SPATIAL DISTRIBUTION OF ALPINE AVENS (*Geum rossii*) AND NORTHERN POCKET GOPHER (*Thomomys talpoides*) DISTURBANCE ON THE PIKES PEAK TUNDRA

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TABLE OF CONTENTS

ABSTRACT

Pattern formation in ecosystems via self-organization is an important area of investigation in the field of ecology. Self-organization is the process whereby short-range facilitation and long-range inhibition lead to patterns in ecosystems at varying scales. Can biotic agents, such as key ecosystem engineers, be responsible for patterns of self-organization? We sought to investigate this question on the tundra of Pikes Peak outside Colorado Springs, CO. Aerial images of Pikes Peak reveal distinct patches of alpine avens (*Geum rossii*) dotting the tundra. Are there any patterns in the distribution and characteristics of these alpine avens patches? Closer examination reveals that evidence of northern pocket gopher (*Thomomys talpoides*) soil disturbance also speckles the tundra. Are there any links between gopher disturbance and alpine avens patches? We sought to answer these broad questions through a series of three investigations. We examined the large-scale spatial distribution of the avens patches relative to each other, surface gopher disturbance in relation to individual avens patches, and the underground characteristics of the tundra below the patches.

Our findings indicate that while a link can be established between gopher disturbance and avens patches, it is not the complete picture. We found that contrary to the expectation that avens patches would follow a regular distribution at smaller distances, they were in fact randomly distributed at small distances and clumped at greater distances as shown by Ripley's K tests. In line with our hypotheses, we found that gopher disturbance was clumped, and occurred more often within avens patches than would be expected given disturbance frequency across the tundra, p=0.001 (chi-squared=10.88, DF=1) for quadrant one, and p=0.0001 (chi-squared=306.96, DF=1) for quadrant two. Finally, we discovered an interesting pattern of what appears to be disintegrated bedrock beneath the avens patches,

which may have implications for avens patch resilience on the tundra. In t-tests comparing mean resistivity of soil underground inside and outside the patch, $p<0.05$ for all depths except the lowest depth in one patch. In sum, it appears from our findings that while gopher disturbance may be necessary for avens patches on the Pikes Peak tundra, it is not sufficient. This is given the fact that gopher disturbance occurs in areas where avens patches do not, and avens patch boundaries are crisply defined while gopher disturbance is diffuse. Evidence does seem to point to self-organization on the tundra, with gopher disturbance creating short-range facilitation for alpine avens, and some mechanism of long-range inhibition preventing avens patches from occurring everywhere on the tundra.

INTRODUCTION

How ecosystems are spatially organized is a central question in the field of ecology. It is a question that can be viewed on many different scales, from the individual to the spatial patterning of species across landscapes, and many levels in between. The multitude of species contained in an ecosystem create a complex spatial, dynamical structure due to interactions such as food-web connections, and modulation of landscapes induced by biotic-abiotic interactions (Gilad et al. 2004). The complexity of these relationships can make it difficult to distinguish the central driving forces in the spatial organization of an ecosystem. In general, patterns arise from external factors or internal dynamics. When discussing pattern formation in ecosystems, it is important to consider the emergent property of spatial self-organization. Self-organization is the process whereby large-scale, coherent spatial structures result from disordered local interactions (Rohani et al. 1997). Examples of spatial self-organization include regular spatial patterns via Turing pattern formation, traveling waves, and spatial chaos (Alonso et al. 2002). However, non-emergent properties, such as dependence on patchily distributed underlying abiotic conditions, can also play a role in determining the spatial organization of ecosystems. This brings us to the habitat-modifying role of some organisms, which can be referred to as ‘ecosystem engineers’. Can biotic entities act as agents of self-organization in an ecosystem? Take the example of Engelmann Spruce trees in alpine Rocky Mountain tree lines. In some areas these spruce, along with sub-alpine fir, grow in narrow strips perpendicular to the prevailing wind direction. This facilitates the accumulation of snowdrifts in between these 'ribbon forests', discouraging seedling establishment between the ribbons while promoting it within them (Rietkerk et al. 2007). Essentially, the alpine trees construct their own habitat, and as a result form a large-scale pattern of ribbon forests. The formation of tree stripes is caused by short-distance positive feedback and long-distance negative feedback (Rietkerk et al. 2007). This mechanism of short-range facilitation and long-range inhibition forming patterns is key in self-organization and pattern formation. Short-range facilitation fosters species' success at some spatial scales, while long-range inhibition prevents success in 'in-between' areas. Hence, large-scale patterns are formed.

One relatively uninvestigated mechanism by which spatial self-organization might occur is through species that modify their habitat significantly and thereby impact the environment for other species. These habitat-modulating species can be referred to as 'ecosystem engineers' (Gilad et al. 2004). Through modifying the physical structure, these species affect the flow of resources as well as the density of other species in the system (Gilad et al. 2004). So how do we define an ecosystem engineer? Reichman et al. propose two criteria for the ecosystem engineer title: that they are responsible for biologically mediated changes to the physical environment which are distinctive from processes that are solely abiotic, and that they have a large relative effect when compared to the purely physical processes (such as wind, erosion, etc.) acting on the system (2002). In the above example, spruce and sub-alpine fir trees act as ecosystem engineers. Beavers are a classic example of an ecosystem engineer, modifying the stream habitat through their construction of dams. Another example can be found in water-limited systems where cyanobacteria and shrubs act cooperatively to accumulate soil-water to the benefit of other species (Gilad et al. 2004). The focus in the field of ecology has long centered upon the role of 'keystone species', or 'keystone consumers' as governing their respective systems (Bruno et al. 2003). However, whether we use the term 'ecosystem engineers', 'habitat-forming species', 'foundation species' or 'geomorphic agents', species that physically alter their habitat play a crucial role. Through their actions they affect a cascade of other species in the ecosystem (Bruno et al. 2003). The diversity of habitats created, and therefore species richness, depends to a large extent on the structural alterations created by the ecosystem engineers (Gilad et al. 2007). In some cases the absence of an ecosystem engineer leads to an overall decline in species diversity due to the decreased availability of varied microhabitats (Bruno et al. 2003). Ecosystem engineers spatially organize their ecosystem through physical alterations to the landscape, which may be driven by factors such as resource management and habitat construction. In the case of gophers, territoriality, physical alteration of the habitat through burrowing and herbivory, and the spatial structure of these actions may lead to pattern formation

An intriguing potential example of self-organization can be found on the tundra above treeline on Pikes Peak near Colorado Springs, Colorado. When viewing aerial images of Pikes Peak, one may notice an interesting pattern of darker-colored dots speckling the tundra above treeline (Fig. 1). These patches, upon closer examinations, reveal themselves to be composed mainly of alpine avens (*Geum rossii*) in well-defined patches in contrast to the surrounding tundra. To the unaided eye, the patches may even appear to follow a pattern of regular distribution across the tundra. These observations raise some interesting questions about tundra ecosystem dynamics and spatial self-organization on Pikes Peak. Fragile alpine ecosystems can provide valuable insights into how ecosystems function in the absence of significant human disturbance such as agriculture and recreation. It is important to have this baseline of knowledge for future monitoring efforts, as human disturbance and global climate change play an increasingly important role in the operation of ecosystems.

To examine these questions, we must first understand alpine avens and their environment. Avens patches on Pikes Peak at our field site are approximately two to five meters in diameter, and are very crisply defined from the surrounding tundra. Abundance tests within the patches revealed frequencies of 66.17% alpine avens, 26.87% alpine clover, and 11.19% grass. Outside abundance data yielded 35.53% grass, 25.24% alpine avens, 17.7% blue alpine phacelia, and 17.22% lichen (Jensen 2014). As demonstrated by the data, avens occur throughout the tundra but are concentrated in these patches. Extra-patch species composition is more heavily grass-dominated. In total, vegetation within the patches is taller and more lush than the surrounding tundra (Jensen 2014). The dominant factors affecting tundra vegetation dynamics and diversity include insolation, wind speed and direction, precipitation, soil moisture, and topography. Slope-aspect additionally affects the aforementioned factors. Finally nutrient levels, while not the focus of this study, play a role in determining tundra vegetation dynamics (Isard 1986). Could any of these factors play a decisive role in avens patch formation?

