Abstract

Understanding patterns of biodiversity is one of the pressing research areas in ecology given global conservation demands. The mechanisms that produce biodiversity are still debated; however, environmental productivity is often thought to be responsible for generating biodiversity since species richness and environmental productivity are generally positively correlated. Species richness is the measurement of the number of species within a given area. Few studies have examined the relationship between species richness of small mammals and environmental productivity across elevational gradients with multiple measures of environmental productivity. For ten sites along an elevational gradient in Colorado’s Front Range, we examined several factors as possible measures of environmental productivity, including temperature, precipitation, food resource abundance (arthropod and understory plant biomass), and small mammal abundance. Small mammal populations were estimated from mark-and-recapture data from the summer of 2010, and we evaluated four estimation methods, including minimum number of individuals known alive (MNKA), modified Lincoln-Peterson and Schnabel methods, and the Jackknife estimator (Program CAPTURE). Mark-and-recapture is a trapping technique that allows for population sizes to be mathematically estimated according to the number of individuals marked, and the number of individuals recaptured. The population estimate of MNKA, is the number of individuals marked in a trapping effort. The modified Lincoln-Peterson, Schnabel methods, and Jackknife estimators use mark-and-recapture data to mathematically derive population estimates. All population estimates were highly correlated (average \( r^2 = 0.9800 \)). Small mammal diversity was strongly positively correlated to understory plant biomass \( (r^2 = 0.6404, \ p-value = \)
0.0033), temperature ($r^2 = 0.6212, p = 0.0041$), precipitation ($r^2 = 0.6438$, p-value $=0.0032$), and small mammal abundance (MNKA; $r^2 = 0.5142$, p-value $=0.0118$).

However, multivariate regression models for small mammal diversity and small mammal abundance only included understory plant biomass ($r^2 = 0.7005$ and $0.6695$, respectively) as the single necessary predictor among the various measurements of environmental productivity. In our preliminary analysis of the first year of sampling, understory plant biomass seems to be a good predictor of local small mammal diversity in the Front Range, Colorado.

**Introduction**

Understanding patterns of biodiversity is one of the pressing research areas in ecology. Biodiversity is currently being lost at an unprecedented rate, and conservation efforts need to become more efficient and effective to preserve species across the globe. Understanding the mechanisms that produce biodiversity should likewise aid these efforts in the face of threats such as human population growth, climate change, and habitat destruction. There is strong support in the published literature that environmental energy correlates positively with species richness (Currie 1991, Currie et al. 2004, Evans et al. 2005, Kerr and Packer 1997, Mittelbach et al. 2001, Waide et al. 1999). Species richness is a measurement of the number of species within a given area. Species-energy relationships are often tested through different measurements of environmental productivity (Currie 1991, Currie et al. 2004, Evans et al. 2005, Kerr and Packer 1997, Mittelbach et al. 2001). Two of the most common species-energy relationships reported are a positive relationship between environmental productivity and species richness, or a
unimodal pattern between environmental productivity and species richness (Evans et al. 2005, Kerr and Packer 1997, Mittelbach et al. 2001, Waide et al. 1999). The spatial scale at which a study occurs has a significant influence on species-energy relationship observed. Typically micro-scale studies have unimodal patterns while macro-scale studies have monotonically increasing curves. Unimodal patterns produce peak species richness at intermediate amounts of environmental productivity, while monotonically increasing curves have the highest species richness at the highest amounts of environmental productivity (Evans et al. 2005, Mittelbach et al. 2001, Waide et al. 1999, Whittaker et al. 2001).

understanding of these species-energy relationships was due to the problematic assumption that these mechanisms are already understood and therefore do not need testing. Evans et al. (2005) argue that it is very important to test each of the nine proposed mechanistic explanations because each one can share certain predictions when explaining species-energy relationships. The most common shared prediction of these mechanisms is that high-energy areas support the highest population densities of species (Evans et al. 2005). Multiple mechanisms can contribute to the same documented pattern, and experiments are unfortunately not designed to explicitly test and distinguish between mechanisms (Evans et al. 2005).

