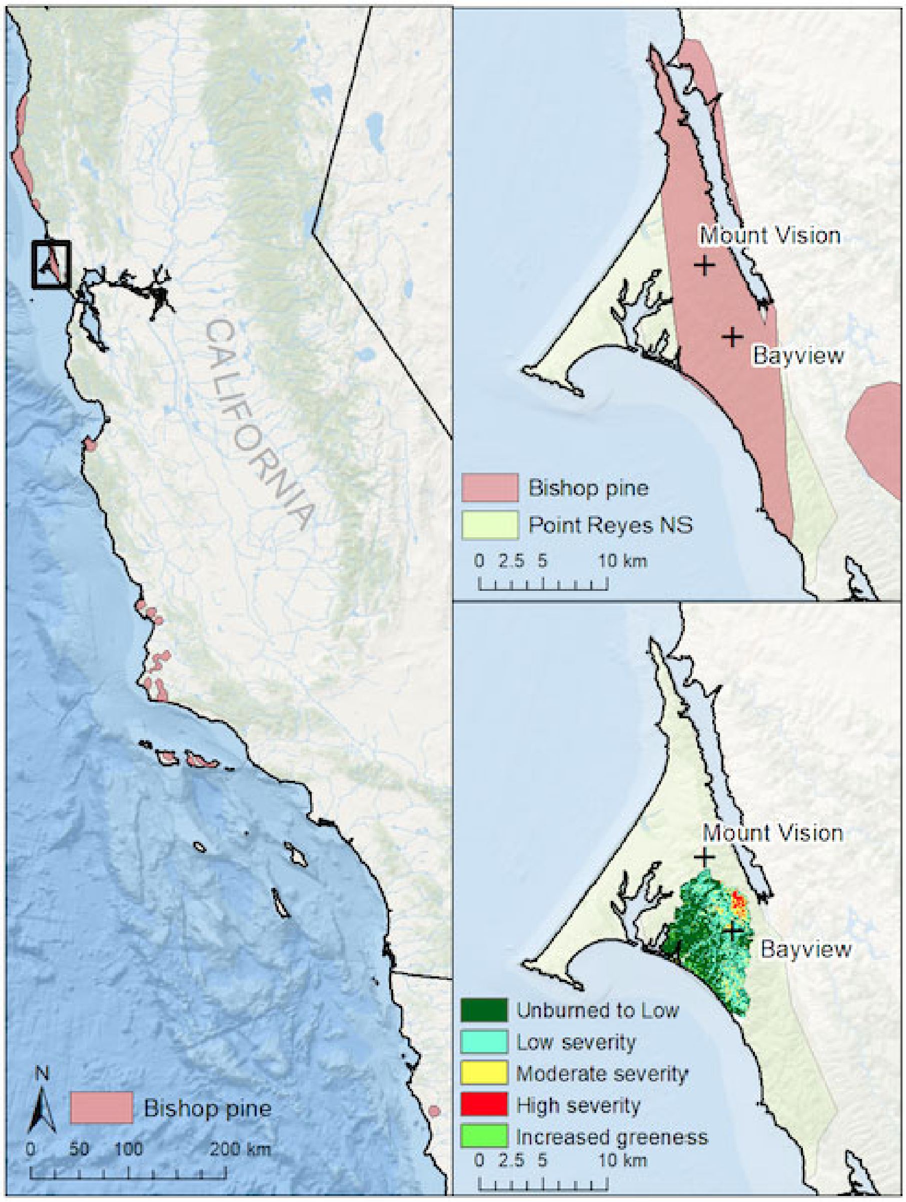

Fig. 1. Map of Point Reyes National Seashore region in central coastal California, USA, showing study plot location and local distribution of Bishop Pines.

the tree until exposed to fire, which causes them to release a large crop of seeds over a short period of time. In the first few years of succession, rapid changes in species composition and structure are observed, and stands generally exhibit high species diversity (Ornduff and Norris 1997, Ornduff 1998, Harvey and Holzman 2014, Harvey et al. 2014). Mid-sere, stand-replacing fires cause regeneration of the Bishop pines into a uniform age and size-class, a dog-hair forest that is nearly a monoculture with almost no understory, in which the dynamics of the stand are dominated by density-dependent mortality (Harvey and Holzman 2014). Over time, the dense forest structure that undergoes this self-thinning process becomes a more open, lower-density and higher diversity stand (Harvey et al. 2011, Harvey and Holzman 2014). In our study, we focus on one mature stand of trees and one mid-seral stage stand with extremely high tree density within the post-fire site.

Wildfire records and records of management have been maintained by PRNS since the establishment of the park in 1962. Brown et al. (1999) documented relatively frequent wildfires (every 8–9 yr, on average) from the 1700s through 1945 for Olema Valley and general Point Reyes area, including four large fires in the early 20th century (1904, 1906, 1923, and 1945). Of these, we believe the 1923 fire is the most likely to have affected our study sites. These fires are thought to be human-caused, and low-severity rather than stand replacing. In October 1995, the Vision Fire, a high-severity (large, infrequent) wildfire, burned 12,354 acres (5000 ha, or 50 km^2) within the Point Reyes National Park unit (National Park Service 2005). Our study targets areas within and outside of the post-fire landscape.

Site descriptions

Field sites were chosen within the boundaries of PRNS, on the Pacific coast of California, USA, ~50 km northwest of San Francisco. According to data from 1964 to 2012, PRNS experiences a Mediterranean-type climate, with mild winters and cool summers (with most of the ~100 cm annual rainfall occurring in winter, and a substantial amount of moisture received from fog drip in the summers; Dawson 1998, Forrestel et al. 2015).