At a closer range, the Pikes Peak tundra is also dotted with evidence of activities of the northern pocket gopher. Northern pocket gophers are the dominant ecosystem engineers of the Pikes Peak tundra (Zhang et al. 2003). For reference, northern pocket gophers have the widest range of any species in their family. They are fossorial mammals, spending the majority of their lives underground. Gophers subsist on a diet of shoots and roots. Cox et al. found that forbs account for 97% of shoot matter consumed, with grasses at 2.4% (1989). At Niwot Ridge, a field site of similar characteristics to that in our study, it was observed that pocket gopher activity is moderate in dry meadows, and more concentrated in the moist-meadow community type (Sherrod et al. 2001). In these tundra ecosystems, pocket gophers play a large role through both their herbivory and their tunneling activities. Anderson and MacMahon (1981) found that northern pocket gophers consumed greater than 30% of net belowground primary production of forbs in an alpine meadow (Williams et al. 1986). The consumption of primary production by gophers is proportionally much higher than for other small mammals due to the high energetic demands of burrowing (Williams et al. 1986). This places a high premium on optimizing burrow location in relation to food sources. According to some estimates, gophers shape their environment as much as the sum of all abiotic influences (Reichman et al. 2002). Estimates of soil moved by gophers to aboveground range from 1-8.5 kg/square meter*year (Huntly et al. 1988). The ecological relevance of this soil movement is multi-faceted. Of primary importance to our study of alpine avens patches is that the burrowing and subsequent mounding activities of the gophers create microsites of distinct physical, biological, and biogeochemical conditions. These microsite have the potential to impact plant species on the tundra (Sherrod et al. 2001).

Does gopher disturbance affect vegetation dynamics? Many studies have examined various aspects of how gopher disturbance affects plant species composition. However, the majority of these studies have focused on prairie ecosystem dynamics, so it is interesting to investigate the tundra ecosystem as well. Huntly et al. found that vegetation on mounds differs in biomass and species composition from adjacent undisturbed areas (1988). It has been suggested by many studies that pocket gophers, through the distinct microsites they construct, create a competitive advantage for plant species they consume, effectively farming their resources (Huntly et al. 1988, Sherrod et al. 2005, Martinsen et al. 1990). This is an interesting preposition that requires further investigation. In the typical ecological scenario, keystone consumers limit the abundance of their preferred prey. The preposition that gophers are creating conditions that aid the proliferation of their preferred prey (avens) is unusual, but as we will discuss further, a likely occurrence. Some effects of gopher disturbance in ecosystems are more evident. Huntly et al. found that abundance and proportional abundance of annual plants and forbs was greater where gophers were present (1988). Of course some of these effects are place-dependent. Williams et al. found contrasting results but this is likely due to the more transient nature of gopher disturbance in the Texas coastal prairie environment (1986). Gopher activities contribute to permanent delayed succession on the tundra. Constant disturbance prevents succession to a steady-state vegetative composition (Zwinger et al. 1996). Is it possible that a connection lies between avens patches and gophers, the dominant ecosystem engineer? Pocket gophers may create spatial organization in the tundra through bioturbation of the soil. Gophers deposit subsoil on the tundra surface through their excavation activities. These mounds represent microsite of distinctly different conditions from the surrounding tundra. Plant re-growth on these mounds may represent short-range facilitation by gophers of alpine avens. This facilitation would occur through gophers advantaging avens over other tundra plants in the process of re-growth up through the soil following burial. Long-range inhibition may limit where alpine avens occur in patches on the tundra. The sum of these local interactions can lead to spatial patterning across the tundra, with patches occurring where short-range facilitation outweighs long-range inhibition.

These interactions provide the basis for our study of the distribution of alpine avens and northern pocket gopher disturbance in the Pikes Peak tundra. Our primary research question is broadly: are there any patterns in the distribution and characteristics of alpine avens patches in the Pikes Peak tundra? More specifically, we wanted to know if we could see any patterns in; (1) the location of patches relative to each other, (2) gopher soil disturbance in relation to patches, and (3) the underground characteristics below the patches as compared to outside the patches. From these investigations, we sought to discover if we could infer any patterns or links between pocket gopher disturbance and vegetation dynamics on the Pikes Peak tundra. We hypothesized to find a regular spatial distribution of alpine avens patches on a large scale, with gopher disturbance being strongly correlated to patch location on a smaller scale.

METHODS

Study Sites

Field data for this study was collected from what we shall refer to as the Oil Creek field site (Fig. 2). Oil Creek (492,133.86, 4,300,292.587 meters UTM) is located on the western slope of Pikes Peak at an elevation of 3,805 meters. It is a west-facing hill slope of about 30 degrees. Oil Creek frames the study site on two sides. The creek provides for a moist meadow ecosystem. Soil composition is coarse and granitic. Oil Creek is accessed by parking at Devils Playground and hiking down the Pikes Peak Crags trail. After about a quarter of a mile the trail is left for a ridgeline to the west, which leads uphill and then down into our field site. The field site is about one mile from the Pikes Peak Highway. Additionally for our study we analyzed aerial images from what shall be referred to as the Windy Point field site. Windy Point (497,628.14, 4,296,957.3 meters UTM) is located on the southeastern slope of Pikes Peak at an elevation of 3,985 meters. Avens patches were labeled within a polygon around the access road, where previous field observations had identified the presence of avens patches.

Large-Scale Spatial Distribution of Avens Patches

In order to examine the large-scale spatial distribution of avens patches in the Pikes Peak tundra, we used GIS to first label avens patches at both the Oil Creek field site (Fig. 3), and at Windy Point (Fig. 4). Imported maps of Teller and El Paso counties from 2011 were utilized. We then used the 'select features' tool to label avens patches by sight using the fact that avens patches appear as distinct points of darker coloration on the aerial map. At Oil Creek, the enclosing corners for the avens site were the four corners of the hillside. At Windy Point, we chose to label avens patches around the access road, as these were known from a previous site visit to contain avens, as opposed to shrubs that also manifest as darker spots in aerial images.

Spatial Distribution of Gopher Disturbance with Respect to Avens Patches

Field data were collected over a total of six days between September and October of 2013. To more closely examine the relationship between avens patches and pocket gopher disturbance at the Oil Creek field site, we selected two quadrants (labeled 1 and 2) of areas 1,380.82 meters squared, and 1,225.84 meters squared respectively (Fig. 7). Each quadrant contained two avens patches. Using a Trimble GPS device, we then mapped the corners of the quadrants, as well as the borders of the avens patches. Areas of patches were as follows: patch one, 21.89 meters squared; patch two, 25.45 meters squared; patch three, 17.32 meters squared; patch four, 18.19 meters squared (see Fig. 9 and Fig. 10 for labeled avens patches). In order to provide insight into the relationship between gopher disturbance and the formations and/or maintenance of the avens patches we mapped each point of gopher disturbance and characterized each by relative age (Fig. 8). 'New' mounds were those which exhibited freshly tilled soils, with high levels of fine soil particles still evident. 'young' mounds were those in which still retained their mound shape, but where larger soil particles were more predominant. Finally, 'old' mounds were beginning to flatten out, and in some cases contained plant growth. Additionally, entrances to gopher tunnel systems were mapped, which manifest as small holes in the tundra with entrances about 10 centimeters in diameter.

Geoelectric Resistivity Profiles

To investigate the subsoil characteristics in and around the avens patches, we used an electrical resistivity meter to create geoelectric resistivity profiles. Stakes composed of a conductive metal were pounded into the soil at intervals of 0.25 meters, and connected by a cable. Each survey contains 24 stakes, therefore covering six meters. We ran three surveys through each patch to encompass the ground below the patches and outside the patches. About one and a half meters are cut off from the ends of each survey due limited conductive pathways at the edge of the survey. To compensate for this, we overlapped six stakes from each survey. The electrical resistivity equipment sends electric current between all possible combinations of stakes using a dipole-dipole array, to calculate the resistivity between the stakes. We utilized the dipole-dipole array because it aids in resolving lateral differences in material. This information is used to create a geoelectric resistivity profile beneath the survey, with color-coded areas showing the resistivity levels at depths up to 0.981 meters (Fig. 13, 15, 17).

Data Analysis

Large-scale patch distribution data were analyzed using a Ripley's K test in the program, 'R'. We wanted to test our hypothesis that avens patches would follow a regular distribution across the tundra. Ripley's K tests compare the sum of all distances between points to the expected distribution of distances if points are randomly distributed. Random distribution of distances between points results in a smooth line flowing proportional to distance squared, as virtually all possible distances between points should be represented. A Monte-Carlo simulation was used to construct a confidence interval around the line corresponding to complete spatial randomness. Regular distribution is demonstrated as a k-function segment below the confidence interval of complete spatial randomness. This occurs because no points will be separated by some amount of low distances until the distance of regular distribution is reached. At this point, the distribution will begin to increase. In contrast, clumped distribution is shown as a k-function segment above that of random distribution. This occurs because certain distances will be represented by more points as a result of clumping. To organize our large-scale distribution data for the Ripley's K test, we obtained x-y coordinates for each labeled avens patch using GIS. We also mapped a best-fit polygon around the patches and took the x-y coordinates of the corners of the polygon. We then imported these x-y data into R and ran Ripley's K tests.