The present study tested two of the mechanistic explanations for species-energy relationships reviewed in Evans et al. (2005). These are referred to as the ‘sampling mechanism’ and the ‘increased population size mechanism,’ which are two of the most commonly tested and hypothesized mechanisms in the literature (Currie et al. 2004, Evans et al. 2005, Kaspari et al. 2000a, 2000b, 2003, McGlynn et al. 2010). The ‘sampling mechanism’ predicts that increased energy availability will result in positive correlations with species abundance and richness; therefore species richness should be a positive decelerating function of total abundance and energy availability (Evans et al. 2005). A positive decelerating function of species richness should be expected because this mechanism assumes that increasing the number of individuals in a population will add more common species than rare species. This mechanism assumes that energy availability limits total abundance in a population assemblage. A complete test of the ‘sampling mechanism’ should be able to establish that environmental productivity, total abundance, and species richness are positively correlated (Evans et al. 2005).
The ‘increased population size mechanism’ is similar to the ‘sampling mechanism,’ and the key to distinguishing between these two mechanisms is being able to test for the reduced risk of extinction (Evans et al. 2005). The ‘increased population size mechanism’ stems from the species-area relationship. The species-area relationship is a theoretical relationship that predicts increasing species richness with increasing area of a sample (Arrhenius 1921, Conner and McCoy 1979, Wright 1983, Storch et al. 2005). Mathematically the species-area relationship is represented as $S = cA^z$, with $S$ being the number of species estimated, $c$ is the species constant, $A$ is the area of the estimate, and $z$ is the slope of the species area relationship (Arrhenius 1921, Bakowski et al. 2010, Willig et al. 2003). The risk of extinction effectively decreases with larger areas because there is greater species richness, which is supported by greater species abundance. It is assumed that increased amounts of area will result in greater resource abundance, which will increase population size and effectively decrease the risk of extinction (MacArthur and Wilson 1963). The species area relationship is closely related to the ‘increased population size mechanism’ because both predict that the risk of extinction is lowered with greater amounts of species richness, and that species richness is supported by species density. Therefore, the species at more productive elevations are less likely to experience local extinctions because these populations should occur in greater densities (MacArthur and Wilson 1963, Storch et al. 2005, Rowe 2009, Bakowski et al. 2010). The ‘increased population size mechanism’ is probably one of the most frequent contributors to species-area relationships, because large populations are at a lower risk of extinction (Evans et al. 2005).
The ‘increased population size mechanism’ has two key parts. The first part is that excess energy is accessible to the majority of species in a local population, and that this energy availability sets limits on species abundances. The second part is that species richness is limited by species abundance (Evans et al. 2005). This assumption is intuitive and supported by robust scientific data from field studies where high population numbers positively correlate with greater food availability (Andrewartha and Birch 1954, Forsman and Monkkonen 2003, Hutchinson 1959, Kaspari et al. 2000a, 2000b).

The present study evaluated a number of environmental productivity measures to provide support for a mechanistic explanation for species-energy relationships. By using a number of different environmental productivity measurements, it is possible to evaluate how well the richness and abundance of a given taxon is predicted. Many environmental productivity measures are measurements of climate or solar energy inputs (Evans et al. 2005). These are variables such as temperature, rainfall, primary productivity, net primary productivity (NPP), actual evapotranspiration (AET), potential evapotranspiration (PET), and normalized vegetation index (NDVI) (Currie 1991, Rowe 2009). These latter measurements all attempt to quantify the amount of energy that flows into the landscape due to climate. The present study will use temperature and precipitation as measurements of climatic productivity to examine if either or both are positively related to species richness.

Another way to assess environmental productivity is through abundances of resources available to consumers, these are known as ‘productive energy metrics’ (Evans et al. 2005). Resource abundance has been suggested to influence species richness (Hutchinson 1959, Kaspari et al. 2000a, 2000b, McGlynn et al. 2010). The present study
assessed two different food abundance measurements. The first is the abundance of arthropod food resources for small mammals, via ground-dwelling arthropod biomass. The second food abundance metric is understory plant biomass. The goal was to assess if either arthropod or understory plant biomass or both are positively related to small mammal species richness.

The ‘increased population size mechanism’ predicts that highly productive environments are able to sustain higher population abundances (Kaspari et al. 2000a, 2000b, 2003, McGlynn et al. 2010). It is assumed that the limiting factor to a population’s density is the flow of environmental energy into an ecosystem. Higher population sizes should then able to support greater species richness because species densities limit species richness (Kaspari et al. 2000a, 2000b, Evans et al. 2005, McGlynn et al. 2010). Therefore, small mammal abundance was also used as a measurement of environmental productivity. Questions posed included: Is there a positive relationship between total small mammal abundance and small mammal diversity? Using the various measures of environmental productivity assessed, including temperature, precipitation, food abundance, and small mammal abundance, it was also examined if these measurements produce a similar index to environmental productivity (e.g. are the productivity measures positively correlated with each other).

