**The relationships between size and abundance in non-forest plant communities**

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**Abstract**

The inverse relationship between size and abundance is a well-documented pattern in forests, and the form of size-density relationships depends on the balance between growth and mortality rates in the community. Traditionally, studies of plant size distributions have focused on single species populations and forests, but here we examine diverse communities dominated by plants with varied life histories, including grasses, forbs, shrubs, and succulents. In particular, we test whether the parameters of the individual size distribution differ systematically across community types and whether they fit the contrasting predictions of metabolic or demographic theories. All thirteen of our study sites better fit the predictions of demographic equilibrium theory, but interestingly, fits of both demographic and metabolic models showed little systematic variation across community types, despite large differences in environmental conditions and dominant life forms. Finally, analysis of the cross-community scaling relationship demonstrates that natural and restored non-forest communities conform to patterns of size and abundance observed among forest, plantation, and crop systems. Taken together, our results suggest that common ecological mechanisms govern plant community size structure regardless of the dominant plant life forms.

**Introduction**

A main goal of ecology is to document and explain patterns that reflect a common set of processes across ecosystems. One such general pattern seen in plant and animal communities is the inverse relationship between body size and abundance (White et al. 2007). Studies of "self-thinning" in plant populations demonstrate that the decline in abundance with size arises from the effects of resource competition on growth and mortality (Westoby 1981). Under constant resource supply rates, small plants typically grow with minimal mortality until the size-dependent rate of resource use equals the rate of resource supply and subsequent growth is only possible if resources are liberated by the death of some individuals (Yoda et al. 1963, Westoby and Howell 1986, Enquist et al. 1998, Deng et al. 2012). At this resource equilibrium, plant population density generally decays as a power-law of plant size.

In long-lived mixed-species perennial communities, the situation is more complex. Resource competition is frequently size-asymmetric, with larger individuals dominating their smaller neighbors (Kikuzawa 1999, Stoll et al. 2002) and the balance between competitive and facilitative interactions is also size dependent (Miriti 2006, Chu et al. 2010). Further, the relative importance of resource competition and abiotic disturbance also shifts as plants grow (Coomes et al. 2003), and allocational strategies that prioritize persistence over growth (e.g., dormancy, sprouting, shade tolerance) allow many species to persist for long periods in communities well below their maximum size (Venable and Brown 1988, Kitajima 1994, Walters and Reich 1996, Bond and Midgley 2001). Thus, in natural communities, size distributions reflect not just resource competition, but also life history trade-offs between growth and survival, complex neighborhood interactions, and the disturbance history of the community (Niklas et al. 2003, Coomes et al. 2003, Muller-Landau et al. 2006a, Kerkhoff and Enquist 2007).

The relationship between size and abundance in ecology, in fact, entails up to four different patterns (White et al. 2007). In plant communities, ecologists generally focus on two of these, which White et al. (2007) refer to as *individual size distributions* and *cross-community scaling relationships.* Individual size distributions are simply the frequency distribution (or probability density) of individual sizes in a single local community. Cross-community scaling relationships plot the total density of individuals in a community as a function of the average size of all those individuals, so each observation represents a stand or community. The cross-community scaling relationship corresponds with how data are analyzed in self-thinning studies, and a recent study suggests that natural forest communities conform to the same self-thinning relationship as experimental populations of single crop species (Deng et al. 2012). However, in contrast to the generally narrow range of sizes observed in self-thinning studies, natural communities often exhibit orders-of-magnitude variation in size *within* each community, so even if communities share a single cross-community size-density relationship, the individual size distributions observed within local communities may still be quite varied (White et al. 2007).

