The spatial-temporal structure of Boulder County's prairie dog towns: patterns and processes from an ecological engineer

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Abstract

Ecosystem engineers construct habitats that largely alter landscape structure. Point pattern analysis, growth rates and scaling factors are tools that can infer pattern generating properties of constructed habitat. I used the burrow system engineered by black-tailed prairie dogs as a model system to characterize large-scale landscape alterations. Instead of relying on time-consuming and inaccurate methods of data collection by GPS, the study took advantage of technological advancements in landscape visualization with the use of aerial imagery to identify constructed habitat from space. Imagery for Boulder County for a time series spanning 2002 to 2018 captured the spatial distributions and growth rates of 15 prairie dog towns. I found that burrows are consistently constructed in non-random clustered patterns, prairie dog town growth is size dependent, and town structure is dictated by strong density-dependent effects. In the process of a prairie dog town changing from a young, small town to a large, established town, burrows become more intensely clustered, density is conserved, area scales sub-linearly, and edge growth decreases. Despite some local variability, the study finds regional convergence upon a set of habitat characteristics. The described emergent properties can support land management in areas with heightened human-prairie dog conflict. On a larger scale, the optimization of the prairie dog engineered system with defined social groups can advise human-engineered systems.

1. Background

Certain species actively engineer landscapes by constructing habitat. Humans are the most familiar example, but a variety of divergent species engineer landscapes as well, including, bees, ants, birds, and some mammals. Social or not, individuals in a species rarely construct habitat independently from each other (Rietkerk and Van de Koppel 2008; Pringle and Tarnita 2017). For many species each construction is erected relative to the spatial location of other constructions (Rietkerk and Van de Koppel 2008; Pringle and Tarnita 2017).

Spatial distributions of constructed habitat involve intricate interactions between resource flow and density feedback that proceed to a stable spatial arrangement (Rietkerk 2004; Sleeman et al. 2005). At the same time that succession advances towards stability, disturbance can reverse and breakdown community structure if the system lacks positive feedback (Sankaran et al. 2019). The organisms that construct such habitats and change the landscape are known as ecosystem engineers. The following subsections will provide background information on ecosystem engineers, extended phenotypes and scaling coefficients, and the spatial distributions and growth types of constructed habitats.

1.1 *Ecosystem engineering*

The activities of ecosystem engineers modify the living or non-living materials in their environment with direct or indirect effects on the energy flow of the ecosystem (Jones et al. 1994). The modification of landscapes by ecosystem engineers can influence population persistence (Ellner et al. 2001), often resulting in non-random patterns (Table 1). Aggregation within constructed habitats is generally considered a product of co-existence and cooperation (Lion and Baalen 2008; Lacey et al. 2019), while uniformity is considered a product of competition and territoriality (Dibner et al. 2015: Getzin et al. 2019a). One emergent property of persistent aggregation is clustering intensity (*I*). Intensity describes the average separation of individuals or groups across space. It is a consequence of behavioral separation or of physical boundaries that influence construction of habitat.

1.2 *Extended phenotypes and scaling coefficients*

Clustering can be seen in the two habitats constructed by ecosystem engineers in Figure 1: human suburb (left) and black-tailed prairie dog (*Cynomys ludovicianus*) town (right). Although the constructed habitat is technically abiotic, its study is of interest because its existence is determined from a biotic organism that is influenced by natural selection. The term extended phenotype is introduced because selection is acting on a stationary object beyond a biological boundary (Dawkins 1982; Minter et al. 2012). For humans, the emergent extended phenotype of the group is the city, and for prairie dogs, the emergent extended phenotype of the group is the town consisting of burrows.

At the group level, we can use scaling coefficients for inferring properties of the extended phenotype (Bettencourt et al. 2007). In this case, we are interested in properties of the structure of constructed habitats relative to population size (Bettencourt et al. 2007; Khiali-Miab et al. 2019) (Bettencourt et al. 2007; Khiali-Miab et al. 2019). The phenotype is some measurable property of constructed habitat, such as density or clustering intensity.

Measurable properties of population viability and population size are related using three types of scaling coefficients (Figure 2) (Khiali-Miab et al. 2019). Studies of scaling coefficients in human cities provide a parallel framework for non-human engineers. In human cities, innovations (measured by number of patents or art) and the prevalence of disease (which depends on interaction between individuals) scale supra-linearly with population size (Bettencourt et al. 2007). Opposingly, the number of food stores and gas stations scale sub-linearly with population size, suggesting an economy of scale (Bettencourt et al. 2007). The success of scaling theory for understanding the macroecology of cities seems appropriate for applying to other organisms that, like humans, are engineers that construct habitat on the landscape.

1.3 ***Spatial distributions and growth types of constructed habitats***

Landscapes containing constructed habitats and underlying spatial patterns can also be characterized using point pattern analysis. In a review on pattern formation, Pringle and Tarnita et al. (2017) find evidence that intergroup competition for limited resources in insects generates uniform distributions of structures. There are, however, other species (notably vertebrates) for which spatial distributions of constructed habitats are either random or clustered (Table 1). The spatial distribution of groups of individuals, and the properties of extended phenotypes, can vary over scale and time (e.g. Schooley and Wiens 2001; Bourguignon et al. 2011). To understand the ways in which properties can vary we return to the human city comparative framework.

Urban growth typically happens in one of three ways: infilling, edge growth, and the emergence of outlying communities (Liu et al. 2014). Infill growth takes place within the perimeter and often involves the modification or destruction of existing structures. Edge growth and outlying growth occur when there is space and resource availability around the perimeter. However, structures built on the perimeter can be viewed as less desirable given their non-central location (Khiali-Miab et al. 2019). All new construction is dependent on the distribution of existing structures due to differential access to resources (Samaniego and Moses 2008). Another property of growth is that growth can become bounded. For example, in Boston and New York where water prevents edge growth in certain directions, population may be limited by space availability.

2. Introduction

The construction of habitat by multiple individuals generates large-scale patterns that impact the energy flow of the ecosystem (Jones et al. 1994; Dibner et al. 2015). Such patterns can be documented from an aerial view to support and develop hypotheses surrounding underlying pattern influences and limiting properties (Dibner et al. 2015; Lara-Romero et al. 2016; Sankaran et al. 2019). Using black-tailed prairie dog (*Cynomys ludovicianus*) burrows and towns as a model constructed habitat, I ask whether there are consistent patterns of burrow distributions within and among towns.

2.1 *Capturing spatial distributions of constructed habitats*

Established constructed habitats, such as mounds and burrows generated from animal activity, can be detected from space (Table 1). This increased potential for spatial pattern recognition has accelerated development of landscape ecology over the past 15 years. This is in part due to increased access to free and open remote imagery, including the establishment of Google Earth (GE) in 2005. As a result of research verifying GE as an accurate classification tool (c.f. Hunter 2009; Ploton et al. 2012; Tilahun 2015), there has been an influx of studies using GE to report spatial patterns (c.f. Dibner et al. 2015; Funch 2015; Juergens et al. 2015; Zangerlé et al. 2016). For certain species and geographical locations, advancements in landscape visualization is supporting progress in the understanding of ecosystem-engineered landscape patterning. However, data on spatial scales of constructed habitats remains incomplete.

2.2 *Prairie dog towns as a model system*

To reduce the gap in spatial knowledge, I focus on characterizing the spatial structure and scaling properties of habitat constructed by an ecosystem engineer, the prairie dog. As keystone species, prairie dogs are vital contributors to their ecosystem and allow for a variety of plant and animal species to exist (Kotliar et al. 1999; Bangert and Slobodchikoff 2000). Prairie dogs are one of only a few species that make large-scale landscape alterations and the distributions of their habitat have yet to be quantified. Burrow systems are marked by an entrance on the surface and extend underground in complex formations. After construction, burrows undergo dynamic phases in which they are actively maintained, abandoned, or actively destroyed (Reichman and Seabloom 2002). When burrows are abandoned, plants colonize the patch and the integrity of the hole decays over time frames depending on local conditions (Osborn and Allan 1949). Established burrows are generally elevated above the ground surface in a mound-like shape identifiable by a bare patch of soil and entry hole (Figure 1. Right).

Distributions of burrows may be mediated by social interactions as prairie dogs reside in social groups on landscapes (Hoogland 1998). Notably, prairie dogs display cooperative behavior in social groups that occupy and defend a defined space within the larger town (Hoogland 1998). These groupings, known as coteries, are typically made up of one adult male, 3 to 4 adult females and their offspring (Hoogland 1998). Towns can consist of a few to many coteries, although today's towns are markedly smaller than historic towns that once covered 2 - 15% of landscapes larger than 400,000 hectares (Knowles et al. 2002). Only an estimated 2% of the historic population remains due to targeted eradication, habitat loss and sylvatic plague (*Yersinia pestis*) (Kotliar et al. 1999).