Each of these environmental productivity measures was assessed among elevationally distributed plots as a whole, and how the environmental productivity measures vary among habitat types was also examined. By examining the variation in species-energy relationships among habitat types and in total across all sites, we may be able to detect whether the landscape-scale trends are functions of all habitats combined or
only particular habitats. This is a novel feature of the present study, and may help detect if certain habitats are more significant in contributing to small mammal patterns of richness and abundance.

Elevational gradient studies are one of the strongest ways to test the various mechanisms responsible for producing species-energy relationships (Bateman et al. 2010, Brown 2001, Lomolino 2001, McCain 2005). These natural experiments have become a practical way to study patterns of species richness and species abundance over the past decade (Bateman et al. 2010, Brown 2001, Ferro and Barquez 2009, Heaney 2001, Li et al. 2003, Lomolino 2001, McCain 2005, McCain 2007, Rickart 2001, Rowe 2009). There are many reasons why elevational gradients have become such important models for testing hypotheses about species richness and environmental productivity. Elevational gradients occur over a relatively small spatial scale when compared to latitudinal gradient studies, thus making thorough trapping along a gradient both economically and temporally feasible. The numerous mountains in the world provide for multiple study sites that can be replicated and compared among each other (Brown 2001, Lomolino 2001, McCain 2005). Elevational studies have produced a number of diversity curves that differ in the patterns of diversity observed, which are produced by plotting species richness against elevation. Some of the most commonly documented diversity curves are monotonically increasing or decreasing, unimodal, or plateaus in richness (McCain 2005). This variability can help to inform researchers of the causes behind species-diversity curves by testing various indirect and direct variables that could be responsible for the production of diversity. These variables fall into the broad categories of evolutionary history, area, climate, and biotic interactions (Brown 2001, Lomolino 2001,
Elevational gradients feature non-random climatic changes, for example temperature decreases linearly with increasing elevation. This feature allows studies to test hypotheses relating to climate because abiotic factors such as temperature and precipitation change predictably with elevation (Brown 2001, Lomolino 2001, McCain 2005, Rickart 2001). Studies along elevational gradients are thus well suited to look at local species-energy relationships. The results of these local studies then can be compared with other data sets from over the world to see if local predictors of abundance and diversity are consistent. These findings also can help to inform land management personnel about how to protect and conserve local species distributions.

To our knowledge there has never been a complete elevation survey of small mammals in the Front Range of Colorado. A current understanding of the diversity in the area will provide valuable information about species-energy relationships that could have widespread applications for conservation, particularly for an ecosystem facing rapid climatic change. The present study focuses on how the relationship of small mammal diversity and five measures of environmental productivity (i.e., temperature, precipitation, arthropod biomass, understory plant biomass, and small mammal abundance) changes along an elevational gradient and addresses the following questions:

1. Is there a relationship between environmental productivity of the environment and small mammal diversity?
2. Is this relationship robust to various measurements of environmental productivity (i.e. temperature, precipitation, food resource abundance, and mammal abundance)?
3. Do these relationships vary among habitats, including forest, meadow, and riparian?

**Methods**

**Study Area**

The present field study took place in the summer of 2010 during the months of June, July, August and September. Ten research sites were examined along the Front Range of Colorado. Eight research sites were spread along an elevational gradient within the Boulder Creek watershed from 1700–3700 m separated from each other by approximately 200–300 meters in elevation. An additional two sites were placed in the Big Thompson watershed at 1700 m and 2100 m. Each of these research sites consisted of trapping transects targeting the various habitats at each site. The habitats studied were forest, riparian, rocky outcrops, and meadow. Each set of transects at a site included 300 Sherman traps, distributed approximately in accordance to the relative abundance of each habitat type. Each line consisted of a series of flagged stations separated by 10 meters with a Sherman live trap placed five meters perpendicular to either side of the line. Sherman live-traps were baited on one side with peanut butter and oats, and a seed mixture flavored with vanilla on the other side. We used two sizes of Sherman live traps, medium (9” X 4.5” X 3”) and large (12” X 4.75” X 3”). The captured animals were identified to species, sexed, external reproductive condition noted, marked (ear tag or toe clip), and weighed.