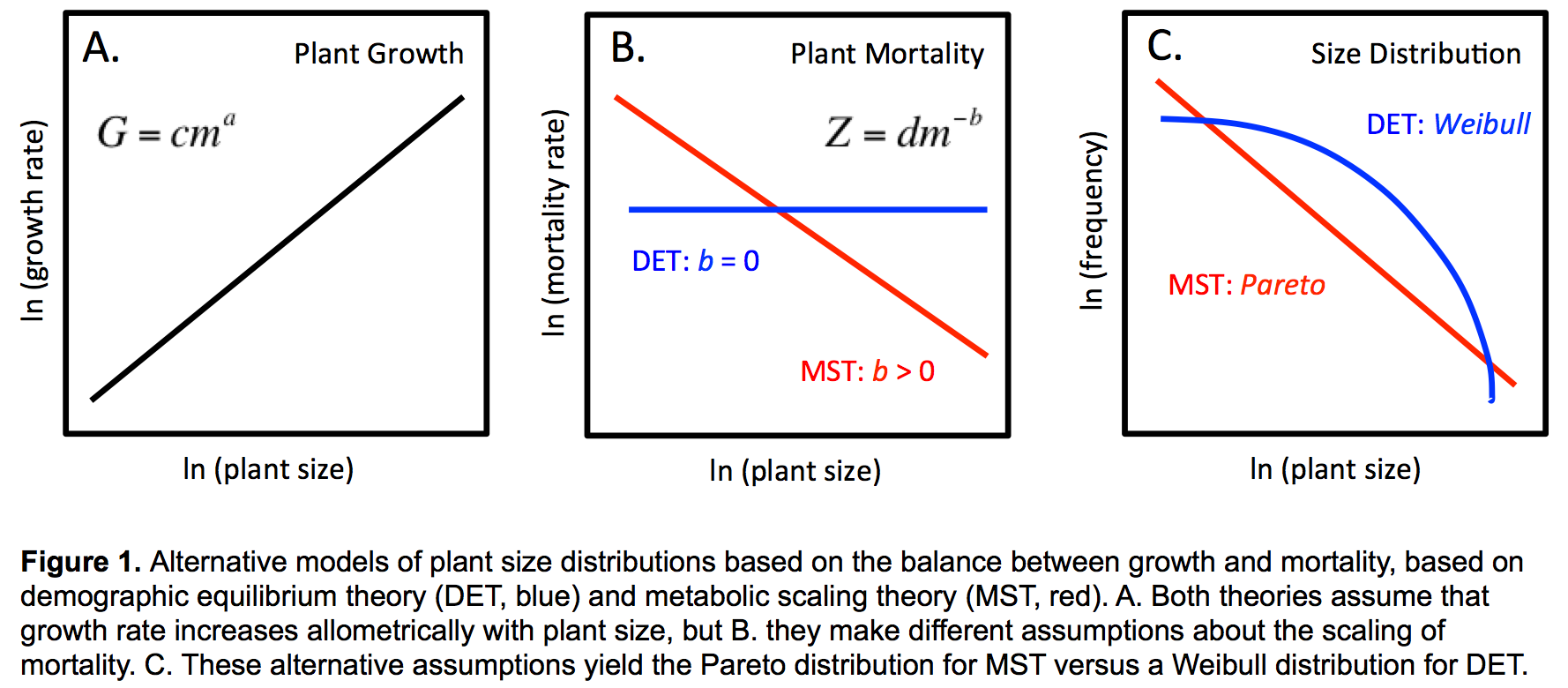
Traditionally, studies of size-abundance relationships in natural plant communities have focused on forests, but herbaceous and shrub-dominated communities may offer new insights into the ecological processes underlying size distributions. Here, we examine the relationships between size and abundance in communities ranging from temperate prairies and herbaceous wetlands, to montane meadows and semi-arid grasslands, to a succulent- and shrub-dominated desert. By examining communities that vary in their range of sizes, dominant growth forms, and limiting resources, we can test the generality of plant size distribution patterns and the explanations offered by the alternative models of how growth and mortality trade-off to influence the relationship between size and abundance.