Cooperation between family groups allows for task allocation of food gathering, predator warning, territory defense and burrow development and maintenance (Rayor 1988; Bangert and Slobodchikoff 2000; Shier and Owings 2007). Previous investigations on the spatial distribution of divergent species provide evidence that rodent burrows, specifically kangaroo rats (Schooley and Wiens 2001) and great gerbils (Wilschut et al. 2015) are clustered. However, prairie dog burrows have yet to be studied, leaving the question whether they depart from regular spatial patterning.

My analysis of spatial structure was motivated by an interest in whether the growth and characteristics of different prairie dog towns follow a general set of rules, suggesting growth is governed by the interplay of social interactions and energetic constraints on population size. Alternatively, different prairie dog towns may have unique properties that reflect differences in available resources and historical events. To explore such patterns, the spatial structure of prairie dog towns in Boulder County were considered over a timespan of almost two decades.

2.3 ***Predictions***

I have organized my thesis around four related hypotheses and corresponding predictions (Table 2). First, I predict the spatial structure of the constructed habitat of black-tailed prairie dog towns is influenced by social interactions and the distribution of resources. In general, I hypothesize that burrow construction and maintenance depend on the burrow’s location relative to other built structures. Burrows are not constructed independently from already existing burrows, and thus will depart in some way from complete spatial randomness (CSR). In a resource-scarce system with pronounced competition, burrows may be arranged such that the distribution maximizes space between individuals. Alternatively, if there is social benefit in a cooperation-based system, one would find burrows constructed in groupings. I predict prairie dog burrows to be clustered within towns as a benefit to cooperative behavior.

Second, the spatial prairie dog town structure reflects a space-filling process dependent on burrow density. If this is true, density will be conserved within towns. Once an area is saturated by burrows, survivorship of new burrows within that area will plummet. Alternatively, if density is too low, benefits of cooperation will be underutilized. If there are density-dependent effects, we might expect scaling coefficients, that estimate large-scale properties, to be sublinear. This would suggest an economy of scale as towns become larger; alternatively, scaling coefficients may be linear suggesting each constructed and maintained burrow occupies an approximately equal size area within the town.

Third, prairie dog towns can grow or shrink depending on local demography and excavation activities of individual animals. These factors may be influenced by regional factors that influence the productivity of grasslands, mainly due to precipitation, and by local factors specific to each town. If regional factors mostly influence growth rates of towns, estimates of growth rates among geographically isolated towns should show similar patterns of growth over time. Alternatively, if local factors play the primary role, estimates of growth rates among geographically isolated towns should be uncorrelated and independent.

Finally, the spatial prairie dog town growth reflects a space-filling process dependent on town age, size and density saturation. If this is true, town growth will happen by edge growth when towns are small and by infilling when towns are larger. Alternatively, if town growth is more of a diffusive process following initial establishment, towns will grow mainly by edge growth regardless of size.

3. Methods

My study area is City of Boulder Open Space & Mountain Parks (OSMP) land in Boulder County, a semi-arid area located at the base of the Colorado Rocky Mountains. Black-tailed prairie dog (*Cynomys ludovicianus*) burrows are abundant in the study area with 118 towns identified on OSMP land. Data for 15 prairie dog towns was collected using publicly available aerial imagery provided by the City of Boulder for years 2002, 2006, 2008, 2010, 2012, 2014, 2016 and 2018 (Figure 3. L). The imagery ranges from 3-12 in/pixel and was imported directly in QGIS 3.10 as map server connections. Towns range in size and location within the study area. The following subsections detail the unique data collection method and then describe analyses completed for three categories of understanding: spatial distributions, density dependence and growth rates.

3.1 ***Acquisition of burrow locations***

Instead of relying on time-consuming and inaccurate methods of data collection by GPS, the study takes advantage of technological advancements in landscape visualization with the use of aerial imagery. Burrows were manually located and verified for each town using QGIS 3.10. To identify burrows, a 10 by 10 m grid layer was added over the raster, covering the extent of the test area.

Beginning with the most recent timestamp, I scanned the town from left to right, one grid box at a time, until a region with increased brightness was noticed. At this time the region of interest (ROI) was inspected for roundness of form, a dark center, and a light-colored halo. If at least two of the three characteristics were present, the point feature was used to mark the center point. Then the scanning process resumed. I saved the completed shapefile layer as a new file and overlaid it onto the next most recent time-stamp image. That image was then evaluated using the copied data. Using the same scanning process, I identified and marked any additional ROI. Additionally, if a marked region was darkly colored and there was no light-colored marking near the marked reference point, the mark was removed. This process continued until the least recent time-stamped image was annotated.

Marked burrows were exported as latitude-longitude values in a csv file from QGIS. Given differences in images across years, there was geospatial error resulting in the apparent existence of two or more burrows when, in reality, there was a single burrow. Geographically fixed landmarks were measured, and associated variances were taken as a threshold. If the distance between two (or more) nearby burrows was less than the error associated with defining the location of the fixed landmark, the burrows were collapsed and assigned a latitude-longitude value based on the average value of the burrows. A presence-absence matrix was determined so that the survivorship of a single burrow could be assessed throughout the time series (Figure 3.C).

3.2 *Spatial Distributions*

Within the time series data, the burrows could be arranged in clustered, random or uniform distributions (Figure 3. T). Nearest-neighbor analyses do not consider information beyond the closest event and thus fail to account for scale dependence of point patterns (Pringle and Tarnita 2017). Applicable across multiple scales, Ripley's K function has become an increasingly common statistic for point pattern analysis of constructed habitats following its development in 1976 (Ripley), (Knowles et al. 2002). Here Ripley's K and L allowed me to estimate the structural properties of prairie dog towns, including whether there are identifiable "neighborhoods" defined by burrow clusters within towns, without bias of discrete scale lengths.

I employed Ripley's K and its L transformation using the spatstat library in R (Figure 3. T) (Baddeley and Turner 2005). The metric quantified if the number of events (points) observed within a given radius deviated from the theoretical Poisson, or complete spatial randomness (CSR). The isotropic correction scaled the naiveK estimate to the proportion of the circle (with radius r) that falls outside the study area to the circle that lies inside the study area.

L, the square root transformation, stabilizes variance and transforms the Poisson Distribution, Lpois(r), to a straight line allowing for clear graphical interpretation. Values of $L(r) = 0$ suggest a random pattern while values of $L(r) < 0$ suggest regularity and values of $L(r) > 0$

suggest clustering (Table 2. row 1). To test the prediction that prairie dog burrows will be clustered I compared patterns for years 2002-2018 for 15 towns to a pointwise confidence envelope calculated from 99 Monte Carlo simulations under CSR.

To quantify the extent of spatial patterns the maximum intensity of clustering, *I*, was recorded as the maximum L(iso) value for each year and site (town location). Higher values of *I* indicate larger degrees of burrow clustering. I ran a linear model to consider large-scale relationships between intensity of clustering and the number of burrows among towns. Mean *I* and mean number of burrows over the time series were collected for each town. I transformed the relationship to a log-log scale to account for normality and to consider scaling relationships.

3.3 *Density Dependence*

Scaling relationships were further considered for investigating trends in town density. To quantify density of burrow packing I used Voronoi tessellations, computer generated diagrams that partition points into polygons such that the area around each point expresses the maximum distance the point takes up in space (Figure 3. R) (Turner 2020). Voronoi tessellations were generated using the deldir package version 0.1-16 in R. I log transformed the areas of generated polygon tiles to fit a normal distribution. Tile area is an inverse measure of density such that smaller tile areas represent areas with high burrow density and larger tile areas represent areas with low burrow density.

To test predictions about density dependence, I first created a singular mixed effect model with three predictor variables to explain the average tile area. The number of burrows present in the town was included as a fixed effect while site (town location) and year were included as random effects to account for non-independence of observations across a single year or within a single site. I log transformed average tile area and number of burrows to conform to the model assumption of a Gaussian distribution.

During data exploration, site was considered as a fixed effect and as a random slope. All models, including those not explicitly described, were compared using AIC. The model with the lowest AIC value was considered the best fitting model.

Finally, I was interested in whether there was evidence of a single scaling coefficient that describes the growth of towns over time, or whether each town grows in ways that are unique to localities. To evaluate this, I constructed individual linear models for each town with the log town size (estimated by the number of burrows) as a predictor variable and the log of the average tile area (inverse density). For each site, a slope and effect size were extracted from the site-specific model. Such slopes revealed whether density was dependent on town growth.

3.4 *Growth Rates*

Town growth rates for years 2002-2020 were considered at three levels: growth of town area, growth of total burrow number, and infilling versus edge growth. I quantified area growth using the geometry library in R. Polygons were drawn around each town for each year using a minimum convex hull.