**Sampling plots**
At each 15th trap station, a vegetation and arthropod sampling plot was established. This insured that all habitat types were sampled. The sampling plot was centered on one of the two traps at the station, randomly chosen as to the right or left trap. Flags were placed in the four cardinal directions at one, three and five meters away from the center of each vegetation plot. To survey understory (< 1 m height) vegetation coverage of grass, forbs, shrubs, cacti, and bare ground, we used the Braun-Blanquet coverage classes to survey within the circle of one-meter flags. We measured the height of understory vegetation at the center of the plot as well at each three-meter flag. Tree number, tree richness, and tree size were estimated within the five-meter flag circle. Tree size was estimated using diameter at breast height (DHB) measurement for trees with a DBH greater than three centimeters. Canopy coverage was estimated using spherical concave densiometer readings [Forest Densiometers, Bartlesville, OK] at each of the three-meter flags facing toward the plot center.

Two arthropod traps were set within each sampling plot, three meters east and west of the center of the plot. In the event that pitfalls could not be placed at these orientations, they were placed as close to these positions as feasible given soil substrate. The arthropod pitfall traps were constructed of two nested 16 ounce plastic cups buried in the soil with their rims flush with the ground. Three wooden shims approximately 50 cm long were placed in three angles off of the cup, in an attempt to funnel arthropods into the trap. The top cup was filled approximately 1/3 full with Sierra antifreeze (propylene glycol). This is an environmentally safe chemical for preserving the arthropods, and preventing desiccation and decomposition. A simple plastic plate covered the cup and was balanced on top of the shims and three rocks to allow a small window for arthropods
to enter the trap. Rocks were placed on top of the plate to keep the cover secure. Traps were monitored throughout the summer to ensure that they had sufficient levels of antifreeze. In cases where the cup was full of arthropods, we collected the sample and refilled the cup with antifreeze. Pitfall traps were in place for 90 to 93 days depending on the site, except for the highest site (Niwot Ridge tundra at 3500–3600 m) where marmots (Marmota flaviventris) repeatedly pulled out the pitfall traps from the soil. After three unsuccessful attempts to marmot-proof the Niwot Ridge tundra traps, the pitfalls were removed. Therefore, this highest site on Niwot Ridge was not included in the arthropod food resource analysis.

Small Mammal Abundance Estimates

Small mammal abundance was estimated with four different methods in this study: (1) a modified Lincoln-Peterson estimator, (2) a modified Schnabel estimator, (3) the jackknife estimator within Program CAPTURE (Rexstad and Burnham 1992), and the minimum number of individuals known alive (MNKA) (Slade and Blair 2000). The modified Lincoln-Peterson was calculated by looking the total number of captures, total recaptures and total marked individuals. The equation was equal to \[ \frac{(\text{Total Captures} + 1) \times (\text{Total Marked} + 1)}{(\text{Total Recaptures})} - 1 \] (Krebs 1989). The Schnabel method was calculated by looking at the total number of marked individuals, the captures on the last trapping day, as well as the total recaptures on the last trapping day. This was equal to \[ \frac{\text{(Total Marked X Captures on last day)} / (\text{Recaptures on last day}) + 1}{(\text{Krebs 1989})} \]. The jackknife estimator from Program CAPTURE is designed to be a robust population estimate that takes into account the heterogeneity of capture probabilities, because different animals will exhibit different probabilities of being captured. The jackknife
estimate has been found to be the most robust estimate of population projections when accounting for the effects of heterogeneity (Otis et al. 1978). MNKA is the number of individuals marked in each transect (Slade and Blair 2000). Each estimate was performed for each individual species within a given habitat type. These species estimates were then summed to get an overall habitat and site abundance estimate for small mammals. These population estimates were compared to each other for robustness of the population values using linear regression analyses.

*Resource Abundance Estimates*

To estimate arthropod biomass as a measurement of food resource abundance, we used the average biomass from 40 standardized pitfall estimates per site. Arthropods from each pitfall were first cleaned by conducting several washes with water, then debris (e.g. gravel, sticks) removed using tweezers. The cleaned samples were then weighed with an Ohaus Scout Pro scale accurate to 0.1 gram, and placed in alcohol for preservation. Samples were then averaged according to habitat type to get the average biomass for each habitat by site as well as the total average for each elevation.