*Alternative Models of Individual Size Distributions in Plant Communities*

Theoretical models used to fit and explain individual size distributions vary principally in their assumptions about how rates of growth and mortality scale with plant size. Like many biological rates and times, growth rates (*g*) and mortality rates (*z*) can be described by allometric power functions of individual plant mass (*m*) (Enquist and Niklas 2001, Coomes et al. 2003, Muller-Landau et al. 2006b)

, (1)

. (2)

Here, *g* is the growth rate (mass time-1), *c* is the growth coefficient (mass(1-*a*) time-1) , *a* is the scaling exponent for growth, *z* is the mortality rate (time-1), *d* is the mortality coefficient (mass-*b* time-1), and *b* is the scaling exponent for mortality. In this study, we examine two specific alternative theories that make contrasting assumptions about the parameters of equations 1 and 2: metabolic scaling theory and demographic equilibrium theory. Both theories assume that growth rate scales as an increasing power function of plant size (*i.e.,* *a* > 0) but the theories differ with regard to the scaling of mortality rate. These alternative assumptions lead to different probability density functions describing the size distribution of individuals in the community (Coomes et al. 2003, Muller-Landau et al. 2006b, Lai et al. 2013, Figure 1).

Metabolic scaling theory assumes that, like growth, mortality also follows a power-function. Specifically, based on the assumption that the forest community is utilizing all available space and resources, mortality rate follows the same scaling relationship as a mass-specific metabolic rate (Enquist and Niklas 2001, Stegen and White 2008). The resulting probability density function is a Pareto distribution, defined as:

, (3)

where *fP(m)* is the frequency of individual plants of mass *m*, *m0* is the minimum plant size (which depends on the sampling design), and *λ* is the scaling exponent that describes the decline of abundance with mass. Importantly, the derivation of the Pareto distribution also implies that *λ* = –*a – d/c,* and assumes that the growth and mortality scaling exponents sum to one(*a* + *b* = 1) (Muller-Landau et al. 2006b) which conforms with metabolic scaling theory.

Applications of metabolic scaling theory frequently assume particular values for the scaling exponents of growth (*a* = ¾) and mortality (*b* = -¼). Based on an empirically observed -2 scaling exponent for tree diameters, Enquist and Niklas (2001) derived a mass distribution exponent of *λ* = -¾. However, because individual size distributions are probability density functions and tree diameters (*D*) scale with mass as *m* ∝ *D*8/3, the -2 diameter exponent corresponds to a mass exponent of -11/8 rather than -3/4 due to the changing dimensions of the variables (Stegen and White 2008). While Enquist and Niklas (2001) supported the Pareto distribution for tree diameters with abundant data and simulations, subsequent debate in the literature regarding both the generality of the derived value for the exponent and the mechanistic underpinnings of the theory has led to the consideration of alternative models of plant community size distributions, including models based on demographic equilibrium theory (Coomes et al. 2003, Muller-Landau et al. 2006b, 2006a, Lai et al. 2013).

Demographic equilibrium theory assumes that mortality is a size-independent process (*i.e.,* in equation 2, *b* = 0, so *z*(*m*) = *d*, a constant). Growth is still assumed to vary as a power function of mass, as in equation 1. The resulting Weibull distribution (Muller-Landau et al. 2006b, Lai et al. 2013) is defined as:

, (4)

where *fW*(*m*) is the probability density function, ** = *d*/(*c*(1-*a*)) is the scale parameter, and ** = 1 – *a* is the shape parameter. The Weibull distribution was shown to be the best fit (and better than the Pareto distribution) for data from 14 large-scale tropical forest plots (Muller-Landau et al. 2006a).

*Models of Cross-Community Scaling Relationships in Plants*

Cross-community scaling relationships, whether in multi-species forest communities or single-species self-thinning populations, generally take the form of a power-law,

, (5)

where *Ntot* is the total plant density of the stand (number area-1), is mean plant mass, *n* is the scaling coefficient (number mass-), and  is the scaling exponent. Much of the theoretical work on cross-community size-density relationships is focused on the values of the scaling exponent .