First, to test if area growth rates of towns are correlated with each other (Table 2. row 3), I recorded the polygon areas. Next, I calculated net rates of burrow growth from the total captured burrows each year and constructed a linear model to predict log area growth from the log number of burrows. Then, to determine relative growth rates, I obtained individual growth rates of infilling and edge growth from the sp library in R (Figure 3.B). Points (burrows) from time t+1 were overlaid on the minimum convex polygon from time t and separated into infilling or edge growth categories. Finally, I calculated percent growth for each category of growth for each year and site (town location) to test predictions 4 A and B (Table 2. row 4).

I performed a t-test to determine differences between growth rates of infilling and edge growth. The number of burrows present in a town and the type of growth were used as predictors for burrow growth rate (percent) in a random-effect mixed model. I log transformed growth rates and number of burrows to conform to the model expectation of Gaussian distribution. To compare relative rates of growth across towns (Table 2. row 3), I included site and year as random effects and an interaction between the number of burrows and growth type. All models, including those not explicitly described, were compared using AIC. The model with the lowest AIC value was considered the best fitting model.

4. Results

The models, scaling coefficients, and point pattern metrics revealed that except for the case of town area growth, habitat constructed by black-tailed prairie dogs consistently departs from null hypotheses of complete spatial randomness, density independence and constant growth type rates. The following subsections describe clustered burrow patterns, the relationship between burrow number and density, local growth rates, and growth type dependence on town size.

4.1 *Clustered patterns of burrows*

For all years and sites, prairie dog burrows were significantly clustered ($L(r)-r > 0$) at scales greater than ~5 meters (Fig 4. Left). At scales less than ~5 meters, the distribution did not significantly deviate from complete spatial randomness (CSR). Burrow pattern intensity (I) varied with site, year and scale. I increased with scale and the average I was 38.37 (SE+/- 2.25). Pattern variation was more common in small and unestablished towns (Short, East). With fewer burrows, density-dependent effects are less influential (Hassel 1975), and spatial distribution is more likely to follow a random pattern. Values of *I* that are particularly high indicate the presence of sub-towns within the site. The sub-towns themselves are clustered from each other. Density of burrows was not correlated with *I* (r= 0.16).

Town size significantly drives mean town clustering intensity (Table 3). The positive sublinear relationship had a slope of 0.37 +/- 0.08, indicating density dependence (Figure 4. Right). Smaller towns with fewer burrows had significantly lower intensity of clustering relative to larger towns. There was more variation in the number of burrows in a town from years 2002-2020 than there was variation in *I*.

4.2 ***Relationship between burrow number and density***

In addition to predicting intensity of clustering, the number of burrows in a town also positively predicted burrow density, supporting the hypothesis that prairie dog town spatial structure reflects a density-dependent burrow space-filling process. In the 15-site mixed model, log number of burrows predicted log tile area ($\chi^2(1)$ =57.25, p=3.833e-14), indicating that town size is density regulated (Table 4). Within towns, density increased with town size, and among towns, density was conserved (Figure S1). When the scaling exponent is negated to capture density, it is 0.40 +/- 0.04, which is significantly less than 1. Burrow density increased sub-linearly with the number of burrows.

When the random slope and intercept model was compared to the random intercept model, the likelihood ratio test showed no significant difference between the models. The random intercept model was chosen given the fewer estimated parameters. This indicates that while sites vary in intercept, the slope/scaling coefficient is strongly conserved. The random effects of site and year contained variation in total town area with town sizes ranging from 0.73 to 63.9 acres.

The null model predicted an intercept of 4.86 (+/- 0.08) with a slope of zero, or that the log tile area would be 4.86 at each site. This finding was reiterated in the average log tile area across all sites of 4.87 (Figure S1. grey dashed line). Consistent burrow density among fifteen towns with variable area indicates strong density-dependence where the probability of birth and survival for burrows decreases above and below the ideal burrow density (Hunter 2009).

Individual site models considering the relationship between the log number of burrows in a town and the log tile area over time reveal a general trend. Regardless of town, prairie dogs create habitat that follows a density-conserved arrangement (Figure 5). The estimated coefficients varied between approximately -1 to 0.28 across the 15 towns. The 95% confidence intervals for coefficients from 10 of the towns overlap with the mean, suggesting there may be a general density-dependent scaling process underlying the structure of prairie dog towns. Twelve out of fifteen towns had a slope that deviated from zero.

Of the sites whose slopes are not significantly different from zero, two sites lie outside the upper outer fence (Q3 + 1.5*IQR), DB and Flatirons (Figure 5). DB (and Sam's, although Sam's did not lie outside the outer fence) had little variation in the number of burrows present over the time series. Consequently, there was not a clear signal of a trend. Flatirons departed from expectations likely due to loss of burrows around town edges. When I removed the two sites outside of the upper outer fence, the mean scaling coefficient was -0.59 (Figure 5, red line). Since tile area is an inverse measure of density, the inverse scaling coefficient, 0.59, is more intuitive for making conclusions.

4.3 *Local growth rates*

I can conclude from prairie dog town area growth measurements that temporal advances and declines support the hypothesis that town area growth reflects local factors. Individual town area growth rates varied from year to year and from other town area growth rates (Figure 6). Mean positive growth was 9.36% per two years, mean negative growth was -5.69% per two years and overall mean growth was 2.84%. However, there was a large spread in the data with variances of 202.92, 75.14 and 202.38, respectively. Variation in the evolution of town structure and function indicates presence of local adaptation.

While area growth does not follow temporal trends, town area growth scaled sub-linearly with the number of burrows in a town (Figure 7). The scaling exponent, 0.52 +/- 0.05, was significantly less than 1. The area required by an individual burrow decreases with increasing construction. Since the log-log model considers means at each site, n is small (15), however, there is low residual variation (r2 = 0.87), suggesting constraints on the scaling relationship.

4.4 *Growth type dependence on town size*

There is a relationship between infilling and edge-growth rates and town size (Table 5), supporting the hypothesis that growth reflects a space-filling process dependent on town age, size and density saturation. Log number of burrows affected growth type ($\chi^2(1) = 36.088$, p = 1.458e-08) and predicted variation in log growth rate (Figure 8). The effect of the number of log burrows in a town on town growth was dependent on growth type. There was an interaction between condition and log number of burrows such that the slope of the edge growth line was more negative (Table 5). There was minimal change in percent growth by infilling between small and large towns. Edge growth, however, was significantly higher in smaller towns than larger towns (Table 5).

5. Discussion

Analysis of the spatial distribution of constructed habitats—prairie dog burrows—revealed several density-dependent patterns. First, Ripley's L analysis of prairie dog burrows revealed that the distribution of burrows is clustered on the landscape. This pattern is similar to other social mammals (Table 1). Moreover, the intensity of clustering increases with density. Second, the growth rates of different towns appear to be largely independent, suggesting the dynamics of increases and decreases in number of burrows reflects local, rather than regional, prevailing conditions. Third, the data show that whether towns grow by infilling or edge growth depends on town size, a result predicted based on the geometry of constructed habitats. Finally, the scaling coefficients from regression of the log of tile area (a measure of density) on the log of the town size (estimated by the total number of burrows) aggregated around -0.6, suggesting that regionally, prairie dog town structure follows conserved density limitations. Here, I will discuss each pattern in detail, followed by an explanation of how the results can be applied to land management and urban development.

5.1 *The spatial organization of towns*

New habitat construction appears to be dependent on the spatial distribution of existing construction. While all towns were shown to be clustered at scales larger than the single coterie (~6 meters), the intensity of clustering varies by site. I suspect, but did not test, that site to site differences are due to factors such as boundness, geography and resource availability.

Clustering happens because of several processes. First, constructed habitat that is clustered may directly benefit cooperative living of social animals (Rayor 1988; Bangert and Slobodchikoff 2000; Shier and Owings 2007). Benefits of group living such as task allocation and territory defense is enhanced by the physical closeness of group members' homes (burrows).

Clustering of prairie dog burrows is consistent with the prior research on rodents that construct habitat, e.g. kangaroo rats (Schooley and Wiens 2001) and great gerbils (Wilschut et al. 2015).

Second, coteries exist as clusters of genetically related individuals (Manno et al. 2007). On average, individuals within a coterie are more closely related to each other than to other individuals of the town and each coterie is defended by resident individuals, resulting in spatial separation (Dobson et al. 1998). Furthermore, small coteries tend to disappear, and large coteries undergo fission (Manno et al. 2007). When fission happens, connections across large tunnel systems are blocked, holes decay, and the two daughter coteries separate in space (Manno et al. 2007). Thus, behavioral interactions associated with kinship influence the clustered spatial patterns observed in habitats constructed by prairie dogs.