Average understory vegetation height (< 1 m) and the average Braun-Blanquet plant coverage classes of forbs, grass, and shrubs were used in combination to estimate understory plant biomass. Vegetation height below 1 meter was estimated at 5 points in each plot (center, four cardinal directions at 3m from center) using a meter stick. The Braun-Blanquet coverage classes [1–5] were used to estimate the understory vegetation coverage within the circle of one-meter flags at each vegetation plot for forbs, grasses and shrubs. Each number corresponded to a percentage coverage of vegetation within the 1 m-radius circular plot, 5 = >75% vegetative coverage, 4 = 50–75% vegetative coverage,
3 = 25–50%, 2 = 5–25%, and 1 = <5%. The understory vegetation coverage estimate for each sampling plot was an average coverage class among forbs, grass, and shrubs. The average understory plant biomass was the product of the averages of understory vegetation height and vegetation coverage class. For each research site, the understory vegetation height and Braun-Blanquet coverage class were averaged across sampling plots within each habitat type and among all habitats at a given elevational site.

Data Analysis

Linear regressions were used to assess how well correlated the population estimate MNKA was to the modified Lincoln-Peterson and Schnabel Methods, and to the estimates from program CAPTURE for the jackknife estimator. Simple and multiple linear regressions were used to assess the relationship between species richness and environmental productivity (i.e., temperature, precipitation, arthropod biomass, understory plant biomass, small mammal abundance). Temperature and precipitation data were obtained from BIOCLIM (Hijmans et al. 2005). Finally, linear regressions were also used to assess the concordance among the environmental productivity measures. The $R^2$ value describes how well the data is predicted by a purported relationship, and the p-value describes the probability of getting a smaller value than detected. The null hypothesis is simply that there is no significant relationship between the two variables and we assume that if the p-value is smaller than 0.05 then the null hypothesis is rejected. Each of these analyses compared at the total site values, as well as, the within habitat trends.
Results

Relationships Among Population Abundance Estimators

All population estimators were highly correlated with the minimum number of small mammals known alive (MNKA) (Table 1–1). The average $r^2$ for the MNKA with the modified Lincoln-Peterson, Schnabel Methods, and program CAPTURE was 0.9700, with an average p-value < 0.0001. The relationship of MNKA with the other population estimates was the most variable within the meadow, whereas other habitat types showed a more consistent population trend among estimates (Table 1–1; meadow average $r^2 = 0.8122$; meadow p-value = 0.0025).

Relationships among Species richness and Environmental Productivity Measures

Total species richness was significantly correlated with every environmental productivity measure used except arthropod biomass (Table 1–2, Figure 1–1). Total species richness was best predicted by precipitation ($r^2 = 0.6212$, p-value = 0.0032; a negative relationship), followed by understory plant biomass ($r^2 = 0.6404$, p-value = 0.0033). The only significant relationship among habitats was within the forest, with small mammal diversity being positively related to understory plant biomass (Table 1–2; $r^2 = 0.3671$, p-value = 0.0492).

Two multivariate regression analyses were used to assess the relationships of small mammal species richness and small mammal species abundance when including all the measurements of environmental productivity (temperature, precipitation, understory plant biomass, arthropod biomass, small mammal abundance). Once the significant correlations among variables (temperature, precipitation, and MNKA) were accounted for through multiple regressions, species richness was best predicted by understory plant
biomass alone ($r^2$ value = 0.7005, p-value = 0.0049, Table 1–4), as was small mammal abundance ($r^2 = 0.6695$, p-value =0.0070, Table 1–4).

*Relationships among Environmental Productivity Measures*

Total understory plant biomass was significantly correlated with every environmental productivity measure except arthropod biomass (Table 1–3, Figure 1–2). MNKA and total understory plant biomass showed the strongest relationship ($r^2 = 0.6345$, p-value = 0.0035). Precipitation exhibited a significant negative correlation with understory plant biomass among all habitats ($r^2 = 0.3645$, p-value = 0.0380), within the forest habitat ($r^2 = 0.4350$, p-value = 0.0317), and within the meadow habitat ($r^2 = 0.6695$, p-value = 0.0043).