Early models of self-thinning based on geometric isometry of plant form (Yoda et al. 1963, Westoby 1984) predicted that  = - 2/3, but subsequent models based on allometric growth, in which plant form changes systematically with size (Westoby 1977, White 1981, Weller 1987a, 1987b), better explained the observed variation in self-thinning and interspecific size density relationships. More recently, alternative explanations based on resource use and the allometric scaling of metabolic rate have been proposed (Enquist et al. 1998, Niklas et al. 2003), which predicted  = -¾ . However, that prediction depends on the assumption that plant metabolic rate scales as the ¾-power of plant mass, which may hold for large but not small plants (Reich et al. 2006, Enquist et al. 2007, Mori et al. 2010). Most recently, Deng et al. (2012) demonstrated that both the biophysical models of plant packing in space and models based on the scaling of resource use can result in a prediction of  = -¾, quite similar to the pattern they observe over a range of crop populations and forest stands spanning approximately 11 orders of magnitude in mean plant mass, .

Here, we examine the individual size distributions and cross-community scaling relationship for 11 herbaceous and shrub-dominated communities and one forest using exhaustive surveys of hundreds to thousands of individual plants across a wide range of abiotic environments. Specifically, we ask: 1) which model (Pareto vs. Weibull) provides the best fit to the individual size distribution in each surveyed community, 2) whether ecologically similar communities share similar size distribution patterns distinct from other community types, and 3) whether herbaceous and shrub-dominated communities follow the same cross-community scaling relationship shared by more extensively studied forests and monospecific populations such as crops.

**Methods**

To test these alternative hypotheses we compiled extensive individual plant size data from forest and non-forest communities. Thirteen different plant communities (Table 1) were surveyed at the Brown Family Environmental Center (BFEC) in Gambier, Ohio (40.39° N, -82.42° W), the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38.90° N, -106.98° W), and Tumamoc Hill Desert Laboratory (THDL) in Tucson, Arizona (32.13° N, -111.00° W).

*Locales*

The BFEC is situated in a temperate rural mosaic of agricultural fields, woodlots, and restored ecosystems including prairies and wetlands. Three different communities were surveyed at the BFEC: a temperate forest, a wetland, and a restored prairie. The temperate forest plot is a two-hectare area within a natural mixed age forest that experienced some selective logging in the early 20th century but was likely never entirely clear-cut. The restored prairie was established on previously agricultural land in 1992 and is maintained by controlled burns each spring. We sampled local prairie communities using three randomly placed 1.2 x 1.2 m plots spread across roughly one hectare. The perched wetland is adjacent to a small headwater stream, which flows into the nearby Kokosing River. In this habitat, we sampled two 1.2 x 1.2 m plots, placed approximately 50 and 100 m from the stream. Soils in the wetland sites are continuously saturated throughout the growing season, while the prairie and forest sites depend on rainfall.

The RMBL in the southern Rocky Mountains provides an alpine environment with an elevation gradient ranging from 2468 to 3380 m above sea level and spanning a geographic distance of approximately 39 km (Bryant et al. 2008, Sloat et al. 2015). The five sites range from an arid grass-sagebrush steppe near Almont, CO (2468 m), through a stream-side wet meadow outside Mount Crested Butte, CO, up to three subalpine meadow sites in Washington Gulch that extend nearly to treeline (3380 m). The three subalpine meadow communities rely heavily on seasonal snowmelt and soils can transition from completely saturated at the beginning of the growing season to quite dry by the end of the summer. Each site was sampled using a single 1.3 x 1.3 m plot.

The THDL in Tucson, AZ, is located in a Sonoran desert habitat dominated by stem succulents, shrubs, and small trees. Here, water availability is the limiting resource for plant growth. The climate is highly seasonal with mostly hot dry weather broken up by a late summer monsoon season as well as seasonal rainfall in January and February. All individuals within a one-hectare area were sampled.