We placed 256-m^2 study plots in two Bishop pine (*P. muricata*) stands and censused each for all aboveground, live vascular plants ≥1 cm in height in April 2012 (Table 1). The higher elevation Bayview plot at 252 m (825 ft) elevation was placed in an area of PRNS that burned in the 1995 Vision Fire and was previously a Bishop pine-dominated area (known to influence patterns of succession; Harvey et al. 2011, Harvey and Holzman 2014). The Bayview plot is a dog-hair type stand of thin, closely growing trees, in which the ages of the Bishop Pines are uniform, and the understory is sparse (Fig. 2). The slightly lower-elevation Mount Vision plot was located at 213 m (698 ft), 6.1 km (~3.8 mi) away from Bayview, in a mature Bishop pine stand with a more diverse and lush understory (Fig. 2). At each site, all individual live plants counted with double-

Table 1. Locations and other descriptive metrics for research plots used in this study.

Site name	Bayview	Mount vision
Latitude/longitude	38.05936°, −122.85071° (±3.6 m)	38.10283°, −122.89338° (±1.8 m)
Elevation	251.5 m (825 ft)	212.8 m (698 ft)
Time since major disturbance	17 yr	No recorded disturbance history since 1923, although maximum estimated tree age is 48 yr
Slope, aspect	0%, S	62.5%, NE
Tree density/ha	5780 stems/ha	550 stems/ha
Total basal area	48.6 m^2/ha	71.9 m^2/ha
Trees cored (total cores obtained)	4; (6)	13; (14)
PRNS catalog numbers	PORE 18080 through PORE 18083; PRNS Accession number: PORE-00866	PORE 18084 through PORE 18096; PRNS Accession number: PORE-00866
Total species (S_0)	16	27
Total abundance (N_0)	486	1844
Total area (A_0)	256 m^2	256 m^2

Note: PRNS, Point Reyes National Seashore.

Fig. 2. Photographs of (a) interior of mature Bishop pine stand at Mount Vision site, and (b) side view of mature stand; (c) interior view of Bishop pine stand that burned in the 1995 Vision Fire at Bayview plot, and (d) exterior view of stand structure 17 yr after the Vision Fire.

observers, and each plant's spatial location in the sampling grid was recorded with a cell number representing a 1-m^2 subdivision of the larger plot. Plants were identified to species in the field when possible using the Jepson Manual (Baldwin et al. 2012) and other field guides for the local region (Keator and Heady 1981, Howell et al. 2007); or otherwise assigned to morphospecies (plants with a large number of shared characteristics that were given a unique species identifier for analysis with reference notes and photographs). METE's predictions are robust to the lumping or splitting of species, provided that such decisions are made consistently (Harte et al. 2013).

Patterns of fire severity leading to landscape heterogeneity are described in Forrestel et al. (2011), which focused on vegetation succession and Bishop pine communities following the October 1995 Vision Fire. Forrestel et al. found that Bishop pines increased in extent by 85% within the park and had an altered spatial distribution following this high-severity, stand-replacing fire. Species compositions between plots cannot be considered different stages of the same successional trajectory due to beta diversity (Harvey and Holzman 2014), but the post-Vision Fire site lacks the well-developed understory common to mature stands, and is considered in a state of ongoing succession for our purposes.

We believe that the disturbance history of the sites is responsible for generating the macroecological patterns of interest, because the diverse, open understory mature forests only exist outside the fire-affected area, whereas within the boundaries of the Vision fire, all Bishop pine stands have the dog-hair, dense, and low-diversity structure. As we are interested primarily in species richness, abundance structures, and spatial clustering of species (that is, ratios of S_0 to A_0, and of N_0 and S_0, and relationships between the total abundance of a given species and A_0), it is clear that the disturbance history is the primary reason for the differences between sites.

Establishing disturbance histories

Four and 13 live trees were cored at Bayview and Mount Vision sites, respectively, using increment borers (Haglöf Sweden). Cores ages were estimated using an age–height correction (Appendix S3), for all cored trees in each plot. Results were corroborated with aerial photographs of this area in the PRNS archive. We examined land-use history records (including aerial photographs, contemporary accounts, historical ranch maps, and post-wildfire incident records) in the archives at PRNS, in consultation with National Park Service archival staff. Other fire records examined include CALFIRE's Department of Forestry and Fire Protection FRAP Fire Perimeters (available online at http://frap.cdf.ca.gov/data).

The maximum information entropy approach

Plant census data from multiple plots within the PRNS Bishop pine community were used to test METE predictions for the SAR and the related z-D universal scale collapse relationship, a Fisher log-series SAD, and a geometric distribution for each SSADs. Shannon information entropy is maximized with respect to two predetermined constraints, which are the ratios of state variables (Brummer and Newman 2019). Solutions to information entropy maximization take the form of the Lagrange multipliers λ_1 and λ_2, and these values capture information from the empirical system and are used in throughout METE's predicted metrics. Here, $\lambda_1 = \beta\text{-}\lambda_2$ and $\lambda_2 = S_0/(E_0{-}N_0)$; and β satisfies the approximate relationship:

$$\beta \ln\left(\frac{1}{1-e^{-\beta}}\right) \approx \frac{S_0}{N_0} \qquad (1)$$

Additional information on METE's predicted distributions is available in Appendix S4.