**Discussion**

Overall, strong relationships with environmental productivity and small mammal species richness were found along the elevational transect in the Front Range, Colorado. The results of the present study suggest that small mammal species richness is driven directly by the effects of understory plant biomass on small mammal abundance and indirectly through climatic effects on vegetative growth.

All estimates of population abundance for small mammals were highly and positively correlated (Table 1–1, Figure 1–4). This is consistent with the findings of Slade and Blair (2000) that the minimum number of individuals known alive of small mammals (MNKA) is highly and positively correlated with various estimates of small mammal population size such as the modified Lincoln-Peterson and CAPTURE jackknife estimator. Therefore MNKA is equally robust to the modified Lincoln-Peterson, Schnabel
Methods, and CAPTURE jackknife estimator of population abundance. MNKA was therefore used as the preferred productivity measurement of small mammal abundance in testing for the relationships of species abundance with species richness.

Arthropod biomass was not significantly correlated with any variable in this experiment; consequently arthropod biomass was neither a good predictor of small mammal abundance or species richness (Figure 1–3). It is commonly assumed that arthropod abundance correlates with temperature since insects are ectothermic (Kaspari et al. 2000a, 2000b, 2003). Therefore, it was particularly surprising that arthropod biomass was not significantly correlated with temperature (Figure 1–3). Ants have been categorized as thermophillic since studies detected a strong positive relationship between net primary productivity (NPP) and ant species abundance in individual studies and meta-analyses (Brown 1973, Kaspari et al. 2000a, Kaspari et al. 2003). Temperature has been found to be a significant factor in the production of NPP, and it was found that temperature alone accounted for 13.8% of the variability in abundance in an ant meta-analysis (Kaspari et al. 2000a). The results of our data are nearly opposite of these previous findings as our highest elevation arthropod biomass sample (3400 m) had the highest average biomass despite being the coldest site sampled. This discrepancy is most likely due to the generalized comparison between arthropod biomass to ant abundance. These are two very different taxonomic classifications. Future analysis of our pitfall data into finer groupings of biomass, diversity and abundance within the various arthropod groups, along with detailing the diversity and abundance of ant species along elevation gradients in Colorado will clarify if this opposing trend is robust.
Support for a Mechanistic Explanation of Species-Energy Relationships

The results of the present field study, that understory plant biomass was the best predictor of both small mammal species abundance and small mammal species richness, provides support for both the ‘increased population size mechanism’ and the ‘sampling mechanism’ as drivers of species-energy relationships and is consistent with previous findings (Kaspari et al. 2000a, 2000b, Evans et al. 2005). These two mechanisms cannot be explicitly distinguished in the present study, as the risk of extinction was not directly tested. However, useful predictions can be made with these data to begin to differentiate the two and evaluate the risk of extinction at certain elevations, which is sole difference between these two mechanisms (see below).

Understory plant biomass was the sole significant predictor of small mammal species abundance and small mammal species richness according to the multivariate analysis results (Table 1–4). As discussed earlier, it is appropriate to treat understory plant biomass as an accurate measurement of environmental productivity (Evans et al. 2005), and here it was also shown to be strongly positively correlated with temperature and negatively correlated with precipitation (both indicating a climatic productivity relationship). Understory plant biomass is responding to inputs of climate (temperature and precipitation), and small mammal species richness and abundance is responding to understory plant biomass. Therefore small mammal species richness and abundance are indirectly responding to climatic productivity.

The elevations with the highest amount of average understory plant biomass were the elevations with the highest abundance of small mammals. These high abundances of small mammals also supported the highest amounts of species richness. Positive
relationships between environmental productivity and species abundance were found as well as positive relationships between species richness and species abundance in the present study. It has been suggested that increased resource abundance will decrease the risk of extinction (Wright 1983). Species at more productive elevations are therefore less likely to go extinct since the greater available resources presumably support greater local population sizes (MacArthur and Wilson 1963, Storch et al. 2005, Rowe 2009, Bakowski et al. 2010). Therefore, albeit somewhat indirect, there is theoretical support for the ‘increased populations size mechanism’ in the form of reduced extinction risk in the present study.