*Plant Sampling Methods*

The herbaceous communities at the BFEC and the RMBL were all sampled using the same method. At peak biomass (near the end of the growing season) each individual plant in the sample plot was harvested above-ground, dried at a temperature of at least 60**°**C for over one week, and weighed to the nearest 0.001g. Individual plants were defined by the aboveground biomass associated with an individual stem or stem cluster at ground level, and bunched grasses were taken as a single individual when their stems could not be reliably separated at ground level. Thus, individuals generally represent ramets rather than genets. In each case, individuals were identified to species or (often) morphospecies, but we group all individuals across species in this analysis, since we are concerned with the community size-frequency distributions.

In the BFEC forest plot, all individual trees were censused in a 2-ha area established in 2006 and 2007. All individuals with a diameter breast height (DBH) greater than 1 cm were measured, mapped using an ultrasonic transponder, and identified to species. Mapped individuals were relocated and re-measured in the summer of 2011, and all newly established individuals were added. The DBH was then converted to mass using allometric equations (Jenkins et al. 2003). Here, we analyze the size distribution for the forest plot survey in 2011.

In the THDL plot, the basal stem diameter, height, and canopy spread (north-south and east-west) were recorded for each individual plant (including both herbaceous and woody individuals) in a 1-ha area, and all individuals were mapped using a total station theodolite. The height, diameter, and canopy measures were converted to biomass values based on individuals of the same species that had been similarly measured, harvested from other local sites (road and golf course rights-of-way), dried and weighed. For most species, we estimated allometric equations based on between 6 – 149 conspecific individuals (median 27.5 individuals) across a wide size range. For species without harvested individuals, we used individuals from a congeneric and/or morphologically similar species or all individuals within the appropriate functional group (woody, succulent, herbaceous) to estimate biomass.

*Data Analysis*

We used maximum likelihood estimation (Muller-Landau et al. 2006a, White et al. 2008, Lai et al. 2013) to fit the two alternative size distribution models (Equations 3 and 4) using code written in ‘*R’*. Model fits were compared based on Akaike’s Information Criteria (AIC) value, and we selected the model with the lowest AIC score as the best fit, using the rule of thumb that models whose AIC values differed by less than 4 (*i.e*., ΔAIC<4) were indistinguishable from one another. In the results below, the data are displayed in the figures using logarithmically normalized binning (White et al. 2008), but it is important to note that the maximum likelihood estimate fits were based on the raw data values and not fit directly to the binned points.

Finally, to examine the cross-community scaling relationship, we calculated the mean plant size in each community and plotted the log density (total number of individuals / plot area) against the log mean plant mass. For comparison, we also included data from Deng et al. (2013) for crop plants grown at their optimal density as well as a global compendium of data from forests, plantations, and bamboo communities.

**Results**

The communities varied substantially in the range of plant sizes, plot sizes, and dominant growth forms, but each included a large sample of individuals, ranging from 160 to 2630 plants (Table 1).

In all communities, the size distribution displayed curvature on a log-log scale suggesting a Weibull (rather than a Pareto) distribution. At every site, the Weibull distribution provided a better fit to the individual size distribution than the Pareto (Figure 2), with ΔAIC > 70 at a minimum (Table 2), which suggests that even when the individual size distribution appears to be quite linear under log-normalized binning (*e.g.,* RMBL grass/sage, Figure 2), the curvilinear fit is more appropriate.

Although the shape of the individual size distribution varied substantially across the communities, we did not observe systematic variation across the three locales or among communities with different dominant growth forms (Figure 2). Environmental variation may influence the shape of the individual size distribution, as the shape parameter (**) values (which describe the curvature of the Weibull distribution) appeared to be systematically higher in the wet communities (BFEC wetland and RMBL wet meadow: 0.67 – 0.74, all others: 0.30 – 0.57, Table 2). However, the nature of our sample precludes us from confidently making any formal statistical inferences about the effects of locale, growth form, or environment on the shape of the individual size distribution.