For SAR and z-D scale collapse model comparisons, we compare models with R^2 values derived from one-to-one predicted vs. observed graphs (White et al. 2012: Appendix A), because no method is available to generate likelihood functions required for Akaike's information criterion (AIC) comparisons. For comparison to the commonly used power law SAR (Brown et al. 2002, White et al. 2008), best-fit power laws were calculated from the SAR data for each site and applied to the SAR and z-D graphs. If the SAD is uneven and there is increased variation in aggregation in the SSAD across species, approximate power law behavior is expected in the SAR (Wilber et al. 2015). Models for SADs and SSADs were generated and compared to candidate distributions using Akaike's information criterion value corrected for small sample sizes (AICc).

Macroecological analyses were carried out in Python (van Rossum and Drake 2001) with the open-source software macroeco (Kitzes et al. 2014, Kitzes and Wilber 2016). Although *macroeco* is programmable through a stand-alone graphical user interface, Python code can be used to reproduce analyses as well and is presented here with data from this study in Data S1. SAR, SAD, and SSAD scripts were available from the beta version of this software (accessed June 2015). Other analyses were carried out in R versions 3.0.1 and 3.1.1 (R Core Team 2013–2015).

RESULTS

Summary statistics and calculated parameters

A total of 2330 individual plants in 32 species were censused across the two study plots. Species richness and abundances differed greatly between the plots (Table 1; Appendix S5). The Bayview plot, which burned in 1995, was surveyed at 17 yr after the Vision Fire and contained 16 species and a total of 486 individuals (148 of which were Bishop pines). Six tree cores had estimated ages from 11 to 16 yr (mean = 15.2 yr, mode = 16 yr). Density of Bishop pines in this plot was measured to be 0.578 trees/m^2 (or 5780 stems/ha). The Mount Vision plot contained 27 species and 1844 individuals total (14 of which were Bishop pines). Bishop pine density in this plot measured 0.055 trees/m^2 (or 550 stems/ha), including the very few seedling trees in the plot. Live tree density estimates are consistent with estimates from other studies (Harvey et al. 2011, 2014). Trees varied in age from an estimated 40–48 yr old (mean = 43.5 yr, mode = 41 yr, which implies that some management, grazing, or logging activity was not recorded in the PRNS archives). In both plots, Bishop pines were the only tree in the overstory and were the largest plants in each plot by estimated biomass. See Appendix S5 for species observed in each plot, and other supporting analyses.

For comparison to METE-predicted metrics, we calculated the value of the parameter $\beta = 6.515 \times 10^{-3}$ for the Bayview plot for the measured values $N_0 = 486$, $S_0 = 16$, and

$\beta = 2.429 \times 10^{-3}$ for the Mount Vision plot, with measured values $N_0 = 1844$, $S_0 = 27$. The values for the Lagrange multipliers λ_1 and λ_2 are not independently calculable because state variable E_0 was not measured for either plot.

Species–area relationship and scale collapse

Generally, the METE prediction for the SAR appears to be a good fit for both data sets, whereas the z-D (scale collapse) graphs show more deviation from the METE prediction for the mid-seral stage Bayview plot (Fig. 3). To determine the best model fits for the SAR, comparisons of R^2 values on a one-to-one line for predicted vs. observed distributions (White et al. 2012) were carried out for both the Bayview and Mount Vision plots. Best-fit power laws were plotted on SAR and z-D graphs (Fig. 3 a-b, d-e). R^2 values on ranked data are generally always high. R^2 values for the mature Mount Vision plot support METE's predicted SAR over the best-fit power law predictions ($R^2_{\mathrm{METE}} = 0.991$; $R^2_{\mathrm{PowerLaw}} = 0.989$), whereas the power law fit is a better fit for the mid-seral stage Bayview plot