One emergent property of clustering intensity is that as towns increase in size, become older and more established, intensity increases (Figure 9). From this observed pattern we can infer that coteries become more fixed and distinct with town age. While density may increase within individual coteries, they maintain distance from each other (increasing in *I*). Intraspecific competition within coteries limits individual clusters from becoming too dense (Manno et al. 2007). This emergent property can be compared to the human urban city framework. Human groupings, such as cultural groupings, are often less distinct in smaller communities. In large cities, however, clusters known as “Little Italy” and “Chinatown” form. Prairie dogs seem to have similar region wide patterns in which intense clusters form in large towns.

5.2 *Growth rates and types*

In the evolution of town structure in terms of area growth it is important to note that there is an absence of regional patterning. Growth is largely variable among towns and reflects local adaptation (Figure 6). I hypothesize that measuring indexes such as the Normalized difference vegetation index (NDVI) may reveal that local conditions, such as vegetation cover/type, precipitation and boundedness, influence individual town area growth rates. However, the current research can only say that growth rates are variable among towns and reflect local factors as opposed to regional factors. Local structure and function imply that management may need to be tailored to individual towns depending on context.

Although total area growth is variable, there does seem to be characteristic patterns of infill growth versus edge growth for prairie dog towns. As opposed to a diffusive process of continual edge growth, pressures driving dynamics of the system over time result in differing rates of infilling and edge growth. Town size, measured by the number of burrows in a town, is shown to be a predictor of infilling growth and edge growth (Table 5). Infill growth remains relatively constant with increasing town size and decreases only slightly. Despite limits of space and density, towns are always destroying, building and maintaining within the perimeter of the town. Towns with fewer burrows (smaller towns) are more likely to grow by edge expansion than larger towns (Figure 9).

One factor in decreasing edge growth is that larger towns are more likely to reach boundedness, in which edge growth is no longer possible. If towns do not reach boundedness there are still other checks that prevent infinite growth. The tendency of towns to increase in size to some maximum capacity is similar to limits to human city growth. In future studies, modeling carrying capacity may provide useful information into whether regional characteristic patterns of edge growth and infilling are mirrored by a regional burrow carry capacity.

5.3 *Density dependent patterns*

Burrow density limits are evident in the relationship between area needed per burrow and burrow number (Figure 7). The total area of the 15 towns in the dataset vary by approximately two orders of magnitude, yet burrow density is highly conserved. In the best fitting model, the slope is remarkably consistent and only varies by intercept. The scaling exponent is less than one, so the area required per individual decreases with increasing numbers of individuals. In human hunter-gatherer societies, similar scaling exponents less than one have been recorded (Hamilton et al. 2007). Again, benefits of cooperation for social animals determine space use, known in the human population as an economy of scale (Hamilton et al. 2007).

Individual models reveal that although a trend of density dependence is followed by the majority of towns, there are exceptions. For sites DB and Sams, there is little variation in burrow number over the timeseries so their presence as outliers is likely due to the lack of signal. Flatirons, however, departs from expectations; it maintains a high burrow density after a year of negative burrow growth (burrow loss). Contrary to the other towns, Flatirons burrow density decreases with burrow number. A look at the town's area growth over time (Figure 6. asterisk) indicates a disturbance event in which town area drastically decreases (2014 to 2018). I hypothesize the decreasing density was observed because burrow death was concentrated to the edge of the town and the central burrow density was maintained.

The intercept and slope in the density model (Table 4) predict a regression line that yearly burrow densities oscillate around. As density increases there is resulting positive feedback with energetic efficiency of space use (Rietkerk and Van de Koppel 2008). However, there is also increased negative feedback with occurrence of social and/or biological disease that is overall detrimental to the integrity of the structure (Rietkerk and Van de Koppel 2008). The sublinear relationship between burrow number and density suggests that density cannot increase at the same rate as burrow number due to harmful density effects. Notably, positive and negative density feedback effects that impact prairie dogs such as task allocation, predator warning, territory defense, resource competition, and frequency of agonistic interactions secondarily affect the survivorship of burrows (Shier and Owings 2007). Towns with low density are typically small and young and there is more variation in burrow spatial distribution due to the absence of density-dependent pressures (Hassell 1975). At markedly high burrow density, the town risks overuse of resources and increased susceptibility to disease (Cully et al. 2010): either burrow death or edge expansion must occur.

In larger towns, prairie dogs are living in denser clusters but further from neighbors. A phenomenon known in human cities as social distancing. This trend may be a response to the deadly effect of sylvatic plague (*Yersinia pestis*) on prairie dog populations (Kotliar et al. 1999; Nowak and Walker 1999). Larger towns are more susceptible to plague (Cully et al. 2010), and clustering may be one emergent property of prairie dog burrow distributions that enhances a town's ability to prevent the spread of disease. Future studies should test this hypothesis by comparing the intensity of clustering with the susceptibility of a town to infectious disease.

5.4 ***Applications***

Fleas that harbor potential bloodborne pathogens, including Bartonella and Yersinia can infect prairie dogs with the plague, invoking fear in neighboring human populations (Pauli et al. 2006; Hanson et al. 2007). In addition, towns of prairie dogs and their dynamic growth patterns often put prairie dogs and humans at odds. Prairie dogs occasionally colonize lands that are privately owned or are utilized for farming, ranching, or planned development (Bangert and Slobodchikoff 2000; Miller et al. 2007). Various land management agencies are tasked with monitoring and managing prairie dog populations. On a local scale, aerial data collection and quantification of town growth patterns can support or replace current prairie dog monitoring conducted yearly by Boulder County Open Space and Mountain Parks (OSMP) in a more efficient and accurate manner.

Analysis of the spatial distribution of prairie dog burrows provides two main insights for land management. Firstly, prairie dogs construct burrows in a clustered formation. This potentially reduces risk of plaguing out with coteries being distant from each other while promoting cooperation of family groups. When burrow drilling is involved with relocations, effective spatial patterns from existing towns with similar characteristics (e.g. NDVI, total area) can be copied and implemented. The data also suggests that for preventative human-prairie dog conflict mitigation, smaller towns are more likely than larger towns to exhibit conflict-triggering edge growth. Young and unestablished towns should be flagged as potential locations of conflict if they are located near human settlements.

Beyond local applications, this research is expanding the intersection of spatial and landscape ecology by exploring large-scale spatial-temporal patterns in previously unstudied species. In addition, the study lays groundwork for how to better understand the engineering of towns and cities.

The parallels between humans and prairie dogs with respect to habitat destruction and construction provides an interesting comparative framework for better understanding the ecology of urbanized landscapes. It is predicted that by 2050 two thirds of the human population will be concentrated in cities (Ritchie and Roser 2018). In addition to the need for efficient distribution and use of resources in populated areas, the COVID-19 pandemic is proof that practices such as social distancing are important for city planning and development. Clustering intensity in prairie dog towns may advise effective practices of distancing in a space-limited environment. Continued infilling and decreasing edge growth for larger prairie dog towns is an emergent property applicable to city development. When a prairie dog town can no longer expand, it continues to modify habitat within the town perimeter. There may be room in human cities to modify structures within cities for more efficient space use.

6. Conclusions

The research described herein tells the story that black-tailed prairie dog towns in Boulder County follow similar patterns of construction that depart from complete spatial randomness. Over time, towns are modified with some local variability and disturbance on a trajectory to a stable set of characteristics. Area scales sub-linearly with population size, density is highly conserved, clustering intensity reaches a maximum and space filling is balanced by edge-growth and infilling. While yearly area growth is variable from town to town, stability looks similar across town and outliers reflect disturbance. Although abiotic, burrows appear to be subject to many of the evolutionary pressures the engineers themselves face, including positive and negative density feedbacks.

Studying the built structures of non-human ecosystem engineers stands to benefit individual species and ecosystems, but more broadly has potential to benefit human engineers in their community development. Non-human species engineered and inhabited spaces have similarities and differences to spaces occupied and engineered by humans (Bettencourt et al. 2007; Samaniego and Moses 2008; Liu et al. 2014). Rosemond and Anderson (2003) outlined four main characteristics of non-human beneficial engineering: (1) mutualistic interactions, (2) facilitation of diversity, (3) effective nutrient cycling, and (4) ecological flexibility. Further quantification of constructed habitats that show clustered formations, like those of burrowing rodents, may provide insight into efficient space use, improve methods of group-living within defined landscapes, and provide case studies for infectious disease.