To test our hypothesis that gopher disturbance in the form of mounds would follow a clumped distribution across the tundra, we also used R to run Ripley's K tests on gopher disturbance in each quadrant. We then wanted to test the hypothesis that gopher disturbance would not only be clumped, it would be clumped within the avens patches. Data from the two quadrants at Oil Creek was analyzed using a chi-squared test to compare distribution of gopher disturbance within and outside the patches. Chi-squared tests compare the expected density to an actual density. P-values less than 0.05 signify that the actual density is significantly different than the expected density. Expected density was calculated to be the density of gopher disturbance in each quadrant assuming a regular distribution of disturbance. To prepare our data for this test we counted frequency of gopher disturbance within the patches in each quadrant, and calculated gopher disturbance outside the patches. Using the total area of the quadrants and the sum of the areas of the avens patches within each quadrant, we calculated expected frequency of gopher disturbance within and outside the patches. We then used an online chi-squared test application to yield our p-values.

Using our geoelectric resistivity data, we wanted to determine if mean resistivity of the soil beneath the patches would be significantly different from the soil beneath the ground outside of the patches. Geoelectric resistivity data were analyzed using non-parametric t-tests (with the exception of depth three in patch two which obeyed the tests for normality) in SPSS to compare the mean resistivity within the patches to the mean resistivity outside the patches at depths of 0.1428 meters (depth one), 0.373 meters (depth two), and 0.648 meters (depth three). Data points were taken every 0.25 meters at each depth. Where stakes overlapped between two surveys across the same transect, an average was taken between the two values for resistivity yielded. If only one stake yielded a resistivity value, then that value was used.

RESULTS

Large-Scale Spatial Distribution of Avens Patches

We hypothesized we would find a regular spatial distribution of avens patches across the tundra. Our results show a different story. At Oil Creek (Fig. 5), a Ripley's K of avens patches demonstrated random spatial distribution at distance of 0-40 meters. Clumped distribution of avens patches was found from distances of 40-60 meters. Distribution was then random again from 60-85 meters, and clumped from 85-95 meters. This was followed by random distribution above 95 meters. At Windy Point (Fig. 6), we found random distribution of alpine avens patches from 0-60 meters, with clumped distribution displayed at distances greater than 60 meters.

Spatial Distribution of Gopher Disturbance with Respect to Avens Patches

We expected to find spatial clumping of gopher disturbance, and that this disturbance would occur more frequently within alpine avens patches. Using a Ripley's K test, we found that surface gopher distance was strongly clumped at distances from 0-10 meters in quadrant one (Fig. 11). Surface gopher disturbance was also strongly clumped at distances from 0-10 meters for quadrant two (Fig. 12). In quadrant one (Fig. 9), a chi-squared test of surface gopher disturbance within and outside the avens patches yielded p=0.0010 (chi-squared=10.880, DF=1). A chi-squared test of surface gopher disturbance in quadrant two (Fig. 10), yielded p=0.0001 (chi-squared=306.961, DF=1). Therefore, gopher disturbance occurs more frequently within patches than would be expected given its frequency of occurrence across the tundra.

Geoelectric Resistivity Profiles

Our initial goal in creating geoelectric resistivity profiles was to map where gopher tunnels occur underground in relation to the avens patches. Instead, we discovered an intriguing pattern. Results indicate that mean resistivity is less in the ground beneath patches than the ground beneath the surrounding tundra. We analyzed geoelectric resistivity profiles by comparing the mean resistivity inside the patches with the mean resistivity outside the patches at the depths of 0.1428 meters (depth one), 0.373 meters (depth two), and 0.648 meters (depth three). Excluding depth two in patch two, which obeyed tests of normality, all other distributions were not normal. We therefore used non-parametric t-tests to compare the means. Data points were taken ever 0.25 meters for each of the three depths. Results for patch two can be seen in Figures 13 and 14. Results for patch three are displayed in Figure 15 and 16, and results for patch four are displayed in Figures 17 and 18. As can be seen, mean resistivity was significantly less for all three depths within the patches than outside, with the exception of depth three in patch three (Fig. 16). We can speculate on causation for this difference. Our main hypothesis is that increased water infiltration and subsequent weathering of granitic minerals to clay products contributes to this decrease in resistivity below the avens patches.

DISCUSSION

Spatial Distribution of Avens Patches is Not Regular

Preliminary observations of aerial images of the Pikes Peak tundra led us to hypothesize that alpine avens patches would follow a regular pattern of distribution across the tundra. How would this relate to gopher disturbance? Does gopher disturbance dictate where patches occur? Firstly, pocket gophers are very territorial. Typically only one pocket gopher occupies each tunnel system, except for during mating season (Reichman et al. 1982). Reichman et al. found that spacing within and between individual burrow systems was highly uniform for all pocket gophers examined. Spacing between individual gopher burrow systems remained constant regardless of resource levels (1982). Social interactions seem to dictate these buffer zones between individual systems rather than resources (Reichman et al. 2002). Though individual burrow systems are perpetually rearranged in negotiations for space and resource, burrow systems were never found to cross (Reichman et al. 1982). Reichman et al. suggest that mounds are clumped at spatial scales less than the size of a gopher territory, but regular in their distribution at large spatial scales as a result of the presence of undisturbed buffers between individual gopher territories (2002). The hypothesis that avens patches correspond to individual burrow systems would have meshed well with a regular distribution of gopher burrow systems. However, this is not what our data indicated. Findings at both the Oil Creek field site and the Windy Point site did not indicate a regular distribution of avens patches. Overall, the data points to a trend of spatial clumping at larger distances. If gophers were entirely responsible for avens patch location through the position of their individual burrow systems, it would have been reasonable to expect a regular distribution of patches. While more data is needed, we can preliminarily say alpine avens patches do not follow regular distribution at smaller distances as we had hypothesized. What we instead found was a generally clumped distribution of avens patches at distances greater than about 60 meters.

Perhaps a larger-scale survey would reveal that these clumps are evenly distributed between one other. More data is certainly needed to answer this question. However, a review of the literature indicates there may be a stronger link between gopher mounds and avens patches than to individual burrow systems.

Gopher Disturbance is Aggregated in Avens Patches

Gophers construct their tunnel systems beneath the tundra, resulting in deposition of subsoil to the tundra surface in the form of mounds of bare, loose soil. These mounds, according to Reichman (2007) follow a clustered distribution reflecting a pattern of 'area-restricted searching' utilized by the gophers. It has been found that gophers are highly accurate at locating their searching efforts in areas of high resource abundance (Huntly et al. 1994). We sought to investigate the relationship of surface gopher disturbance to avens patches through high precision mapping of all gopher disturbance and avens patches within two larger quadrants. Given our review of the literature, we expected to find a clustered distribution of mounds on the tundra. This was verified by our findings that gopher disturbance was strongly clumped at distances up to 10 meters in each quadrant. Next, we hypothesized that gopher disturbance would be concentrated inside the avens patches. Our chi-squared test results indicated that for each quadrant, gopher disturbance did in fact occur more often within the avens patches than would be expected given the overall density of disturbance within the quadrants. So how does this relate to the location of avens patches?

The net effect of gopher activity on the tundra is to mix soil vertically and generate patchy soil conditions horizontally (Gabet et al. 2003). As mentioned earlier, pocket gophers practice a highly accurate pattern of area-restricted searching for resources, increasingly the turn radii and number of tunnel branches in rich resource patches (Reichman 2007). This area-restricted searching is a necessary practice for gophers due to the high energetic cost of underground excavation, which places importance on optimizing burrow location (Reichman et al. 2002). Some fossorial mammals are very precise in their abilities to locate burrows and foraging tunnels in areas of higher productivity, or favored resource abundance (Huntly et al. 1994). For reference, the energetic cost of burrowing underground is about 360-3400 times that of aboveground travel (Huntly et al. 1988). Our finding of clumped distribution of mounds is in agreement with the results of other studies. Huntly et al. state that mounds are virtually always spatially clumped at a variety of scales. This clumping reflects the location of foraging tunnels within an individual territory, location of territories, and local patterns of population density (1994).

If gophers consume alpine avens, it is logical that mounding would be concentrated in avens patches as a result of area-restricted searching. We observed higher productivity and standing crop within avens patches as compared to the surrounding tundra (Jensen 2014). We found no conclusive study as to the diet of northern pocket gophers in the Pikes Peak region. However by compiling the results of other investigations, we can make educated guesses as to the diet of the pocket gophers in our study. Reichman outlines how forb shoots are the preferred diet of pocket gophers (2007). Another study found that forbs are preferred over grasses in the diet of pocket gophers in Oregon (Cox 1989). As avens are one of the most abundant forbs at our field site, it can be reasonably assumed that they make up at least part of the diet of pocket gophers.