Although the Pareto distribution provided an inferior fit, it should be noted that many of the Pareto exponents were close to, but shallower than, the predicted value of 11/8 (Stegen and White, 2008; Table 2). As in the case of the shape parameter of the Weibull distribution, the Pareto exponent did not vary systematically across locales or between community types.

The twelve communities measured here broadly conformed to the cross-community scaling relationship observed in crops, plantations, forests, and bamboo communities (Figure 3). Interestingly, compared to crop populations with comparable mean plant mass, , the herbaceous communities from the BFEC and RMBL generally exhibit lower plant density.

**Discussion**

Overall, our results suggest that herbaceous and shrub-dominated plant communities exhibit the same relationships between size and abundance as more commonly studied forest communities and single species populations. Within communities, the individual size distributions were curvilinear, supporting the Weibull as a better description of the plant size distributions regardless of variation in dominant life forms, environmental stresses, or limiting resources. These results challenge the simplest form of metabolic scaling theory as a generalized explanation for community level size distributions (Niklas et al. 2003, Coomes et al. 2003, Muller-Landau et al. 2006a).

The fact that such a wide variety of plant communities exhibit similar individual size distributions is quite remarkable. The plant communities differed in their limiting resources, dominant plant type (*i.e.,* trees, shrubs/succulents, forbs/grasses), levels of natural and human disturbance, water and nutrient availability, and other environmental and edaphic factors. The fact that such divergent communities display similar size distributions suggests that common processes may govern plant community structure in very different communities (Anfodillo et al. 2013).

If the assumptions of demographic equilibrium theory (Muller-Landau et al. 2006b) hold in forest and non-forest communities alike, individual size distributions arise from a dynamic equilibrium between growth rates that change as a power-law function of size, and a constant (or at least size-independent) mortality rate (Lai et al. 2013). This line of reasoning is based on the idea that size-asymmetric competition will impact growth and mortality when the plant is small, but once a plant is established in the community, mortality is likely independent of size. Thus, if the size threshold of the survey is low enough, we could see deviations from the Weibull model, with the Pareto distribution describing the best fit in smaller sized trees and a Weibull distribution for larger individuals, as observed in several large temperate and subtropical forest plots (Lai et al. 2013). While such a combined model did not provide a superior fit in any of our study plots, we did observe strongly size dependent mortality in the BFEC forest plot from 2005-2011 (data not shown), despite the superior fit of the Weibull. Thus, caution must be exercised in inferring particular assumed processes (*i.e*., size-independent mortality) from the fit of models to emergent patterns like individual size distributions.

While the Weibull provided the best fit to the size distribution in every case, some sites exhibited systematic departures from the predicted pattern. At one extreme, the most abundant size class was frequently not the smallest one; below some threshold size, abundance dropped off. These deviations could reflect sampling errors in finding the smallest individuals within each plot. However, the exhaustive sampling strategy for the herbaceous communities left the plot virtually bare. At the other extreme, the actual size distribution also deviates from the Weibull for largest plants in most of the sites, with the Weibull underestimating the observed frequency of large plants. The high number of large plants could represent systematic deviations from the assumptions of growth and mortality for particular dominant species. These deviations demonstrate that, while simple models provide effective descriptions of plant size distributions, site-specific conditions may lead to departures from their predictions (Coomes et al. 2003, Anfodillo et al. 2013).

Across communities, the fact that all twelve sites conformed to a power law linking forests, plantations, and crop populations is consistent with the conclusion that the cross-community size-density scaling relationship arises from the constraints of geometric packing and/or energy use (Deng et al. 2012). At the same time, the fact that our mixed-species herbaceous communities had lower plant densities than crop populations with a similar mean plant mass suggests that differences in individual size distributions among communities affect the relationship between total plant density and mean plant mass. Specifically, populations or communities with narrow, relatively uniform size distributions (*e.g*., crops) can pack in more individuals than communities exhibiting skewed, higher-variance distributions. The development of formal theory linking variation in individual size distributions to cross-community scaling relationships would greatly expand our understanding of how the varied relationships between size and abundance reflect ecological processes.