7. Acknowledgements

First and foremost, I would like to thank Dr. Martin for always pushing my capacity to conceptualize and think bigger. The opportunity to work with Andy for so many years has been transformative. I would like to give special thanks to Professor Johnson, for being the best statistics teacher and advisor. Who knew stats could be so fun? A big thanks to Professor Renfrow for giving terrific feedback on my writing. I’m always excited to get back your comments. Thank you Professor Collinge for being an inspiration, I’m honored to have you on my committee. Micaela and Sean, thanks for guiding me through the slew of emotions that come with writing an honors thesis. Finally, thank you to the University of Colorado Boulder’s Undergraduate Research Opportunity Program (UROP), the Alexander and Verderber Undergraduate Research Fund, the Open Space and Mountain Parks (OSMP) funded research program, and my parents for making my research goals a reality.

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9. Figures

Figure 1. Aerial view of human settlements and black-tailed prairie dog constructed habitats in Boulder County. **Left.** Human subdivision to the left of the vertical road. Prairie dog town comprised of burrows to the right of the road. **Right.** Closer view of prairie dog burrows from space.

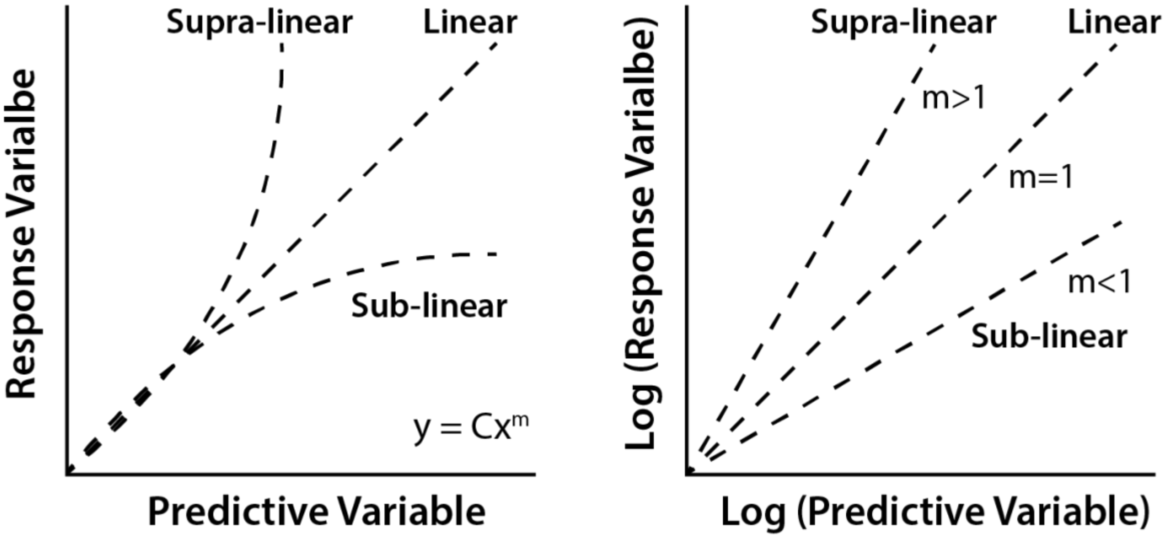


Figure 2. Possible scaling coefficients between predictive and response variables. Equation is $y = Cx^m$ where y = response variable, C = population size, x = predictive variable and m = scaling exponent. **Left.** Three scaling relations between predictive and response variables. **Right.** Log-log plot of scaling relations with three different scaling exponents. When $m = 1$ the amount of resources required per individual has a constant proportional increase. $m > 1$ indicates that each added individual costs the system energy. For $m < 1$ with each added individual the amount of resources required per individual decreases.

Year	Species/ Structure	Collection Method	Analysis	Spatial Distribution			Reference
				Aggregated	Random	Uniform	
2001	Termite mounds	Compass and tape measure	G(r)	X *small		X *large	Korb & Linsenmair
2001	Kangaroo rat mounds	GPS	K(r)	X *large		X *small	Schooley & Wiens
2007	Burrowing owl nests	GPS/ Remote imagery	K(r)	X	X		Fisher et al.
2011	Termite mounds	Grid-based	K(r), *g*(r)	X *small		X *large	Bourguignon et al.
2011	Kangaroo rat mounds	GPS	G(r)	X			Vazquez & Alvarez-Castaneda
2012	Sage grouse	GPS	Patch				Aldrige et al.
2015	Ant mounds	Remote imagery	K(r)			X	Dibner et al.
2015	Termite mounds	Remote imagery	G(r), *g*(r), K(r)			X	Juergens et al.
2015	Termite mounds	Remote imagery	qualitative			X	Funch
2015	Gerbil burrows	GPS	K(r), SV	X			Wilschut et al.
2016	Earthworm mounds	Remote imagery	qualitative				Zangerle et al.
2019a	Termite mounds	Remote imagery	CV, G(r), *g*(r), K(r)			X	Getzin et al.
2019b	Fairy Circles	Remote imagery	*g*(r), K(r)			X	Getzin et al.

Table 1. Selection of studies reporting spatial point patterns of three categories of social insect (light grey), burrowing rodent (dark grey), and subterranean nesting bird (white) ecosystem engineers published after 2000. Insect mounds are shown to be clustered when towns are small and young, and uniform when towns are large and established. Contrastingly, rodent burrows are uniform for small young towns and clustered for large established towns. Literature on nesting birds suggest aggregation but is incomplete. G(r) = nearest neighbor, K(r) = Ripley's K, g(r) = pair correlation function, SV = semi-variogram, CV = 1 - coefficient of variation of G(r).

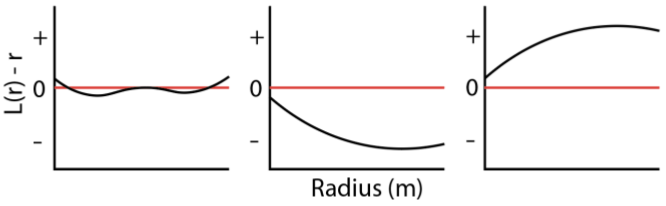
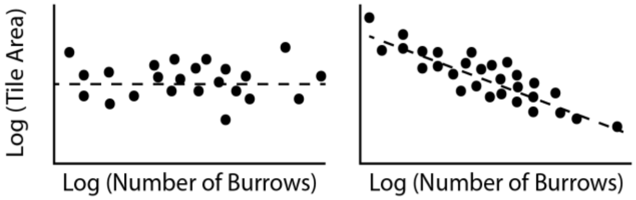
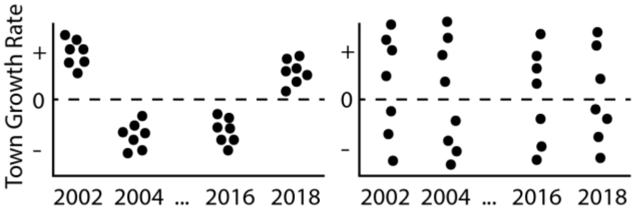
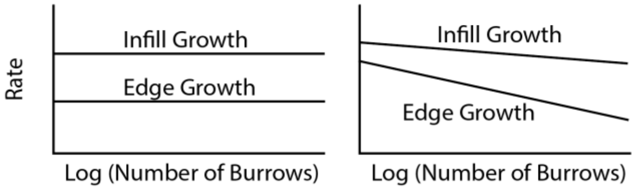
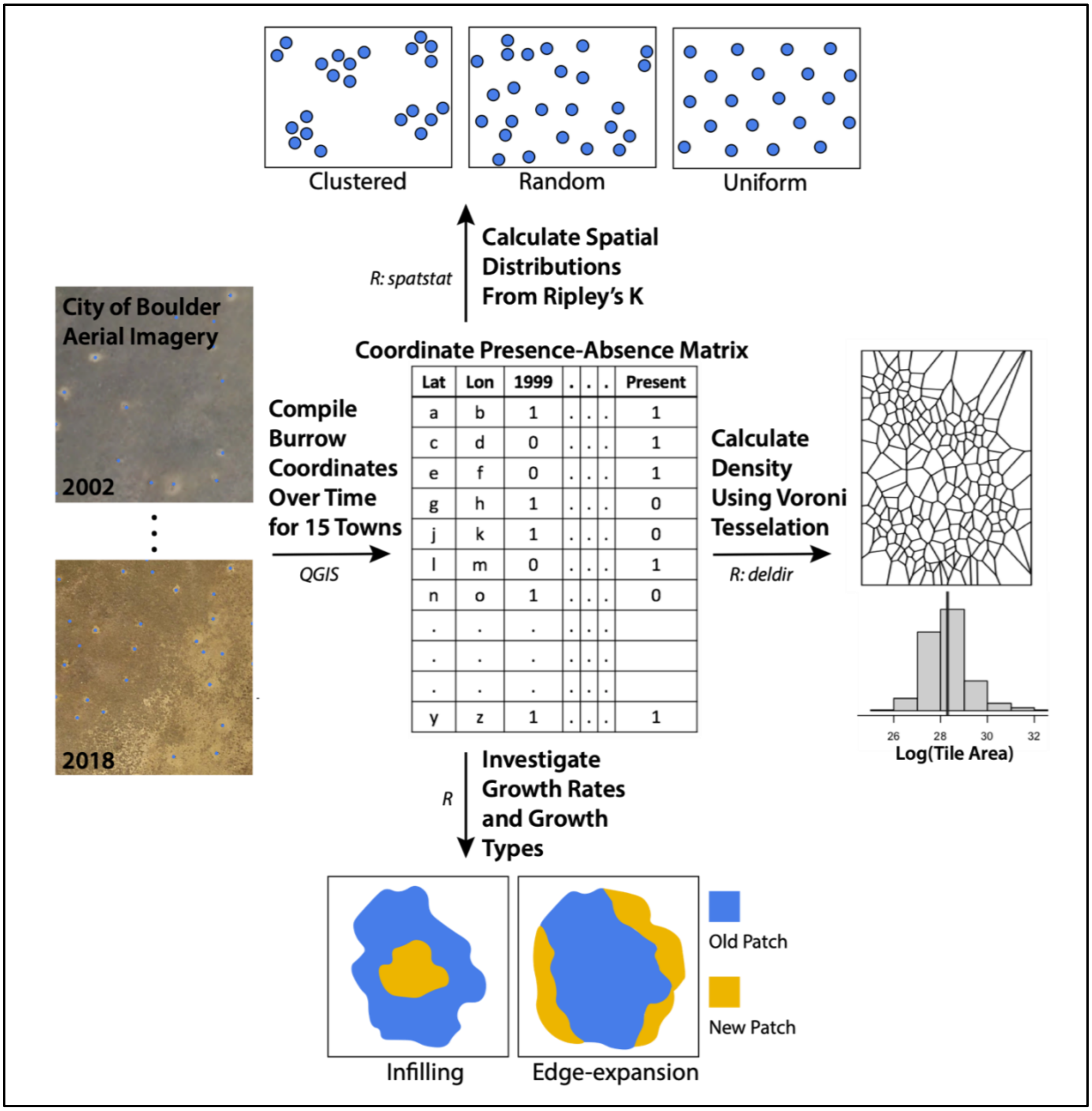
Text based predictions	**Visualized predicted outcomes**	**Relevance**
1A: Burrows in towns are randomly distributed. **1B:** Burrows in towns have a uniform distribution. **1C:** Burrows in towns have a clustered distribution.		Tells whether the spatial structure of towns is due to competition, sociality and/or the distribution of resources.
2A: Growth is density independent. **2B:** Growth is density dependent.		Reveals whether town structures are dependent on density.
3A: Growth rates of independent towns are correlated. **3B:** Growth rates of independent towns uncorrelated.		Town spread can be assessed as reflective of local or range-wide regional factors.
4A: Relative growth rates of infilling and edge growth remains constant with town size. **4B:** Relative growth rates of infilling and edge growth communities change with town size.		Provides the basis for predicting spread and origination of towns.