The question then becomes if there is a link between surface gopher disturbance in the form of mounds, and alpine avens patches. Gopher mounding activities create sites that are distinctly different from the surrounding tundra. Sherrod et al. found that mounds contain little or no plant biomass (upon initial excavation), high incident light, and higher soil temperatures than the bordering ground (2001). Essentially, mounds create microsites with differing properties from the surrounding tundra. Mounds present a clean slate for plant re-growth in the tundra. Which plant species grow up through the mounded soil plays a determining role in vegetation dynamics on the tundra. Plant survivorship is generally low on mounds but final size and reproductive output of plants was found to be substantially higher (Huntly et al. 1994). This may relate to the fact that we observe higher productivity and standing crop in avens patches than the surrounding tundra. Of greatest interest to our study are the finding of Sherrod et al., that alpine avens have more success in response to burial compared to graminoids and cushion plants. This study, conducted in the moist meadows of Niwot Ridge, CO using simulated gopher mounds, found that forbs recovered faster following burial than graminoids or cushion plants after both one growing season and one year. Four species of forbs were studied; alpine avens, rocky mountain sage, american bistort, and parry clover. These species area all believed to be part of the pocket gopher diet (2005). This recovery demonstrates a resilience that confers a competitive advantage to avens over other plant forms, and favors forb dominance in moist meadows with gopher presence (Sherrod et al. 2005). Sherrod et al. suggest that the rapid recovery of forbs following burial may be due to their large belowground carbon stores (2005). This resilience in the face of burial is of primary importance in the colonization of gopher mounds, which effectively bury the surrounding vegetation.

There appears to be a point of tension in our findings between gophers actively constructing burrows for the use of foraging in areas of high avens concentration (if they are a preferred resource), while at the same time creating microsites, which facilitate the competitive advantage of alpine avens over surrounding tundra vegetation. It would seem that gopher predation should decrease the abundance of alpine avens in areas of high gopher activity. Why is this not the case? In a test of various gopher plant resource, it was found that mainland plant species which had been exposed to gopher herbivory were more heavily defended chemically, but also more tolerant to root loss when compared to plants which had never been subject to gopher presence (Reichman 2007). Could we be observing the effects of a mutually beneficial relationship wherein gophers create sites for avens colonization and in return are provided with a food source, which leads to additional long-range inhibition of avens in the tundra?

Soil Under Avens Patches is Less Resistive to Electrical Current

The most unexpected and perhaps most fascinating result of our study was the finding of significantly less resistive soils beneath the avens patches as compared to the surrounding tundra at three different depths. Except the lowest depth level in patch three, mean soil resistivity was significantly less at three different depths below the avens patches than beneath the tundra outside the patches. Through the creation of geoelectric resistivity profiles beneath the mounds, we intended to map where gopher tunnels occurred in the soil above the bedrock. Instead, what we unexpectedly found was a pattern of apparent disintegration of bedrock beneath the alpine avens patches.

Gophers, as we have established, act as ecosystem engineers of the tundra through their tunneling and soil-moving activities. Pocket gophers are agents of bioturbation, defined as the churning and stirring of sediment by organisms (Gabet et al. 2003). This bioturbation has been found to significantly decrease bulk soil density in areas of gopher disturbance (Gabet et al. 2003). A potential effect of this decrease in density is increased percolation of water into the ground in areas of gopher disturbance (Williams et al. 1986, Gabet et al. 2003). While our study did not measure soil moisture, it has been found that the lower soil density of mounds and re-filled burrows leads to the more rapid absorption and loss of soil moisture (Reichman 2007). Therefore, gopher disturbance affects the water balance of the soil. In a study of gopher disturbance in a Texas coastal prairie ecosystem, it was proposed that vegetation buried by gopher disturbance forms a mat, which effectively reduced evaporation from the soil (Williams et al. 1986).

We hypothesize that the decrease in mean soil resistivity within the avens patches at depths of up to 0.648 meters is due to a combinations of bioturbation and subsequent bedrock weathering. Gabet et al. propose that fossorial mammals may indirectly accelerate chemical weathering of bedrock by decreasing the bulk density of the soil, thereby increasing its hydraulic conductivity and bringing already fragmented pieces of bedrock closer to the soil surface (2003). Once this process has begun, fragmented bedrock weathers more quickly due to increased surface area (Gabet et al. 2003). An increase in water content of soils beneath avens patches could manifest as decreased resistivity, as water has a high conductivity. The pressure exerted by the larger taproots of alpine avens within the patches may also work to perpetuate this process. Deeper soil depth provides advantageous conditions for deeply rooted species to perform better in areas of gopher disturbance (Hobbs et al. 1985). An additional effect of the decreased density and subsequent increased water content of the soil could be the chemical transformation of the mineral components of granite into clays. Two key minerals in granite, mica and feldspar, are chemically converted to chlorite and kaolinite respectively when exposed to water (Anderson 2014). Clay, through its partially charged nature, provides exchange sites for positively charged ions including key plant nutrients. Therefore, the decreased resistivity of soils beneath avens patches may indicate a higher clay composition, as the ions attached to clays make weathered granite less resistive than granitic bedrock. An increase in the clay content of the soils has, to a certain extent, positive implications for nearby plants because as mentioned earlier some of the ions attached to exchange sites are key plant nutrients. Weathered bedrock beneath avens patches has implications for the establishment and resilience of avens patches on the Pikes Peak Tundra. If avens patches and gopher function in a co-evolved state of mutual benefit, then the presence of this disintegrated bedrock, with accompanying conditions of increased soil moisture and increased clay content, may contribute to the long-term resilience of avens patches on the tundra.

Synthesis

While our results indicate that gopher disturbance may be necessary for avens patch formation, the disturbance is apparently not sufficient. This is highlighted by the fact that there are areas of gopher disturbance on the tundra where alpine avens patches do not occur. Some factor or combination of factors is restricting patch formation to certain areas within the larger disturbance matrix. Why is this the case? Tundra vegetation dynamics are affected through the soil-moving activities of northern pocket gophers. This is not a phenomenon unique to the tundra. Distinct patches of vegetation in grasslands are associated in many cases with gopher mounds (Hobbs et al. 1985, Huntly et al. 1988). At our field site, we observe distinct patches of vegetation as well as gopher disturbance, which led us to speculate that the two are related. Our key findings of clumped gopher disturbance within the avens patches and the pattern of bedrock weathering beneath the patches seem to indicate gopher disturbance as responsible for the formation of avens patches, but something more must be at work.

Our findings in this study relate back to the fundamentals of self-organization. The mechanisms for self-organization are short-range facilitations coupled with long-range inhibition. Mechanisms for spatial self-organization include oscillating consumer-resource interactions, localized disturbance-recovery processes, and scale-dependent feedbacks (Rietkerk et al. 2007). Localized disturbance and consumer-resource interactions certainly pertain to the role of gophers in the tundra ecosystem. The hypothesis that gophers are positively impacting a crucial resource could be an example of resource optimization by the gophers, resulting in positive consequences for the productivity and diversity of the alpine tundra (Rietkerk et al. 2007). While gophers seem to be ‘farming’ avens within the patch, where facilitation outweighs inhibition, in the surrounding tundra gophers only ‘harvest’ avens. This balance of positive and negative factors limits avens to patches It also appears local abundance of avens somehow facilitates avens growing within the patches. Our goal in labeling the relative ages of mounds was an attempt to discern the potential role of disturbance in patch formation and/or maintenance. More data would be needed to investigate this link. An additional effect of gopher-induced disturbance may be increased moisture content in the soil, and thereby the conversion of granitic minerals to clays. From our initial geoelectric resistivity results, it seems this weathering of bedrock and subsequent decrease in soil resistivity is caused by a positive feedback between avens and gopher disturbance. However, in this chicken-egg situation, the possibility exists that initial abiotic conditions could have drawn the gophers or the avens to these areas.

Our results, paired with the literature, provide reasonable evidence that short-range facilitation is occurring between gophers and alpine avens. The theoretical summative actions of gophers create a positive feedback, defined as when a species helps another survive through facilitation by modifying the environment, and by doing so increases its own fitness. This may be related to the formation of avens patches on the tundra of Pikes Peak. Cox found in north central Oregon that some plants that were abundant on gopher mounds were nevertheless major items in the pocket gopher diet (1989). While it seems herbivory should negatively impact the avens, forbs species could be well adapted to chronic disturbance. Therefore the relatively regularly occurring biotic disturbance caused by gophers is rarely high enough to negatively affect the avens significantly (Martinsen et al. 1990). Instead, we may be observing a unique situation whereby pocket gopher herbivory, or more aptly the side effects of pocket gopher herbivory such as bioturbation, creates conditions that benefit one of their major food sources. These benefits lead to the proliferation of alpine avens across the tundra in the form of patches, rather than their regulation (as would be the case with keystone predation). The feedback is positive in the sense that gophers create conditions which lead to the proliferation of alpine avens. In turn, avens provide a source of food for the gophers, allowing the gophers to create more sites that benefit the avens on the tundra.