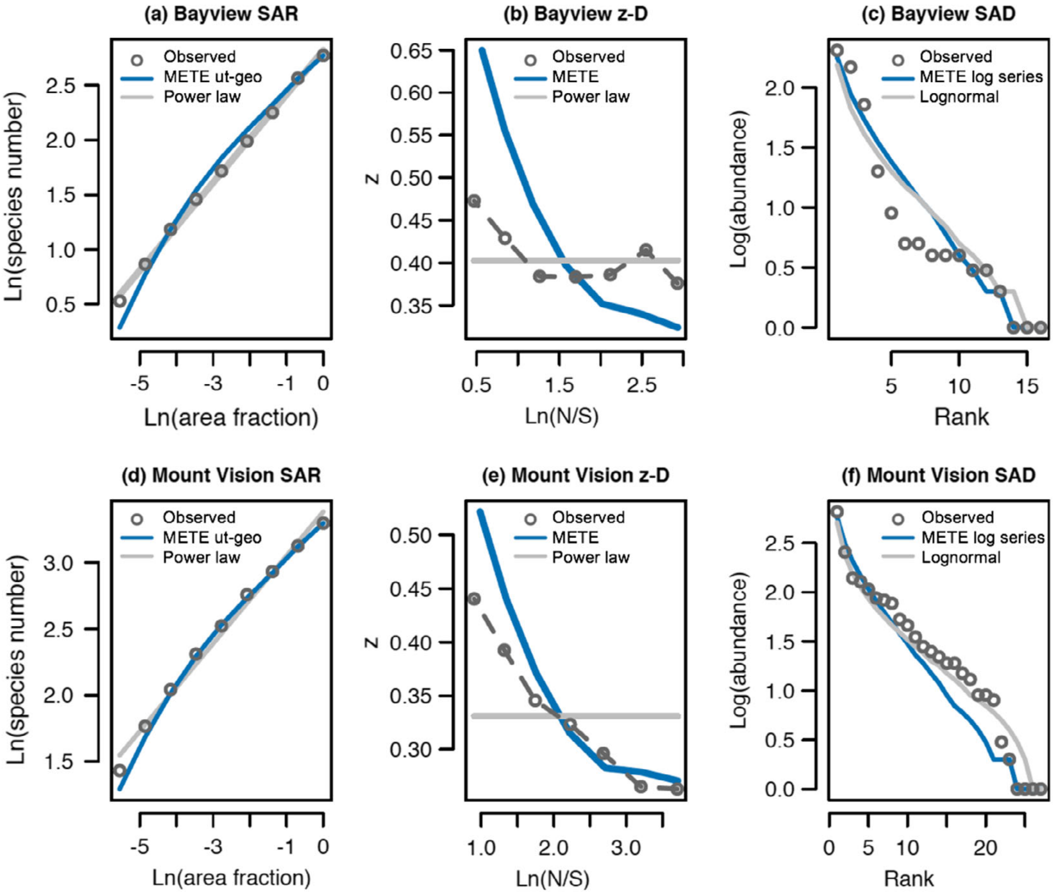

Fig. 3. Species–area relationships (SARs), z-D universal scale collapse graphs, and species abundance distributions (SADs) for the mid-seral stage Bayview plot (a, b, and c, respectively), and for the mature Mount Vision plot (d, e, and f, respectively). For the SARs, empirical data are shown against the Maximum Entropy Theory of Ecology (METE) upper-truncated geometric (ut-geo) prediction, and the best-fit power law for comparison. Universal scale collapse graphs, with METE-predicted and observed values, illustrated at scales of N/S (total abundance/total species) on a log scale for each plot. The best-fit power law is shown again for comparison. Empirical and METE-predicted ranked species abundance distributions (SADs) are shown against lognormal distributions for comparison.

($R^2_{\mathrm{METE}} = 0.977$; $R^2_{\mathrm{PowerLaw}} = 0.998$) on a ln-ln graph. The deviations in model fits to data are clearer in the z-D graphs, confirming the better fit of the METE-predicted distribution over the best-fit power law for the mature plot, and a more power law-like fit for the more recently disturbed, mid-seral stage Bayview plot.

Species abundance distribution

Model selection comparing AICc values for both the Bayview and Mount Vision plots in both cases support the METE-predicted log-series distribution over the lognormal distribution (Table 2) that is often associated with disrupted or perturbed systems. ΔAICc = 5.149 between the models for Bayview, and ΔAICc = 3.717 for Mount Vision. On visual inspection of the SAD graphs (Fig. 3 c, f), there is the pattern of suppression of mid-abundance species in the Bayview plot that may be characteristic of disturbed or disrupted communities, but which is not captured by either the log-series or lognormal distribution. The METE log series does not model this deviation, but because it accurately fits the number of singleton species and the abundance of the single most common species in this distribution, it wins out over the lognormal distribution in AICc comparisons.

Species–level spatial abundance distributions

Species-level spatial abundance distributions were calculated for all species with $n \geq 4$, comprising 21 species in the older Mount Vision plot, and 10 species in the disturbed Bayview plot (Appendix S5). In Fig. 4, two alternate ways of presenting the same data are shown using one species (TRIBOR) as an example; first, a rank-abundance plot (where rank is inversely related to plant abundance in a cell), and second, a cumulative density function. AICc comparisons between two candidate distributions for the SSAD: The binomial and METE ut-geometric predictions for species in the mid-seral Bayview plot and Mount Vision mature plot are summarized in Appendix S5. Higher AICc weights corresponding to better model fits, and number of wins were tallied for model fits in each case (Fig. 5).

For the mid-seral stage Bayview plot, SSADs have AICc values supporting a binomial distribution in eight of 10 cases, with the two remaining cases supporting METE ut-geometric distribution. Bishop pine is one of the species with a distribution that is best described by the METE prediction, with next best-supported model having ΔAICc = 3.851. For the Mount Vision mature plot, we find the opposite pattern: AICc values support a binomial distribution in eight cases, and 13 cases support METE ut-geometric distribution (Fig. 5). The spatial distribution of Bishop pines in the Mount Vision site is, as in the Bayview plot, better described by the METE ut-geometric distribution, with the next best-supported binary model having somewhat less explanatory power (ΔAICc = 1.506). A Pearson's chi-squared contingency test on the distribution of wins indicates that the difference between SSADs at Bayview and Mount Vision is statistically significant at the 95% confidence level.

DISCUSSION

Predicted and empirical distributions in different-aged stands

This study demonstrates how macroecological approaches may inform disturbance ecology. Macroecological predictions of METE perform well in the mature stand in a disturbance-dependent community for the SAR, SAD, and the SSAD

Table 2. Model comparisons of candidate species abundance distributions (SADs) for the Bayview (disturbed) and Mount Vision (mature) plots.

Plot	Model	k	AICc	ΔAICc	w_i
Bayview	Lognormal	2	125.3246	5.1485	0.0708
	METE log series	1	120.1761	0	0.9292
Mount vision	Lognormal	2	271.9128	3.7173	0.1349
	METE log series	1	268.1956	0	0.8651

Notes: METE, Maximum Entropy Theory of Ecology. Here and following, k = *n*umber of parameters in model; AICc = Akaike's information criterion value corrected for small sample sizes; w_i = AICc weight (a measure of strength of evidence for each model); ΔAICc = difference of AICc value compared to the next best-supported model.