Table 2. Predicted outcomes, visualizations and their relevance.



Lat	Lon	1999	.	.	.	Present
a	b	1	.	.	.	1
c	d	0	.	.	.	1
e	f	0	.	.	.	1
g	h	1	.	.	.	0
j	k	1	.	.	.	0
l	m	0	.	.	.	1
n	o	1	.	.	.	0
.	.	.	.	.	.	
.	.	.	.	.	.	
.	.	.	.	.	.	
y	z	1	.	.	.	1

Figure 3. Methods followed to acquire point data for burrow locations and distinguish emergent patterns. **Left (L).** Manual marking of burrows in QGIS 3.10 using Boulder County Open Data over the time series 2002-2018. **Center (C).** Data frame of burrow coordinates and presence absence data for each burrow over the time series. **Right (R).** Use of the deldir package in R to calculate tile area, an inverse measurement of burrow density. **Bottom (B).** Investigations of growth rates (overall area, overall burrow number, infilling versus edge growth) using R. **Top (T).** Use of the spatstat package and Ripley's K in R to determine spatial point patterns.

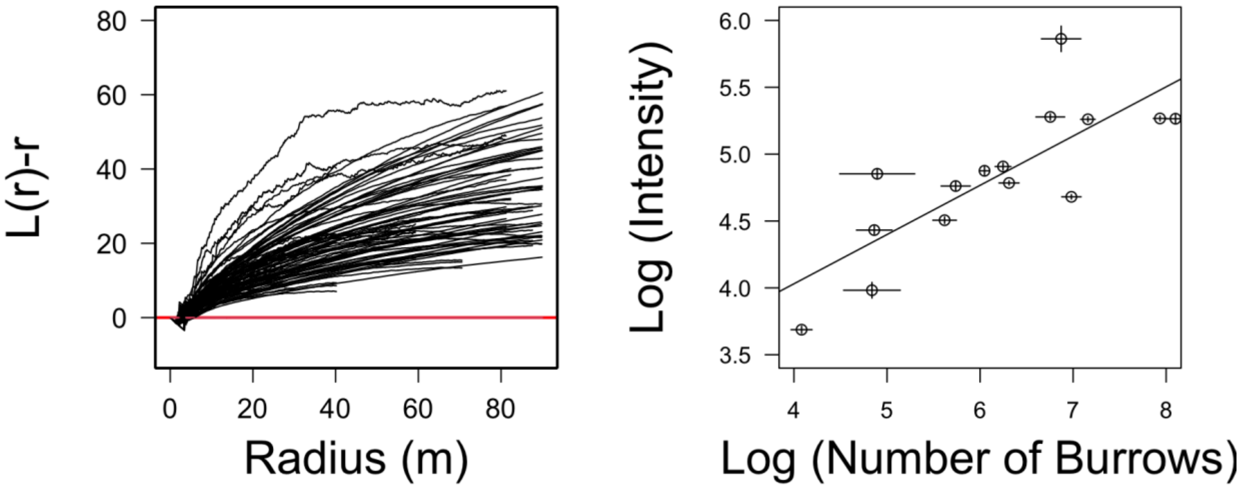


Figure 4. Ripley's L function on 15 towns for six historic years. **Left.** L is scaled to the zero expectation (red line) such that L(r)-r > 0 suggests clustering while L(r)-r < 0 suggests uniformity. Black lines display observed L(r) with an isotropic correction. **Right.** Relationship between log number of burrows and intensity (*I*= max L(iso)) of burrow clusters. Open circles are mean values of estimates over the time series for each site. Error bars are standard errors.

Predictor	**Estimate**	**Standard Error**	**t value**	**Pr (>|t|)**
Intercept	2.55802	0.49080	5.212	0.002
Log (number of burrows)	0.36817	0.07832	4.701	0.004

Table 3. Results from the linear model: Intensity ~ Log (Number of burrows). The number of burrows and intensity for each site is a mean value to consider among town effects.

Fixed Effects	**Estimate**	**Standard Error**	**Df**	**t value**	**Pr (>|t|)**

Intercept	7.34	0.28	78.69	25.90	<0.001
Log (number of burrows)	-0.40	0.04	107.6	-9.94	<0.001

Table 4. Results from the linear mixed effect model: Log tile area ~ Log Number of Burrows + 1|Site + 1|Year.