The theoretical positive facilitation of avens by gophers is not sufficient to explain avens patches on the tundra. Our main reasoning for this conclusion is that gopher disturbance is diffuse, whereas the avens patches have extremely defined boundaries. The fact that alpine avens do not occur in the concentration and size that they do in the patches across the entire tundra indicates that some form of long-range inhibition is keeping them concentrated in patches. This could be due to a number of factors, but we speculate competition with other vegetation for space, gopher herbivory through a predator-prey mechanism of Turing diffusive instability, and/or varying soil conditions across the tundra may be of primary importance (Alonso et al. 2002). Perhaps gopher activities on the tundra also lead to long-range inhibition. This would fit in line with a predator-prey mechanism of Turing diffusive instability (Alonso et al. 2002). In this situation, avens patches would still attract gophers as a favored resource. Gophers have a higher rate of mobility (or diffusivity) than avens. As gophers move in from the edges of the patches, they may contribute to long-range inhibition of alpine avens across the tundra. The results of this inhibition would be the patchiness of avens across the tundra. We can view the space in between the patches as zones of inhibition. Theoretically were gopher herbivory the sole determining factor in the location of avens patches, these zones of inhibition, and therefore the avens patches, would be regularly spaced. From our results, we see that this is not the case. The hypothesis of gophers as a long-range inhibition mechanism does not rule out gophers as providing short-range facilitation for the avens as well, it simply is a possible explanation for the crispness of the avens patch edges. Another short-range facilitation process to be considered is that avens are somehow working to modify their own environment. Our study did not focus on this option, but it is a possibility. The larger size and abundance of avens inside the patches suggests there may be a benefit for avens in living in close proximity to other avens. These are all pieces in the puzzle of why distinct alpine avens patches occur on the tundra

These dynamics have implications for the broader tundra ecosystem. An ecosystem is resistant if it can withstand environmental change and still remain in the same state (Rietkerk et al. 2007). A diverse ecosystem is theoretically more resistant to change. “Models predict regular pattern formation has important emergent effects on ecosystem functioning. Ecosystems with regular patterns might be more resilient to disturbance and resistant to global environmental change as compared with homogenous systems” (Rietkerk et al. 2007). The vegetative difference created by the patches promotes diversity across the landscape and delays succession through continual disturbance. Were the tundra soil left undisturbed, we would see a vegetative composition on par with that of the extra-patch plant abundance data (Jensen 2014). Disturbance, which can be defined broadly to include biological and physical processes, is fundamental to ecological dynamics. Disturbance affects population persistence and species coexistence in dynamic habitats (Pacual et al. 2005). As biotic agents of disturbance, gophers shape the ecosystem dynamics of the tundra. Through burial of vegetation by mounding, gophers create microsites in the otherwise monotonous tundra they inhabit. These microsites provide a competitive advantage for avens, which influences the entire tundra wherever gophers are present (Hughes et al.). In other words, microsites create conditions that are advantageous for different species, promoting competition and therefore a richer variety of species on the tundra. A mosaic of disturbance patches of varying successional age leads to increased diversity, which allows different kind of plants to coexist (Case et al. 2013). We might look at the influence of gophers as a pattern-forming ripple effect across the tundra. This ripple effect stems from gopher presence. Disturbance generated by gopher excavations tends to increase the dominance of forbs, which are a favored pocket gopher resource (Reichman et al. 2002). Gopher disturbance seems to be increasing the abundance of alpine avens on the Pikes Peak tundra by creating microsites of competitive advantage for the avens.

In sum, our results provides compelling evidence for a link between gopher disturbance and alpine avens patch formation on the Pikes Peak tundra, but they are not conclusive. Our data showing significant clumping of gopher disturbance within the patches, coupled with the pattern of weathered bedrock beneath the patches, provide initial insights into the mechanisms involved in the formation and maintenance of alpine avens patches. Crisply defined avens patches are an undeniable aspect of the tundra. However, our results are not conclusive. More investigation is needed into the question of why gopher disturbance is not necessarily a predictor of avens patch presence, and the mechanisms behind the decreased resistivity shown in our resistivity profiles. Certainly this is a multi-faceted question, and a relatively new area of research. The pattern of alpine avens patch formation on the Pikes Peak tundra is a potential demonstration of a biotic agent, the northern pocket gopher, engineering the tundra ecosystem. This engineering may contribute to the patterning of vegetation in the form of alpine avens patches, in what would in the absence of the northern pocket gopher represent a homogenous landscape.

Limitations of the Study

This study was conducted over the course of six field research days in September and October of 2013. Early autumn snowfall prevented us from collecting as much geoelectric resistivity data as we would have liked. A study over a longer time frame would provide for the collection of more data.

Areas for Further Research

The study of the spatial distribution of alpine avens patches and northern pocket gopher disturbance is a relatively new area of research, especially in alpine tundra ecosystems. There are many opportunities for further research in this field. To investigate the large-scale distribution of alpine avens patches across Pikes Peak, a large-scale remotely sensed (aerial photography) GIS-based survey of avens patch distribution would be relevant. This geographic survey could take into account factors such as slope-aspect and gopher presence. Further investigation might reveal if the long-range clumping of patches holds up on a greater scale, or if an alternative pattern emerges. Additionally, a comparison of avens patch location historically to today could provide insight into whether patches stay established in the same location, or if the patch distribution is more dynamic across the tundra.

To further investigate the relationship between gopher disturbance and avens patches, more data could be taken using GPS surveys of disturbance and avens patches. More data on age-classified gopher disturbance would allow for the parameters of a chi-squared test to be obeyed. Chi-squared tests on the different age classifications of gopher disturbance may provide insight into the role of gopher disturbance in the formation and maintenance of avens patches. An investigation attempting to describe how the gopher disturbance outside of the patch relates to the distance away from the patch would be pertinent to this study. It is possible that the density of disturbance decreases as distance from the avens patches increases.

The newest area of research pertinent to this study, and one with the most room for further investigation, is the underground geoelectric profiling. It would be highly relevant to take more transects for various situations across the tundra, to provide a framework for the results obtained in this study. More transects should be run under avens patches to investigate if the pattern of lower resistivity beneath the patches holds. Additionally, it would be interesting to run transects under areas on the tundra with gopher disturbance and no patch, to see if the pattern of weathered bedrock occurs in the absence of an avens patch. Finally, underground transects in tundra with no avens patch or gopher disturbance would serve as a reference point for the data collected in this study.

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APPENDICES

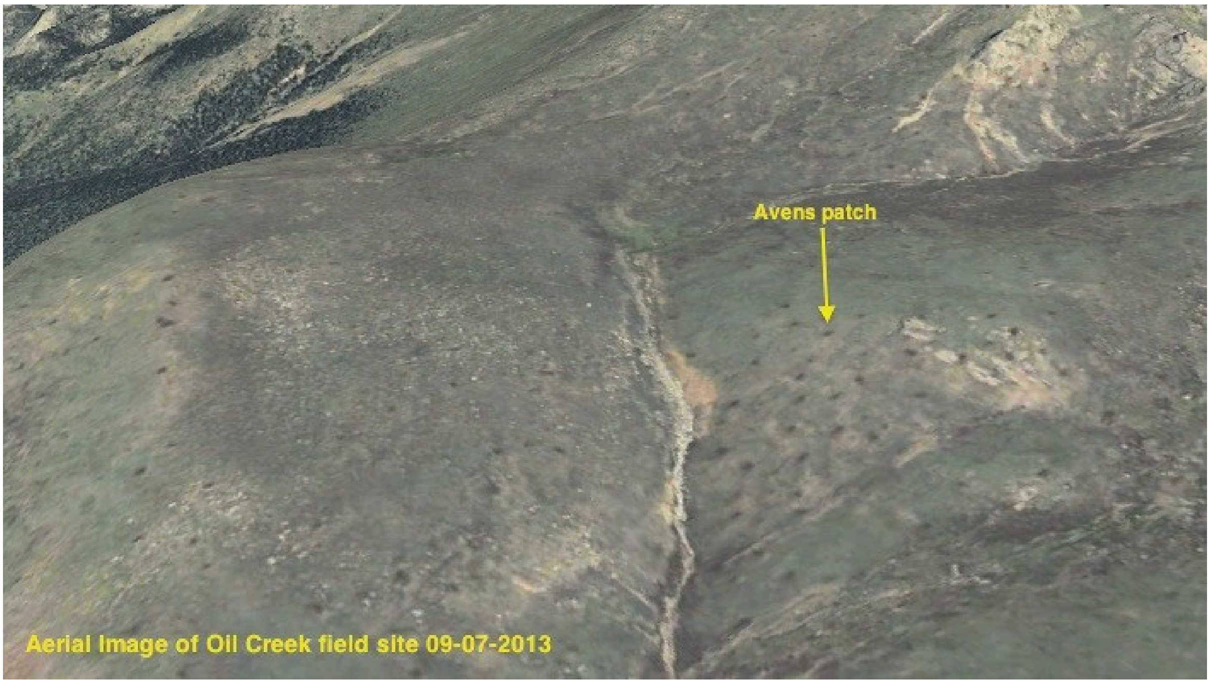

Figure 1. Oil Creek Field Site, avens patches are visible as distinct darker patches on the tundra.