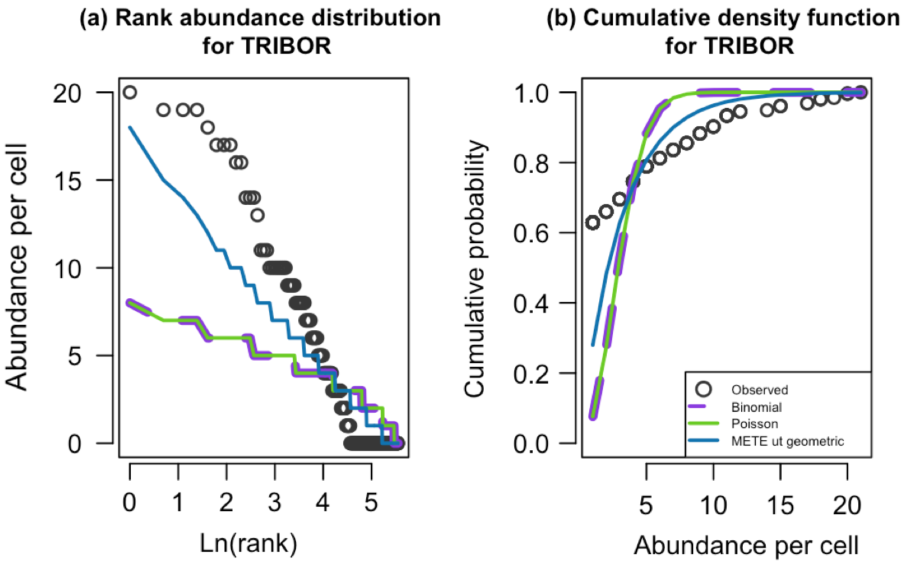

Fig. 4. Species-level spatial abundance distribution (SSAD) example. The species shown is *Trientalis borealis* (TRIBOR) from the Mount Vision plot. In this example, the Maximum Entropy Theory of Ecology (METE) upper-truncated (ut) geometric prediction is compared to other candidate distributions: the binomial and the Poisson. The METE ut-geometric distribution is equivalent to a finite negative binomial distribution with a support parameter of $k = 1$. Here, the binomial and Poisson distributions give the same predictions for the SSAD. The Poisson and binomial predictions give the similar results for each of the SSADs tested; this is because both models correspond to a null hypothesis of random placement, although the binomial has finite support and the Poisson is calculated with infinite support. Because both the binomial and the METE ut-geometric have finite support and the same number of parameters, Akaike's information criterion comparison between the two distributions is strictly based on the likelihood component. METE SSAD predictions are therefore compared to corresponding binomial distributions throughout the manuscript.

of both the dominant species (Bishop pine) and most of the other species in the plant community, compared to other candidate distributions. These results conform to our expectations, because the mature (Mount Vision) stand exhibits similar constancy and demographic stability to the Smithsonian plots where METE has proven successful previously (Harte et al. 2008, Harte 2011, Xiao et al. 2015). METE predictions have variable and lower success in the mid-seral stage Bayview plot, with the SAD better predicted by METE (compared to the lognormal), but with the SAR and z-D plots better described by a best-fit power law, and the SSADs in aggregate better described by the binomial distribution.

We expected that if SADs are more uneven and there is increased variation in aggregation in the SSAD across species, that we would see approximate power law behavior in the SAR (Wilber et al. 2015). In this study, we measured a more uneven SAD and some variation in the SSAD aggregation in the mid-seral stage Bayview plot and did in fact find power law-like behavior of the SAR there. We also found that this more recently disturbed Bayview plot had a Poisson spatial distribution of abundances (SSAD) for most species. This pattern is consistent with null model describing a post-disturbance landscape with opportunities for species to colonize with equal probability anywhere (noting that the colonization by Bishop pines would have taken place immediately post-fire). In contrast, the mature plot deviates from Poisson SSADs and has more highly aggregated METE-like SSADs. This points to other ecological processes than colonization being responsible for generating these patterns.

Deviations from METE's predicted distributions

The Maximum Entropy Theory of Ecology's predictions are most effective in steady-state

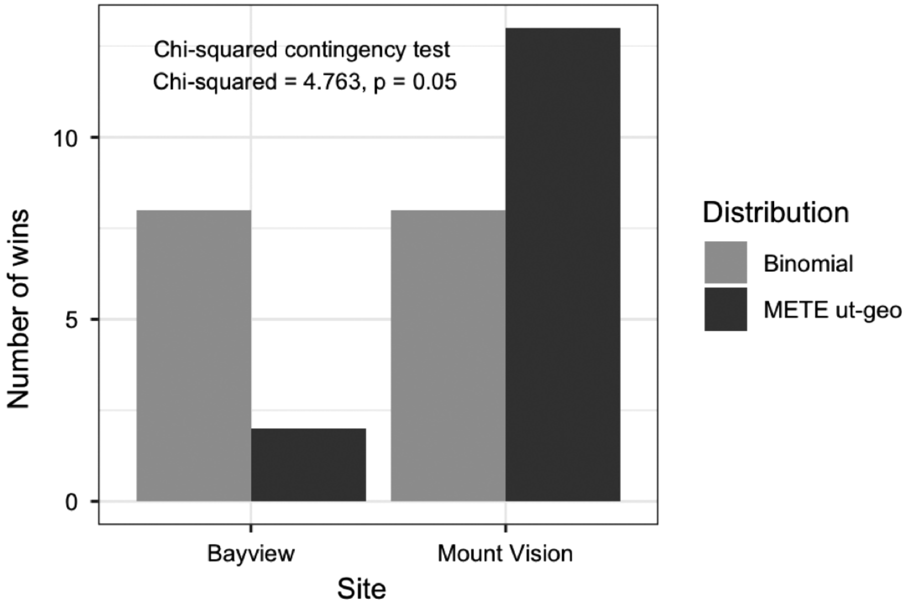

Fig. 5. Bar plots comparing number of wins between species-level spatial abundance distribution (SSAD) models for all species, based on AIC*c* weights. Binomial distributions are better fits to data from more species in the mid-seral stage and more recently disturbed Bayview plot, whereas Maximum Entropy Theory of Ecology upper-truncated geometric (ut-geo) models are better fits overall for species in the mature Mount Vision plot. A Pearson's chi-squared contingency test on the distribution of wins indicates that the difference between SSADs at Bayview and Mount Vision is statistically significant at the 95% confidence level (chi-squared = 4.763, df = NA, *P* = 0.05; simulated *P*-value based on 2000 replicates).