It is commonly assumed in the literature that resource abundance influences the patterns of species abundance and species richness observed in nature. Earlier elevational studies suggested that small mammal species richness would be correlated with species abundance (Heaney 2001, Sanchez-Cordero 2001, Li et al. 2003). Abundance data provided by Heaney (2001) were inadequate to access the relationship between small mammal abundance and richness across the whole elevations transect, but lower elevation sites appeared to display a relationship (Heaney 2001). Early elevational studies of small mammals in the mountains of Oaxaca, Mexico concluded that primary productivity and food resource diversity correlated positively with species richness (Sanchez-Cordero 2001). A similar conclusion was reached by a study on Mt. Qilian, China showing that species richness correlated with primary productivity and the diversity of herbs (Li et al. 2003).

Andrews and O’Brien (2000) assessed mammal species richness in southern Africa and found that climatic has an indirect effect on observed small mammal species
richness. Variation in plant species richness was furthermore found to be responsible for up to 75% of the variation in mammal species richness, and a positive relationship between of species richness of plants and mammal species richness was thus established (Andrews and O’Brien 2000). Studies performed by McCain (2005), Lomolino (2001), Brown (2001) and Heaney (2001) also suggested that small mammal species richness is responding to the indirect effects of climate. The inputs of climate, mainly precipitation and temperature account for the plant species richness produced (Andrews and O’Brien 2000).

Evans et al. (2005) concluded that the strong theory and empirical evidence behind the increased population size, niche position, and diversification rate mechanisms make attractive explanations of species energy-patterns. Further data collection and analysis will hopefully display that these first season patterns are robust findings. There are many other studies that support these three attractive mechanistic explanations. Kaspari et al. (2000a, 2000b) provided support for the ‘increasing population size mechanism,’ in the form of increased ant species density with increasing NPP, and increased species richness with increasing species density. Kerr and Packer (1997) also support the ‘increasing population size mechanism’ as the driver of small mammal species richness.

However, there are other studies that do not provide support for the ‘increasing population size mechanism.’ Kaspari et al. (2003), as well as McGlynn et al. (2010) provided support for the ‘diversification rate mechanism’ in colonies of ants. This mechanism predicts that species richness is the result of increasing amounts of solar energy (temperature and ultraviolet radiation), which can affect the mutations rates in
genetic information because these are frequent causes of mutations (Evans et al. 2005). Srivastava and Lawton (1998) did not find that increasing amounts of resources lead to increased species densities, which would have to be the case for the ‘increased population size mechanism’ to be validated. Currie et al. (2004) did not find adequate empirical support for the ‘increased population size mechanism’ despite the finding that energy correlates well with patterns of species richness. Future studies should test mechanisms that best apply to the taxon of study because it is clear that different mechanisms can apply to different groups of organisms.

The results of this study provide support to the theory that small mammal diversity and abundance is the indirect result of climatic inputs mediated by vegetative food resource abundance. Our measurements of climate were significantly correlated with understory plant biomass, which shows that these variables have a significant effect on understory plant biomass. In addition, the theory behind these results is attractive because net above ground productivity apparently sets limits on herbivore populations. The significant relationships between climatic productivity, understory plant biomass, and small mammal species richness and abundance were detected after an initial season of fieldwork. It will be interesting to see if these patterns remain robust after more field sites are added to this data set. There was not nearly as much data for individual habitats as for the totals at each elevation. Perhaps with more data within forest, riparian and meadow habitats, some of the total trends detected will show divergent patterns among the various habitats.
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Literature Cited


Table 1–1: A comparison of four small mammal population estimation techniques (MNKA=minimum number of individuals alive, LP=Modified Lincoln-Peterson, Schnabel=Schnabel Methods, and Capture Jackknife) across the 10 elevational sites in the Front Range, Colorado.

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<th>MNKA-LP</th>
<th>MNKA-Schnabel</th>
<th>MNKA-Capture</th>
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<td>Riparian</td>
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<td>0.9463</td>
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Table 1–2: A comparison of linear regressions between species richness and productivity measures across the 10 elevational sites in the Front Range, Colorado. (Temp.=Temperature, Precip=Precipitation, and MNKA=minimum number known alive). Yellow shading indicates significant.