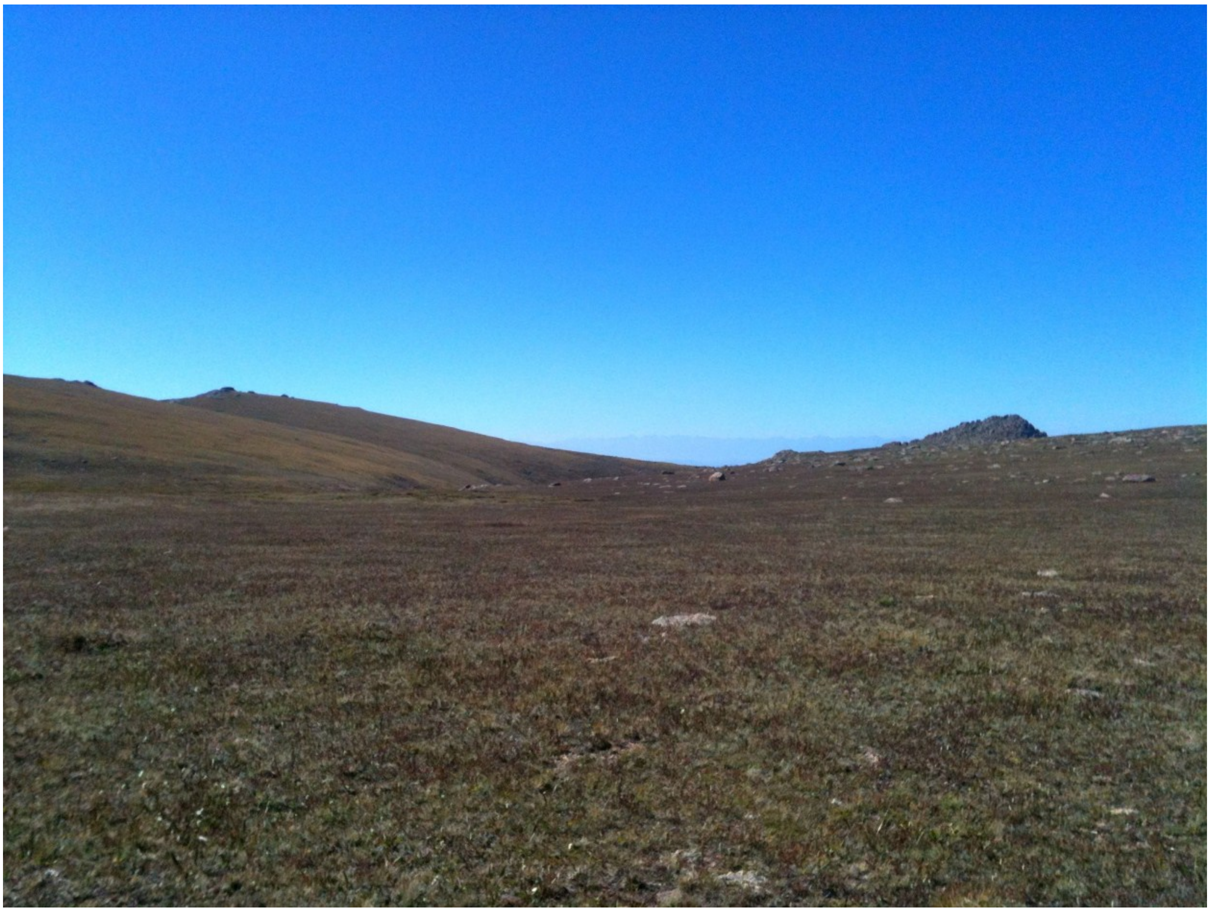

Figure 2. Oil Creek Field Site.

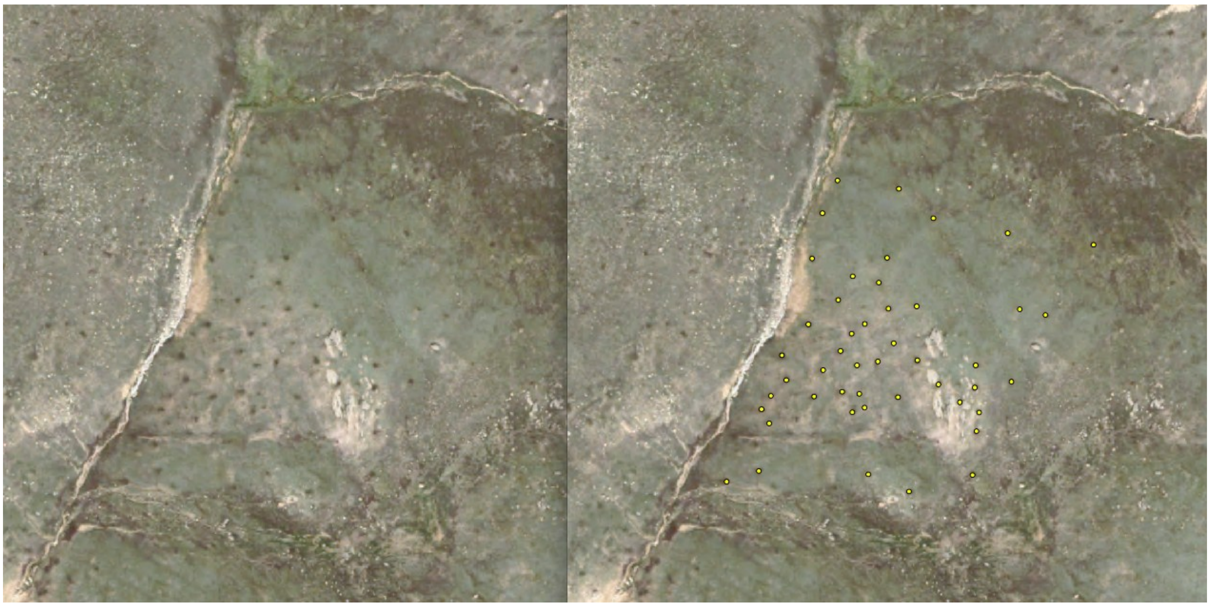

Figure 3. Aerial image of the Oil Creek field site with avens patches labeled.

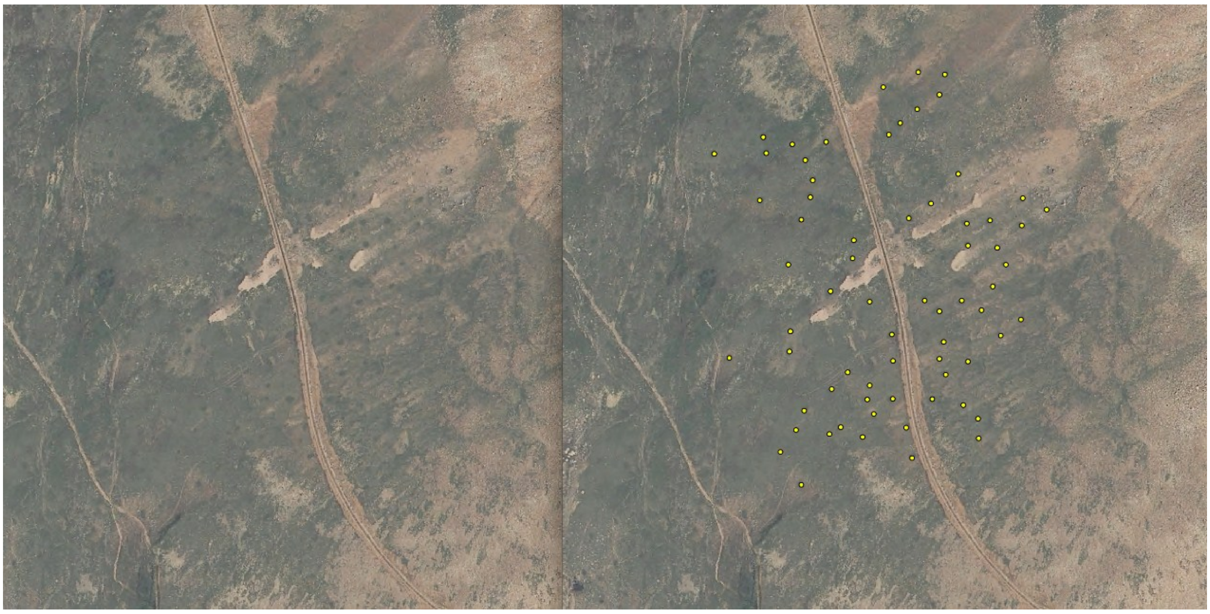

Figure 4. Aerial images of Windy Point with avens patches labeled.