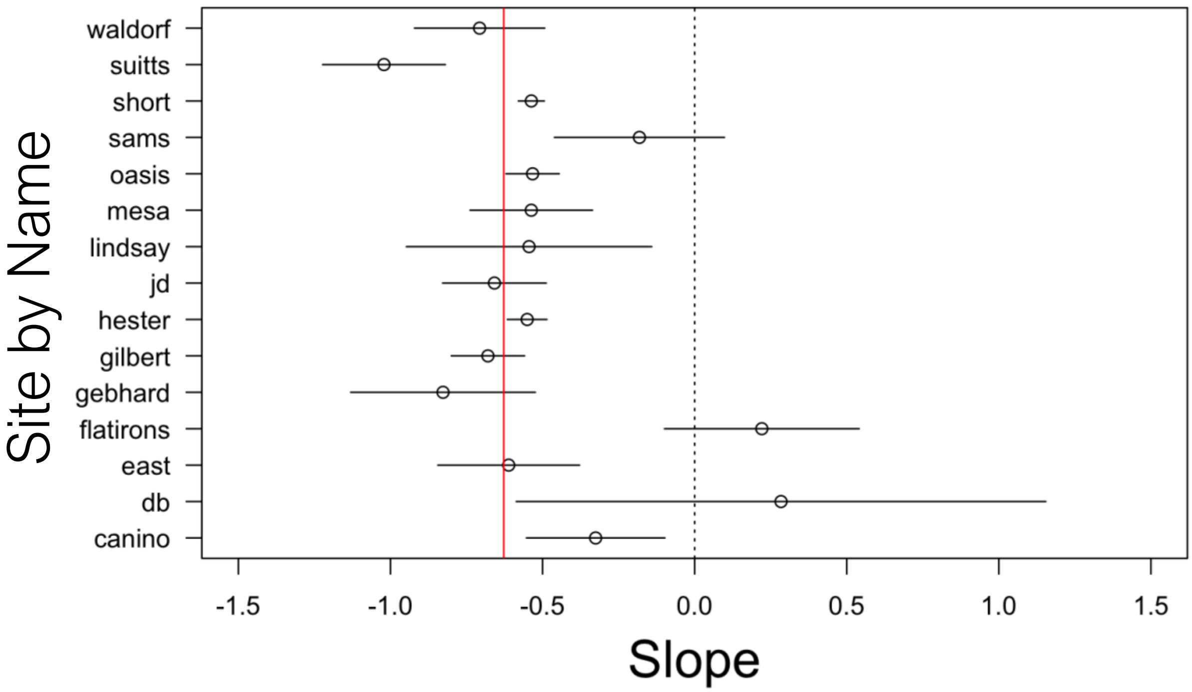


Figure 5. Slope (open circles) and effect size (horizontal lines) for 15 linear models. Each town location (site) is named on the y axis. For each site the slope indicates the relationship between log number of burrows and log tile area. Red line is the average slope of sites that fall within the outer fence (excludes Flatirons and DB). Dashed line is a reference for a slope of zero.

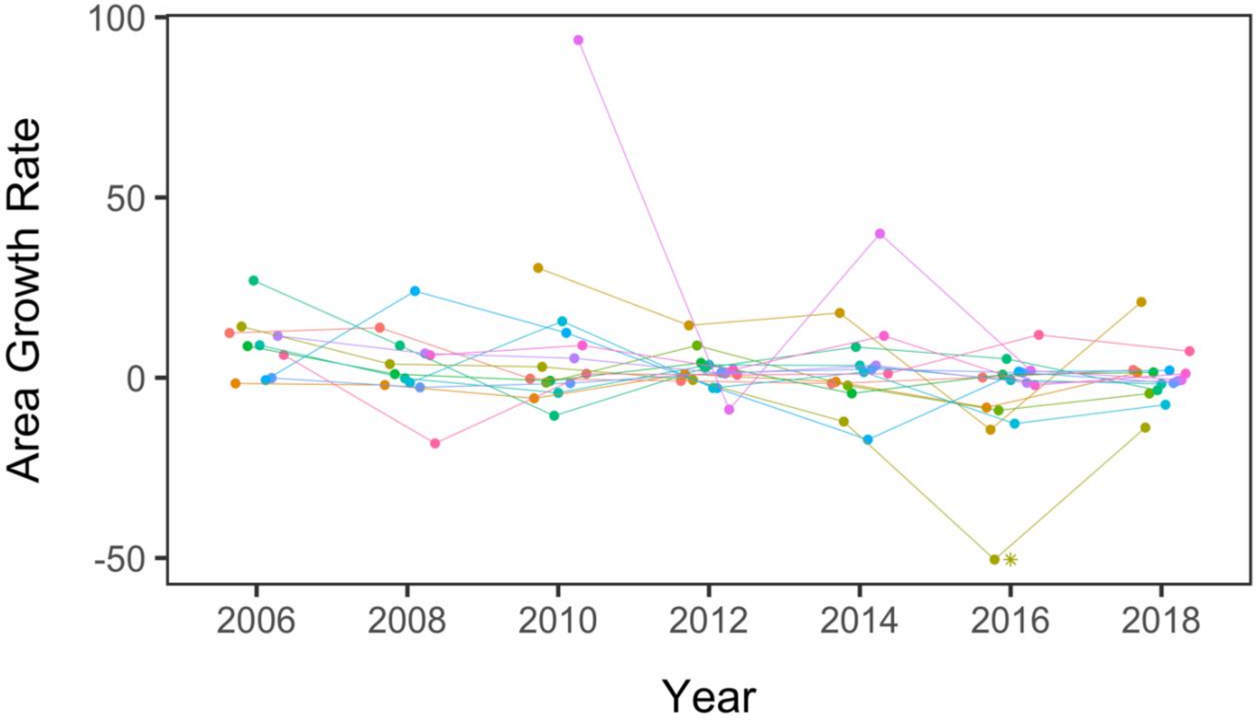


Figure 6. Percent growth in total area of 15 towns (colored circles) for seven historic years. Colored lines track temporal advances and declines for each town.

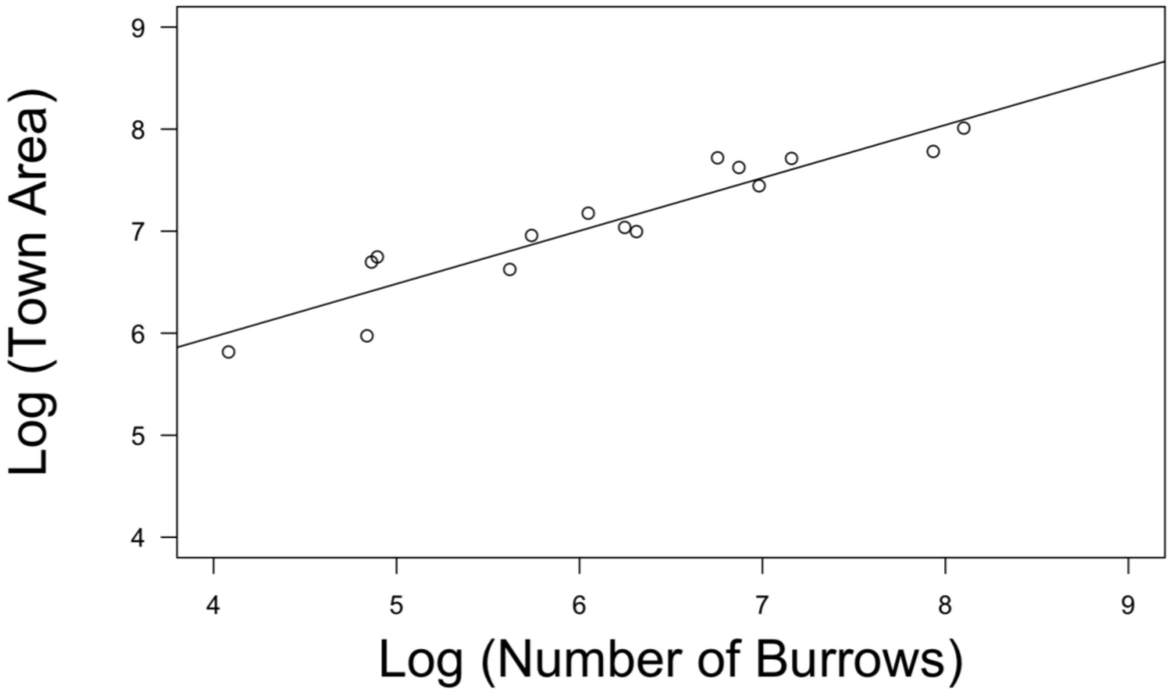


Figure 7. Log-log plot of mean number of burrows and mean town area. Open circles are 15 sites in Boulder county. Solid line is the least-squares regression estimate of the slope of the sublinear relationship (Y= 0.52X + 3.89. $R^2 = 0.87$).