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<tbody>
<tr>
<td></td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
</tr>
<tr>
<td>Total</td>
<td>0.6212</td>
<td>0.0041</td>
<td>0.6438</td>
<td>0.0032</td>
<td>-0.1285</td>
</tr>
<tr>
<td>Among Habitat Types</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>0.1438</td>
<td>0.1696</td>
<td>0.0279</td>
<td>0.3042</td>
<td>-0.1427</td>
</tr>
<tr>
<td>Meadow</td>
<td>0.0366</td>
<td>0.2911</td>
<td>-0.0338</td>
<td>0.4187</td>
<td>0.0126</td>
</tr>
<tr>
<td>Riparian</td>
<td>-0.1944</td>
<td>0.8840</td>
<td>-0.1422</td>
<td>0.6363</td>
<td>-0.0291</td>
</tr>
</tbody>
</table>
Table 1–3: A comparison of linear regressions between environmental productivity measures across the 10 elevational sites in the Front Range, Colorado (MNKA=Minimum number of individuals known alive). Yellow shading indicates significant.

<table>
<thead>
<tr>
<th>Total</th>
<th>MNKA</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Arthropod Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
<td>P-Value</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.1295</td>
<td>0.1647</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0.1320</td>
<td>0.1624</td>
<td>0.9520</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Arthropod Biomass</td>
<td>-0.0644</td>
<td>0.4959</td>
<td>-0.0809</td>
<td>0.5466</td>
</tr>
<tr>
<td>Plant Biomass</td>
<td>0.6345</td>
<td>0.0035</td>
<td>0.4373</td>
<td>0.0222</td>
</tr>
</tbody>
</table>

Among Habitat Types

<table>
<thead>
<tr>
<th>Forest</th>
<th>MNKA</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Arthropod Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
<td>P-Value</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.0724</td>
<td>0.5194</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.0046</td>
<td>0.3590</td>
<td>0.9418</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Arthropod Biomass</td>
<td>0.0064</td>
<td>0.3393</td>
<td>0.2056</td>
<td>0.1232</td>
</tr>
<tr>
<td>Plant Biomass</td>
<td>0.3191</td>
<td>0.0657</td>
<td>0.5083</td>
<td>0.0187</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Meadow</th>
<th>MNKA</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Arthropod Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
<td>P-Value</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.0329</td>
<td>0.2966</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.0194</td>
<td>0.3879</td>
<td>0.9482</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Arthropod Biomass</td>
<td>-0.1667</td>
<td>0.9964</td>
<td>0.0811</td>
<td>0.2505</td>
</tr>
<tr>
<td>Plant Biomass</td>
<td>0.1763</td>
<td>0.1435</td>
<td>0.6151</td>
<td>0.0075</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Riparian</th>
<th>MNKA</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Arthropod Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R^2</td>
<td>P-Value</td>
<td>R^2</td>
<td>P-Value</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.0969</td>
<td>0.5234</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.1294</td>
<td>0.6002</td>
<td>0.9521</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Arthropod Biomass</td>
<td>0.2687</td>
<td>0.1335</td>
<td>0.3810</td>
<td>0.0825</td>
</tr>
<tr>
<td>Plant Biomass</td>
<td>0.2359</td>
<td>0.1521</td>
<td>0.0050</td>
<td>0.3567</td>
</tr>
</tbody>
</table>
Table 1–4: Two multivariate regression analyses assess the relationships of small mammal species richness and small mammal species abundance when including all the measurements of environmental productivity (temperature, precipitation, understory plant biomass, arthropod biomass, small mammal abundance=MNKA). Yellow shading indicates significant.

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2$</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>MNKA Model w/ temperature, precipitation, understory plant biomass, arthropod biomass</td>
<td>0.6695</td>
<td>0.0070</td>
</tr>
<tr>
<td>Diversity Model w/ temperature, precipitation, understory plant biomass, arthropod biomass, MNKA</td>
<td>0.7005</td>
<td>0.0049</td>
</tr>
</tbody>
</table>
See the figure below for the regression results of total species richness and environmental productivity measures (species richness=richness and MNKA=minimum number of individuals known alive). Red lettering indicates significant.
Figure 1–2: Regression results of understory plant biomass with diversity as well as among the productivity measurements (MNKA = minimum number of individuals known alive). Red lettering indicates significant.
Figure 1–3: Linear regression results of arthropod biomass and species richness, as well as among productivity measures (MNKA=minimum number of individuals known alive).
Figure 1–4: Graphs of total population abundance estimates as well as for each habitat type. (LP Abundance=modified Lincoln-Peterson estimator, MNKA=minimum number known alive, Schnabel Abundance=Schnabel Methods estimator, CAPTURE=Capture Jackknife estimator.)