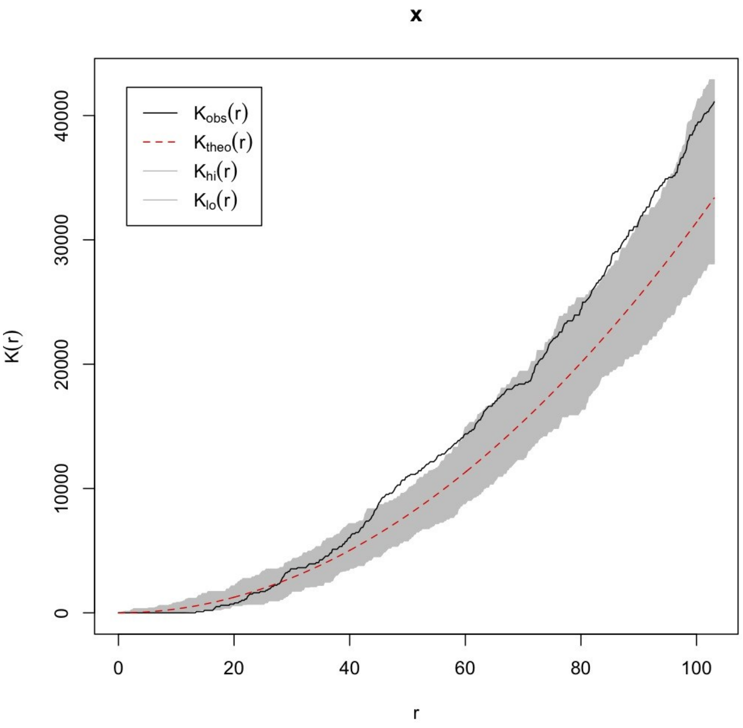

Figure 5. Oil Creek Ripley's K test results. Notice the distances where the black line deviates upward into clumped distribution (between 45 and 60 meters, and again at 80 meters)

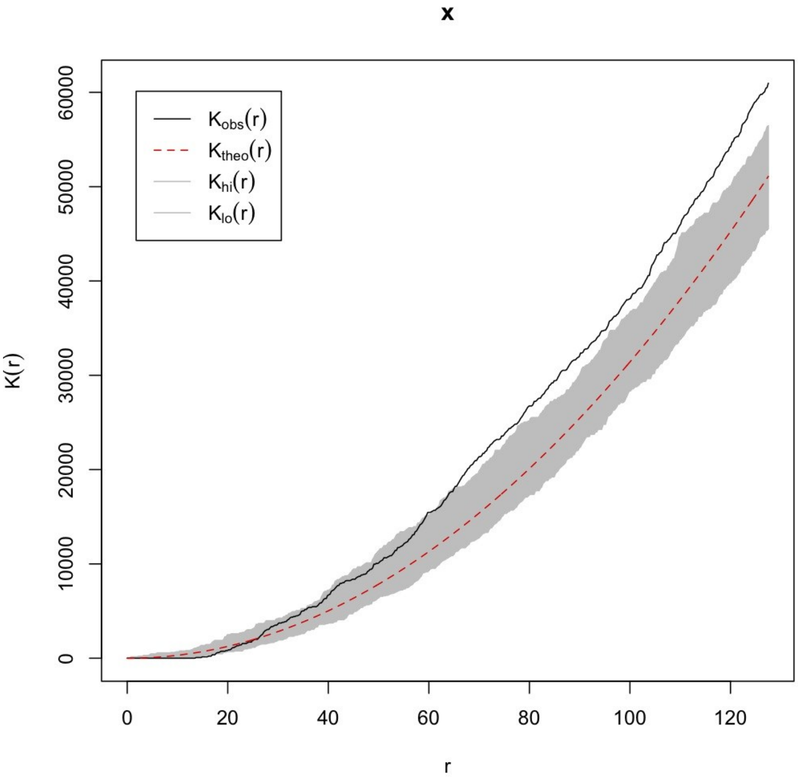

Figure 6. Windy Point Ripley's K test results. Notice where the black line deviates upward into clumped distribution (at distances above about 60 meters).

Figure 7. Oil Creek field site with quadrants labeled where high resolution maps of gopher disturbance and avens patches were created.

Figure 8. Mound age classifications. New mounds showed freshly tilled soils, young mounds were starting to show predominance of larger soil particles, and old mounds were those which were beginning to flatten and in some cases hosted plant growth.

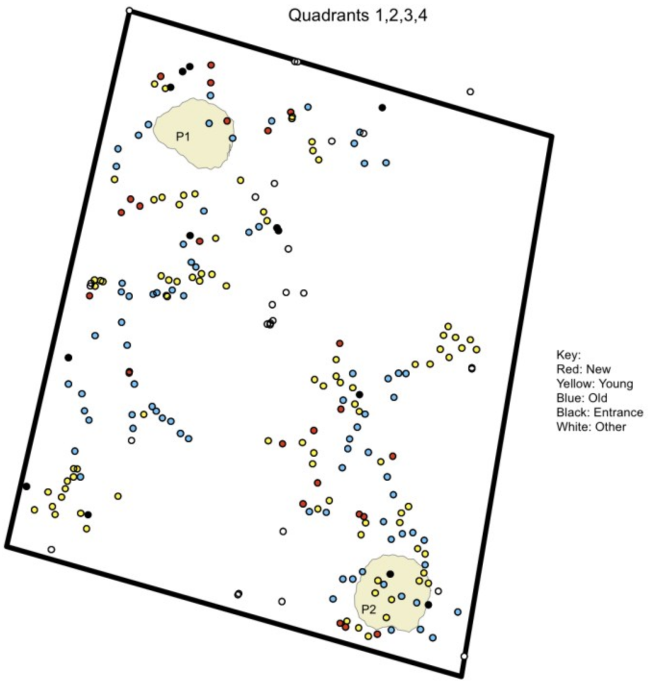

Figure 9. Quadrant one with avens patches and gopher disturbance (see key) labeled. 'P1' and 'P2' denote patch one and patch two.

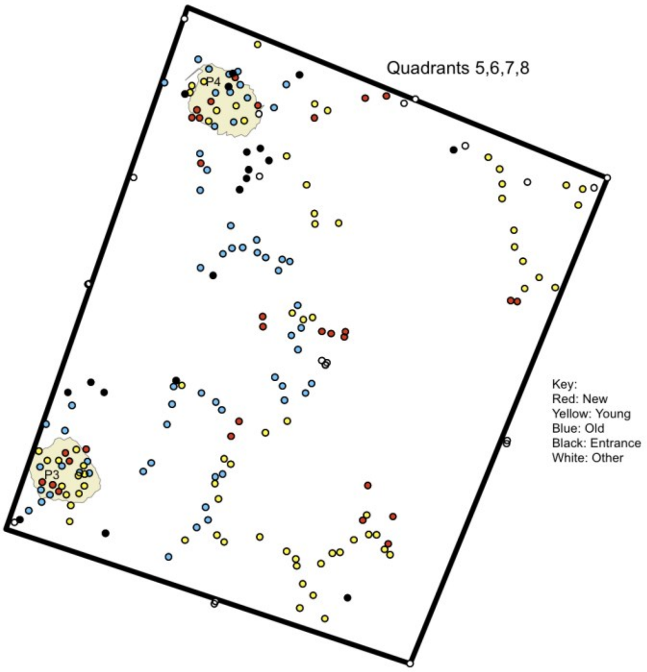

Figure 10. Quadrant two with avens patches and gopher disturbance (see key) labeled. 'P3' and 'P4' denote patch three and patch four.