systems in which detection rates for the taxa studied are high, but like many forms of macroecology (Fisher et al. 2010), the current ASNE formulation does not account for transient dynamics. It therefore does not provide a full accounting of disturbance ecology and disturbance dynamics, but it can provide robust, quantitative descriptions of the pre- and post-disturbance community. Our results from two sites are consistent with the idea that ecological perturbation may result in lognormal SADs (although we only found deviation, not lack of AIC support), and suggest that the SAD may be transformed through successional stages from a geometric shape through a lognormal to a log series (Bazzaz 1975, Whittaker 1975). It is also apparent that time since disturbance affects the shape of the SAD and various other metrics in this study, including the shift of SSADs from the binomial toward the METE ut-geometric. This pattern may be consistent with other forms of spatial clustering of species during transitional phases (Kéfi et al. 2007) and is consistent with shifts in the overall metacommunity (McGill 2010) following disturbance.

We believe that deviations from METE's predicted SAD and the more binomial-type SSAD distributions for the general plant community in the younger stand of Bishop pines are likely explained by a lack of steady-state dynamics. As an information entropy-based statistical framework that employs state variables to describe the macrostate of an ecosystem or plot within that ecosystem, the static ASNE version of METE and the MaxEnt mathematics underlying it automatically optimize for distributions that maximize information entropy. The predicted state therefore always corresponds to a steady-state solution. The fixed, maximized information entropy distributions METE predicts for a given set of state variables likely closely correspond to mature biological communities experiencing very little demographic fluctuations or other large shifts in community composition over time. This in turn may explain why METE works better for the mature stand than for the younger, more recently disturbed stand still undergoing succession in this study. However, it still leaves open the questions of how macroecology can account for disturbance in ecosystems, and what implications this has for predicting their ecological effects.

Other examples of notable deviations from METE's predictions have been observed in the Barro Colorado Island forest plot, in a drought-affected Rocky Mountain meadow (Newman et al. 2014), and in some Hawaiian arthropod communities (Rominger et al. 2016, Harte et al. 2017). For the Barro Colorado Island plot, tree and seed-disperser extirpation on the island following its isolation from the mainland was a consequence of the construction of the Panama Canal. Time since isolation has been associated with an increasingly lognormal SAD. The lognormal SAD is also observed in the Rocky Mountain meadow during a period of unusual drought and high temperatures leading to a novel community of wildflowers that exhibited irregular phenology (Newman et al. 2014). In the Hawaii case, the SAD shows higher-than-predicted numbers of singleton species. Deviation from the METE in this case may be caused by dispersal limitation and the relatively young age of the community (Rominger et al. 2016). In each case, ecological context suggests that these systems are far from steady-state dynamics or missing a key ecological constraint, and provides insight into the ecological patterns observed.

Unifying macroecology with disturbance ecology

To our knowledge, no macroecological studies have focused on patterns in species diversity, spatial, and abundance distributions in natural disturbance regimes. This study examines two very different successional states in a disturbance-dependent ecosystem to identify the differences between METE's predictive abilities in communities with different disturbance histories. By showing precisely how sites with known, recent disturbance histories depart from the predictions of the current formulation of METE, we set the stage for explicit or implicit extensions of the theory and its application to a wider range of ecosystems, including those in states of rapid change, those with repeated natural disturbance, and those that experience combinations of natural disturbances and anthropogenic disruptions.

We show that at the plot-scale, METE predictions are generally better supported for the more mature, less rapidly changing plot that for the more recently disturbed plot that is low diversity and undergoing a period of density-dependent mortality. However, examining single successional states and comparing them, as we do here, may not be sufficient to produce METE-based generalizations of disturbance-dependent ecosystems. For example, a simple relationship such as "the more disturbed, the farther from METE predictions" may fail because of non-linear relationships between ecological processes and constraints on state variables (Hamer and Hill 2000, Xiao et al. 2016). A possible solution is to take a step back and look at a broader landscape scale (~50,000–100,000 ha) that comprises multiple patches with different disturbance histories. Although census information for this scale is generally lacking (and part of the motivation to study macroecology; Brown 1995), a fruitful approach to characterizing disturbance-prone ecosystems is better taken at scales larger than the spatial extent of disturbance events such as large fires and insect outbreaks. Without needing the transient dynamics (e.g., fire behavior, stand-level gap replacement) that apply at fine scales, it is possible that the ASNE version of METE may be applied successfully, as a form of snapshot ecology, to patches within a disturbed landscape to characterize zones of different ages and disturbance histories.

Maximum Entropy Theory of Ecology has been demonstrated to work across several orders of magnitude up to the largest scale of ecosystems (Harte et al. 2009, Harte 2011, White et al. 2012, Harte and Kitzes 2015). Measuring state variables from multiple patches at different successional stages will provide more constraining information for METE metrics and may lead to better predictions of the SAR and SAD. The scaling of macroecological metrics may even provide insight into the scales at which disturbance-dependent ecosystems deviate most dramatically from METE predictions (Hamer and Hill 2000, McGill 2010), as patterns in disturbance-dependent landscapes are known to be scale-dependent (Wu 2004). These patterns may also change between landscapes affected by large, infrequent disturbances (as in this study) and those affected by small, frequent disturbances (Romme et al. 1998, Turner and Dale 1998).