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**Tables and Figures**

Table 1. The sites surveyed in this study; their sample sizes in area and number of plants. The wetland, prairie, and forest data is from the Brown Family Environmental Center, Gambier, OH. The RMBL data is from alpine meadows near the Rocky Mountain Biological Lab in Gothic, Colorado. Tumamoc data is from Tumamaoc Hill plot in Tuscon, Arizona.

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| --- | --- | --- | --- | --- |
| Locale | Community | Plant mass (g) | Plant N / Density (m-2) | Dominant  Life Forms |
| BFEC | Wetland 1 |  | 1,771 / | Forb/Grass |
| BFEC | Wetland 2 |  | 1,668 / | Forb/Grass |
| BFEC | Prairie 1 |  | 244 / | Forb/Grass |
| BFEC | Prairie 2 |  | 320 / | Forb/Grass |
| BFEC | Prairie 3 |  | 315 / | Forb/Grass |
| BFEC | Forest |  | 1,739 / | Tree |
| RMBL | Grass-Sage Steppe |  | 226 / | Grass/Shrub |
| RMBL | Wet Meadow |  | 618 / | Grass |
| RMBL | Sub-alpine Meadow 1 |  | 160 / | Forb/Shrub |
| RMBL | Sub-alpine Meadow 2 |  | 281 / | Forb |
| RMBL | Sub-alpine Meadow 3 |  | 938 / | Forb |
| THDL | Desert |  | 2,630 / | Succulent/Shrub |

Table 2. Comparison of model fits for the Weibull, Pareto, and combined models based on Akaike’s Information Criteria (AIC) values for the for all sites surveyed. Lowest AIC value within each site represents the best fit of the data. All values followed the pattern of Weibull < Combined < Pareto. Shape, scale, and exponent parameters for Weibull and Pareto are also provided.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Site | AIC Value  Weibull | AIC Value  Pareto | AIC Value Combined | Shape  (Weibull) | Scale  (Weibull) | Exponent  (Pareto) |
| Wetland 1 | -303.58 | 1,887.47 | 81.82 | 0.64 | 0.26 | 1.25 |
| Wetland 2 | 394.94 | 2,419.14 | 975.40 | 0.76 | 0.35 | 1.29 |
| Prairie 1 | 51.94 | 351.54 | 119.69 | 0.53 | 0.30 | 1.20 |
| Prairie 2 | 543.83 | 760.02 | 689.53 | 0.48 | 0.52 | 1.28 |
| Prairie 3 | 1,229.20 | 1,748.18 | 1,290.94 | 0.57 | 2.17 | 1.15 |
| Forest ‘06 | 18,562.32 | 19,552.62 | 19,027.00 | 0.27 | 10.40 | 1.22 |
| Forest ‘11 | 17,882.91 | 19,172.73 | 18,125.31 | 0.32 | 28.59 | 1.19 |
| Semi-Arid | -170.88 | -100.45 | -101.66 | 0.31 | 0.038 | 1.35 |
| Wet Meadow | -314.33 | 652.84 | -131.64 | 0.71 | 0.24 | 1.21 |
| Alpine Meadow | 29.48 | 132.01 | 48.52 | 0.31 | 0.14 | 1.21 |
| Alpine Meadow | 164.60 | 326.94 | 228.33 | 0.30 | 0.18 | 1.20 |
| Alpine Meadow | -1,727.56 | -911.75 | -1614.73 | 0.51 | 0.09 | 1.29 |
| Desert | 50,297.00 | 52,961.73 | 50,510.85 | 0.36 | 3,046.23 | 1.17 |