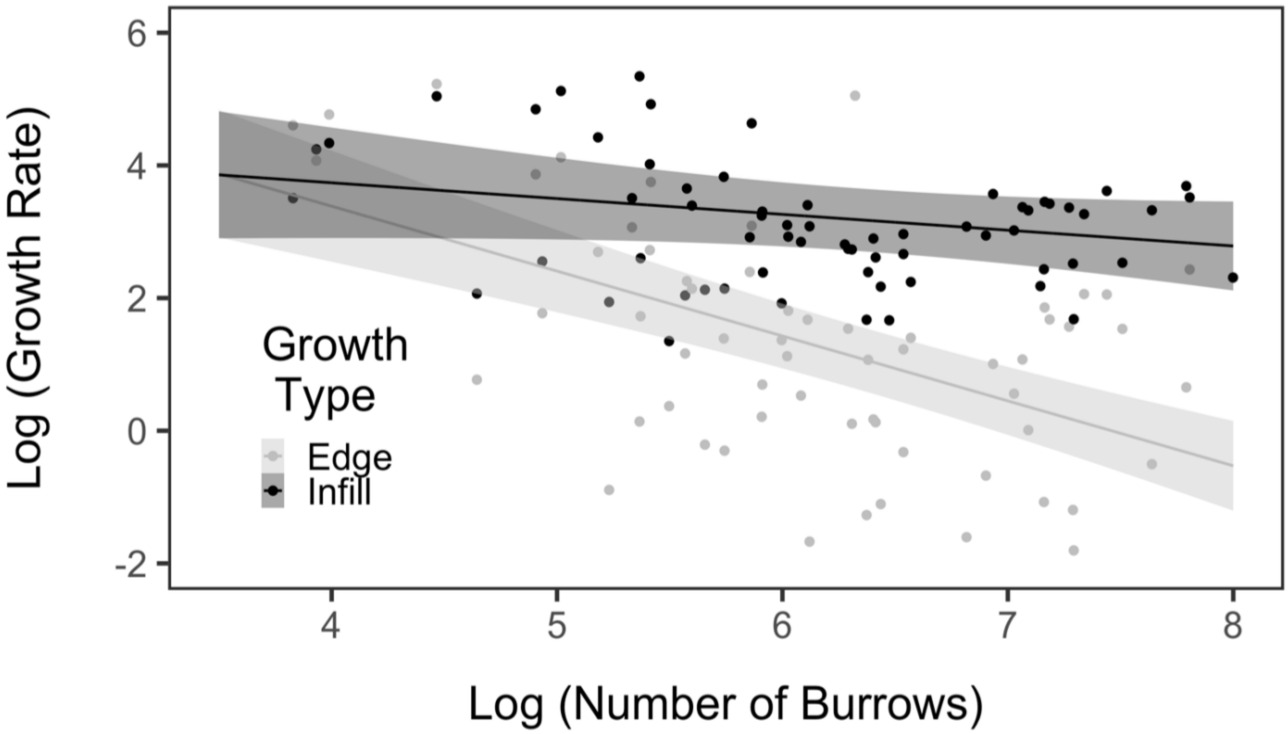


Figure 8. Relationship between log growth rate of burrows and log burrow number for two growth types (data points - closed circles, regression - solid line). Grey bands represent 95% confidence intervals.

Fixed Effects	**Estimate**	**Standard Error**	**Df**	**t value**	**Pr (>|t|)**
Intercept	7.30	0.97	37.69	7.48	<.001
Condition (infill)	-2.61	1.08	123.09	-2.41	0.02
Log (Number of Burrows)	-0.98	0.15	35.6	-6.58	<.001
Interaction Infill	-0.74	0.17	123.1	4.43	<.001

Table 5. Results from the linear mixed effect model: Log growth rate ~ Log Number of Burrows*Growth Condition + 1|Site + 1|Year.

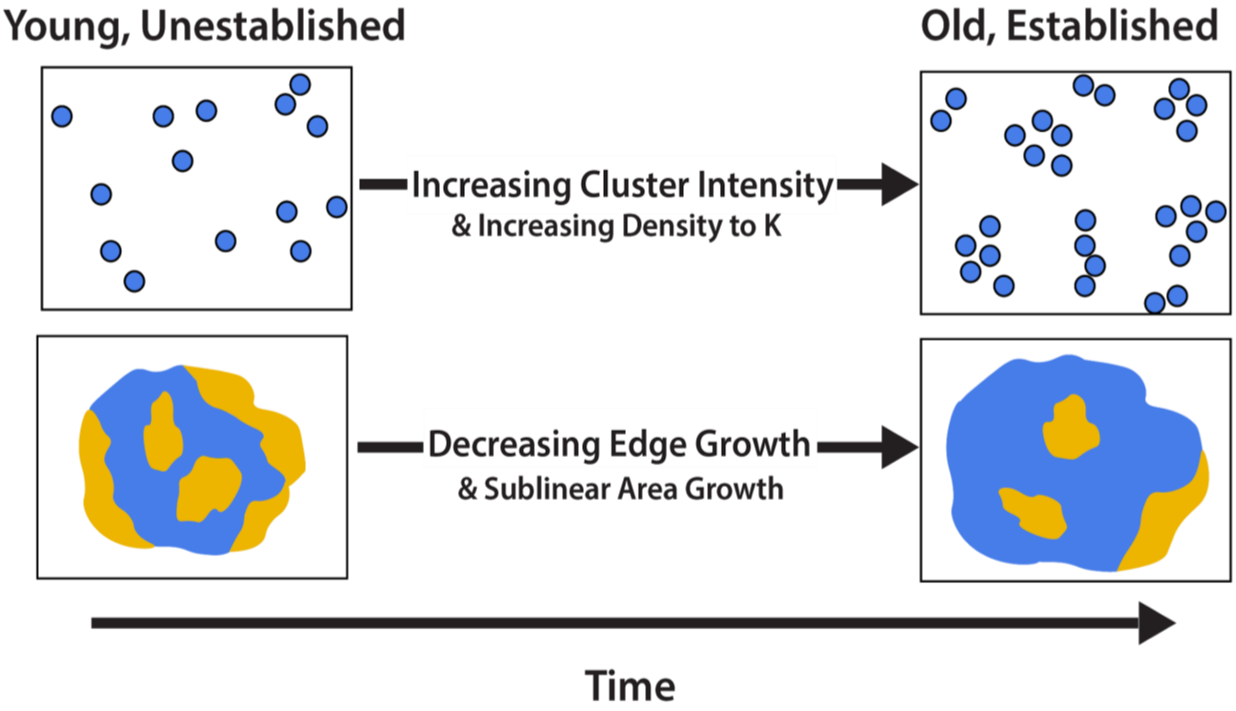


Figure 9. Tendencies for towns to converge upon a structure that is more intensely clustered and increasingly dense to a burrow carrying capacity. Throughout the processes of succession edge growth decreases and area grows sub-linearly with burrow number. Yellow coloration indicates new growth. Blue coloration indicates existing structure.

10. Supplementary Material

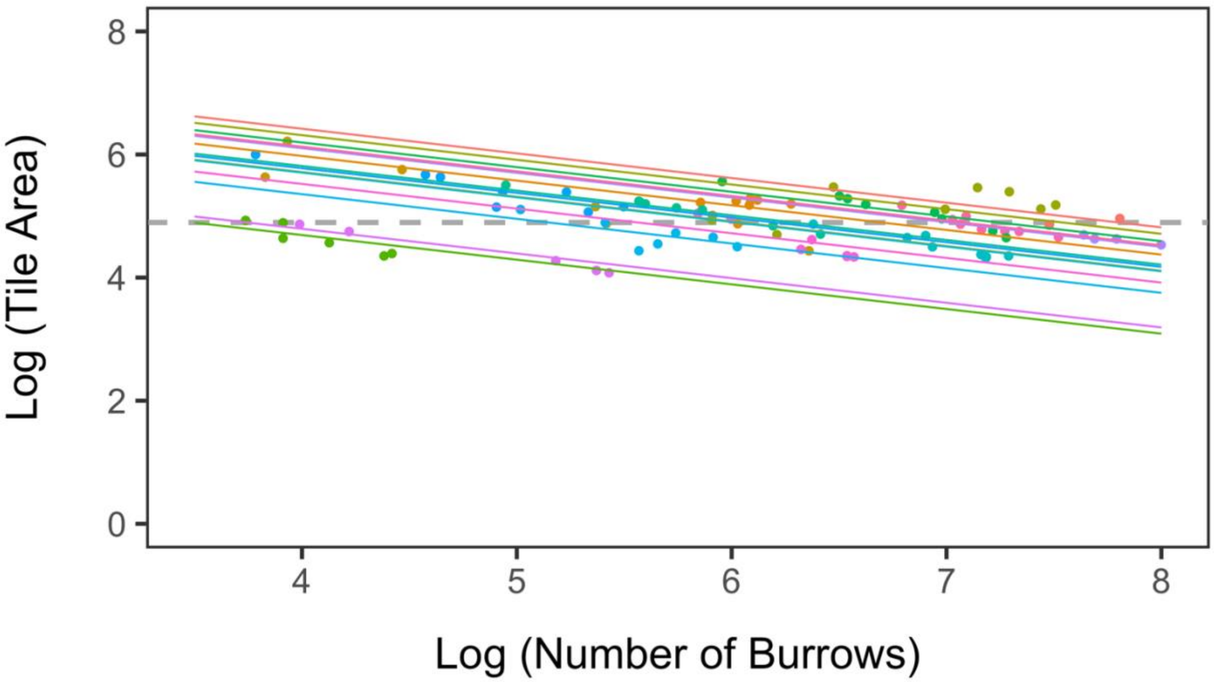


Figure S1. Relationship between mean log tile area of burrows from tessellation objects and log burrow number (data points - closed circles, regression - solid line). Average tile area is represented by the horizontal line (grey dashed).