Acknowledgments

We thank PRNS for providing permits, field sites, logistical support, and facilities. This study was carried out under PRNS Park-assigned permit PORE-2012-SCI-0014, Activity #PORE-00572. We thank B. Becker for permitting assistance; C. Derooy and D. Morgan for curatorial assistance; and D. Hembry, A. Forrestel, S. Beissinger, and B. Harvey for useful discussions and comments on the manuscript. We also thank K. Krasnow and S. L. Stephens for materials and training and K. Hartfield for assistance with mapping. This research is funded in part by the Gordon and Betty Moore Foundation, by the NSF through the Graduate Research Fellowship to EAN, and grant NSF-EF-1137685. Publication fees were provided by the University of California, Berkeley Library.

Literature Cited

Alroy, J. 2015. The shape of terrestrial abundance distributions. Science Advances 1:e1500082.

Baldridge, E., D. J. Harris, X. Xiao, and E. P. White. 2016. An extensive comparison of species-abundance distribution models. PeerJ 4:e2823.

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken. 2012. The Jepson manual: vascular plants of California. Second edition. University of California Press, Berkeley, California, USA.

Bazzaz, F. A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56:485–488.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H., V. K. Gupta, B. L. Li, B. T. Milne, C. Restrepo, and G. B. West. 2002. The fractal nature of nature: power laws, ecological complexity and biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 357:619–626.

Brown, P. M., M. W. Kaye, and D. Buckley. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. Northwest Science 73:205–216.

Brummer, A., and E. A. Newman. 2019. Derivations of the core functions of the maximum entropy theory of ecology. Entropy 21:712.

Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer Science and Business Media, Berlin, Germany.

Dawson, T. E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117:476–485.

Death, R. G. 1996. The effect of habitat stability on benthic invertebrate communities: the utility of species abundance distributions. Hydrobiologia 317:97–107.

Dennis, B., and G. P. Patil. 1979. Species abundance, diversity, and environmental predictability. Pages 93–114 *in* J. F. Grassle, G. P. Patil, W. Smith, and C. Taillie, editors. Ecological diversity in theory and practice. International Cooperative Publishing House, Fairland, Maryland, USA.

Dornelas, M. 2010. Disturbance and change in biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3719–3727.

Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010. Dynamic macroecology on ecological timescales. Global Ecology and Biogeography 19:1–15.

Forrestel, A. B., M. A. Moritz, and S. L. Stephens. 2011. Landscape-scale vegetation change following fire in Point Reyes, California, USA. Fire Ecology 7:114–128.

Forrestel, A. B., B. S. Ramage, T. Moody, M. A. Moritz, and S. L. Stephens. 2015. Disease, fuels and potential fire behavior: impacts of Sudden Oak Death in two coastal California forest types. Forest Ecology and Management 348:23–30.

Gray, J. S. 1981. Detecting pollution-induced changes in communities using the log-normal distribution of individuals among species. Marine Pollution Bulletin 12:173–176.

Hamer, K. C., and J. K. Hill. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conservation Biology 14:1435–1440.

Harte, J. 2011. Maximum entropy and ecology: a theory of abundance, distribution, and energetics. Oxford University Press, Oxford, UK.

Harte, J., and J. Kitzes. 2015. Inferring regional-scale species diversity from small-plot censuses. PLOS ONE 10:e0117527.

Harte, J., J. Kitzes, E. A. Newman, and A. J. Rominger. 2013. Taxon categories and the universal species-area relationship. American Naturalist 181:282–287.

Harte, J., and E. A. Newman. 2014. Maximum information entropy: a foundation for ecological theory. Trends in Ecology and Evolution 29:384–389.

Harte, J., E. A. Newman, and A. J. Rominger. 2017. Metabolic partitioning across individuals in ecological communities. Global Ecology and Biogeography 26:993–997.

Harte, J., A. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species-area curve. Ecology Letters 12:789–797.

Harte, J., T. Zillio, E. Conlisk, and A. Smith. 2008. Maximum entropy and the state variable approach to macroecology. Ecology 89:2700–2711.

Harvey, B. J., and B. A. Holzman. 2014. Divergent successional pathways of stand development following fire in a California closed-cone pine forest. Journal of Vegetation Science 25:88–99.

Harvey, B. J., B. A. Holzman, and J. D. Davis. 2011. Spatial variability in stand structure and density-dependent mortality in newly established post-fire stands of a California closed-cone pine forest. Forest Ecology and Management 262:2042–2051.

Harvey, B. J., B. A. Holzman, and A. B. Forrestel. 2014. Forest resilience following severe wildfire in a semi-urban National Park. Fremontia 42:14–18.

Hill, J. K., and K. C. Hamer. 1998. Using species abundance models as indicators of habitat disturbance in tropical forests. Journal of Applied Ecology 35:458–460.

Hill, J. K., K. C. Hamer, L. A. Lace, and W. M. T. Banham. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. Journal of Applied Ecology 32:754–760.

Howell, J. T., W. Follette, C. Best, and F. Almeda. 2007. Marin Flora: an illustrated manual of flowering plants, ferns, and conifers of Marin County, California. California Academy of Sciences and California Native Plant Society., San Francisco, California, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Jaynes, E. T. 1982. On the rationale of maximum entropy methods. Proceedings of the IEEE 70:939–952.

Keator, G., and R. M. Heady. 1981. Pacific Coast Fern Finder. Nature Study Guide. Wilderness Press, Birmingham, Alabama, USA.

Kéfi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. ElAich, and P. C. De Ruiter. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213.

Kempton, R. A., and L. R. Taylor. 1974. Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. Journal of Animal Ecology 43:381–399.

Kitzes, J., C. Lewis, and M. Wilber. 2014. macroeco v0.2. http://github.com/jkitzes/macroeco

Kitzes, J., and M. Wilber. 2016. macroeco: reproducible ecological pattern analysis in Python. Ecography 39:361–367.

Little Jr, E. L.. 1971. Atlas of United States trees, volume 1. Conifers and important hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1146.

May, R. 1975. Patterns of species abundance and diversity. *In* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Mayor, S. J., J. F. Cahill Jr, F. He, and S. Boutin. 2015. Scaling disturbance instead of richness to better understand anthropogenic impacts on biodiversity. PLOS ONE 10:e0125579.

McGill, B. J.. 2010. Towards a unification of unified theories of biodiversity. Ecology Letters 13:627–642.

McGill, B. J., et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

McGlinn, D. J., X. Xiao, J. Kitzes, and E. P. White. 2015. Exploring the spatially explicit predictions of the Maximum Entropy Theory of Ecology. Global Ecology and Biogeography 24:675–684.

McGlinn, D. J., X. Xiao, and E. P. White. 2013. An empirical evaluation of four variants of a universal species–area relationship. PeerJ 1:e212.

Millar, C. I. 1983. A steep cline in *Pinus muricata*. Evolution 311–319.

Millar, C. I. 1986. The Californian closed cone pines (subsection Oocarpae Little and Critchfield): a taxonomic history and review. Taxon 657–670.

National Park Service. 2005. Vision Fire 10 Year Anniversary Fact Sheet #3—Incident Statistics. http://www.nps.gov/pore/learn/management/upload/firemanagement_visionfire_factsheet3.pdf

Newman, E. A., M. E. Harte, N. Lowell, M. Wilber, and J. Harte. 2014. Empirical tests of within-and across-species energetics in a diverse plant community. Ecology 95:2815–2825.

Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Nummelin, M. 1998. Log-normal distribution of species abundances is not a universal indicator of rain forest disturbance. Journal of Applied Ecology 35:454–457.

Ornduff, R. 1998. Three years after the Vision Fire in Point Reyes. Fremontia 26:26–27.

Ornduff, R., and V. Norris. 1997. Rebirth of a Bishop Pine forest: first year after the Mount Vision fire. Fremontia 25:22–28.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology 29:254–283.

R Core Team. 2013–2015. (Versions 3.0.1 and 3.1.3) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rominger, A. J., et al. 2016. Community assembly on isolated islands: Macroecology meets evolution. Global Ecology and Biogeography 25:769–780.

Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1:524–534.

Schlossberg, S., and D. I. King. 2015. Measuring the effectiveness of conservation programs for shrubland birds. Global Ecology and Conservation 4:658–665.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Stephens, S. L., and W. J. Libby. 2006. Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. Journal of Biogeography 33:648–652.

Supp, S. R., and S. M. Ernest. 2014. Species-level and community-level responses to disturbance: a cross-community analysis. Ecology 95:1717–1723.

Supp, S. R., X. Xiao, S. K. M. Ernest, and E. P. White. 2012. An experimental test of the response of macroecological patterns to altered species interactions. Ecology 93:2505–2511.

Tokeshi, M. 1993. Species abundance patterns and community structure. Advances in Ecological Research 24:111–186.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171–197.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world 1. Ecology 91:2833–2849.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: What have we learned? Ecosystems 1:493–496.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landscape Ecology 8:213–227.

Ulrich, W., M. Ollik, and K. I. Ugland. 2010. A meta-analysis of species–abundance distributions. Oikos 119:1149–1155.

van Rossum, G., and F. L. Drake, editors. 2001. Python reference manual. PythonLabs, Virginia, USA. http://www.python.org

White, E. P., B. J. Enquist, and J. L. Green. 2008. On estimating the exponent of power-law frequency distributions. Ecology 89:905–912.

White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Pages 399–450 *in* Progress in botany. Springer, Berlin Heidelberg, Germany.

White, E. P., K. M. Thibault, and X. Xiao. 2012. Characterizing species abundance distributions across taxa and ecosystems using a simple maximum entropy model. Ecology 93:1772–1778.

Whittaker, R. H. 1965. Dominance and Diversity in Land Plant Communities: Numerical relations of species express the importance of competition in community function and evolution. Science 147:250–260.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. Macmillan, New York, New York, USA.

Wilber, M. Q., J. Kitzes, and J. Harte. 2015. Scale collapse and the emergence of the power law species–area relationship. Global Ecology and Biogeography 24:883–895.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19:125–138.

Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70:439–466.

Xiao, X., D. J. McGlinn, and E. P. White. 2015. A strong test of the maximum entropy theory of ecology. American Naturalist 185:E70–E80.

Xiao, X., J. P. O'Dwyer, and E. P. White. 2016. Comparing process-based and constraint-based approaches for modeling macroecological patterns. Ecology 97:1228–1238.

DATA AVAILABILITY

Data from this study are available in the Supporting Information and through FigShare at https://doi.org/10.6084/m9.figshare.11363051.

SUPPORTING INFORMATION

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

Appendix S1: Acronyms and their meanings.
Appendix S2: Notes on detectability.
Appendix S3: Tree coring data and metadata.
Appendix S4: Mathematical formulae for METE's predictions.
Appendix S5: Supporting results and analyses.
Data S1: Python script and study data for the software *macroeco*.