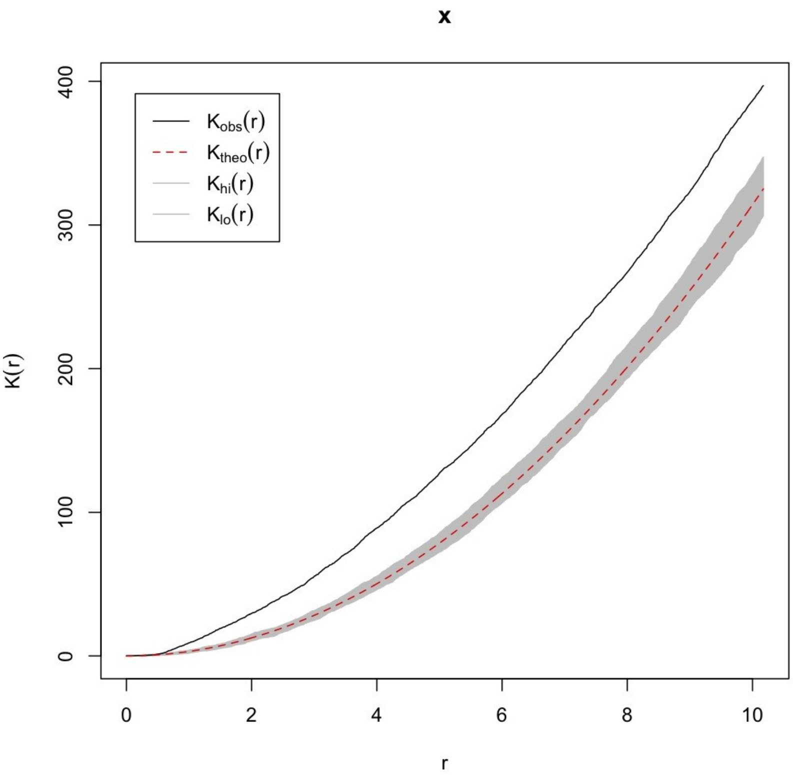

Figure 11. Quadrant one Ripley's K test results. Distribution is clumped for all distances between 0 and 10 meters.

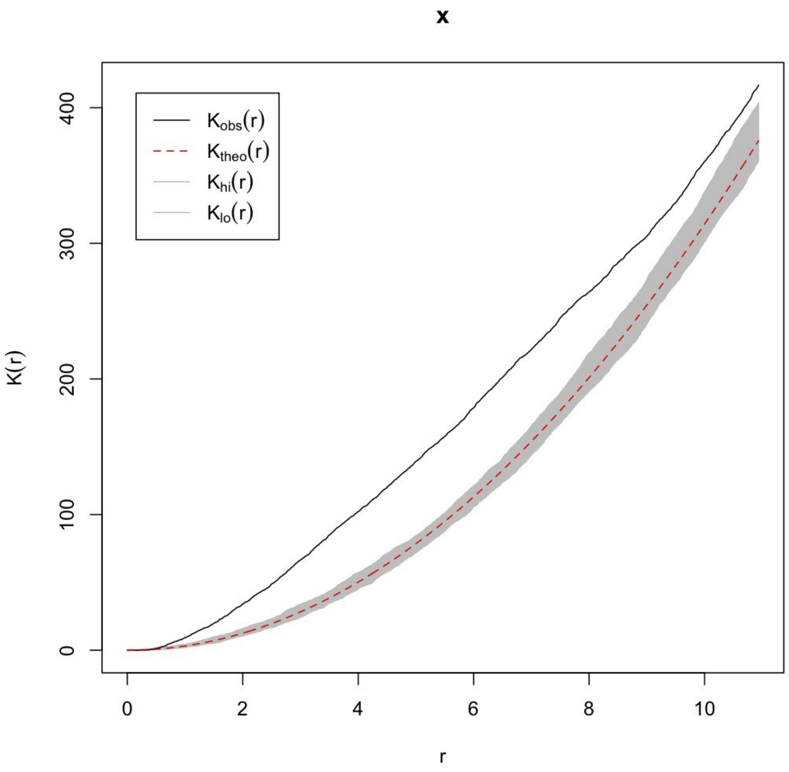

Figure 12. Quadrant two Ripley's K test results. Distribution is clumped for all distances between 0 and 10 meters.

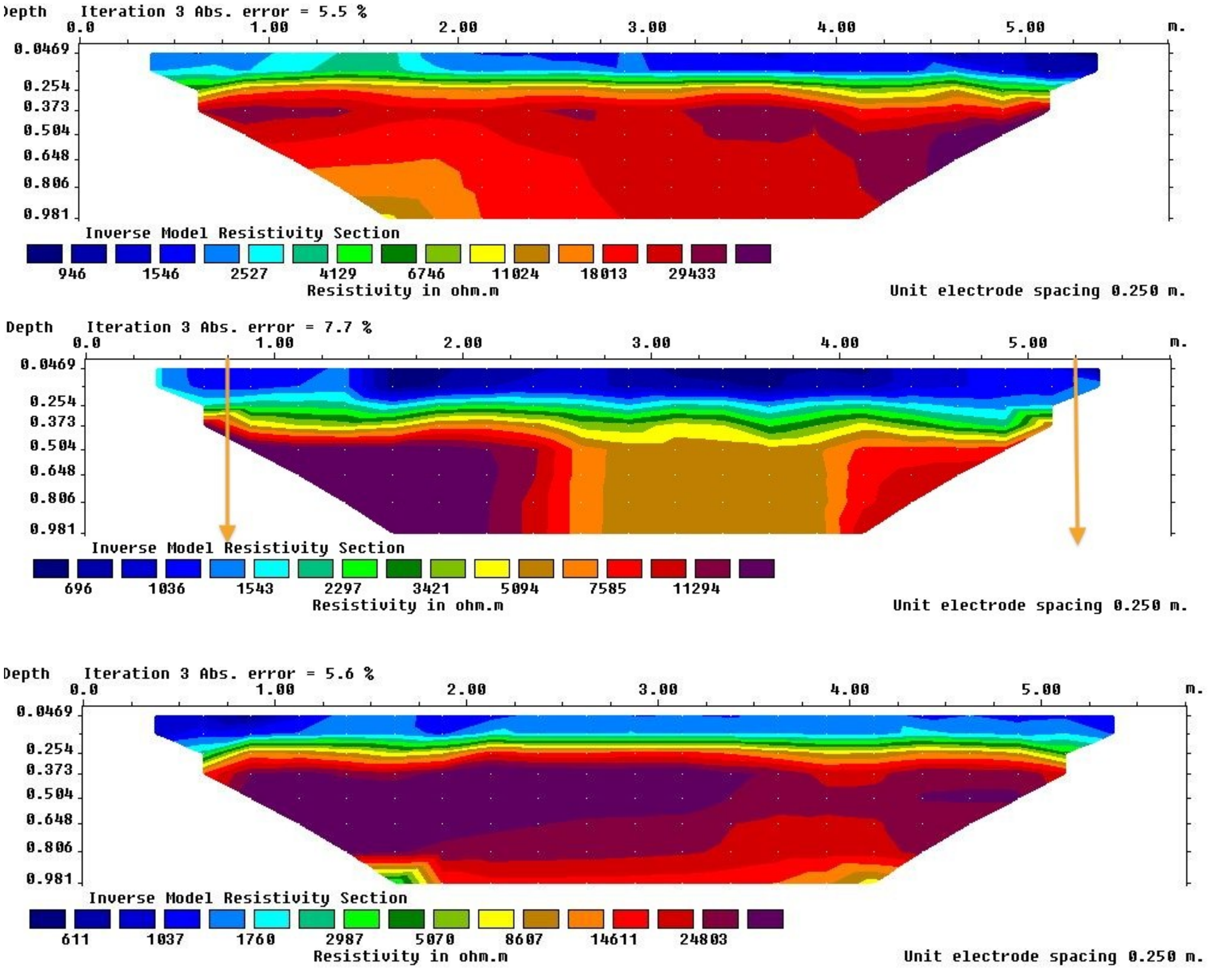

Figure 13. Patch two geoelectric resistivity profile. Note that color-coded resistivity keys follow different scales for each image. Orange arrows delineate avens patch edges.

	Mann – Whitney U	**P-value**	**In patch mean**	**In patch Std. Dev.**	**Out of patch mean**	**Out of patch Std. Dev.**
Depth 1	4.000	<0.0005	1158.468	151.927	2415.503	799.494
Depth 2	n/a	<0.0005	4979.298	4254.321	29660.032	5356.538
Depth 3	0.000	<0.0005	9722.057	4179.522	27837.848	6496.393

Figure 14. Patch two statistical results.

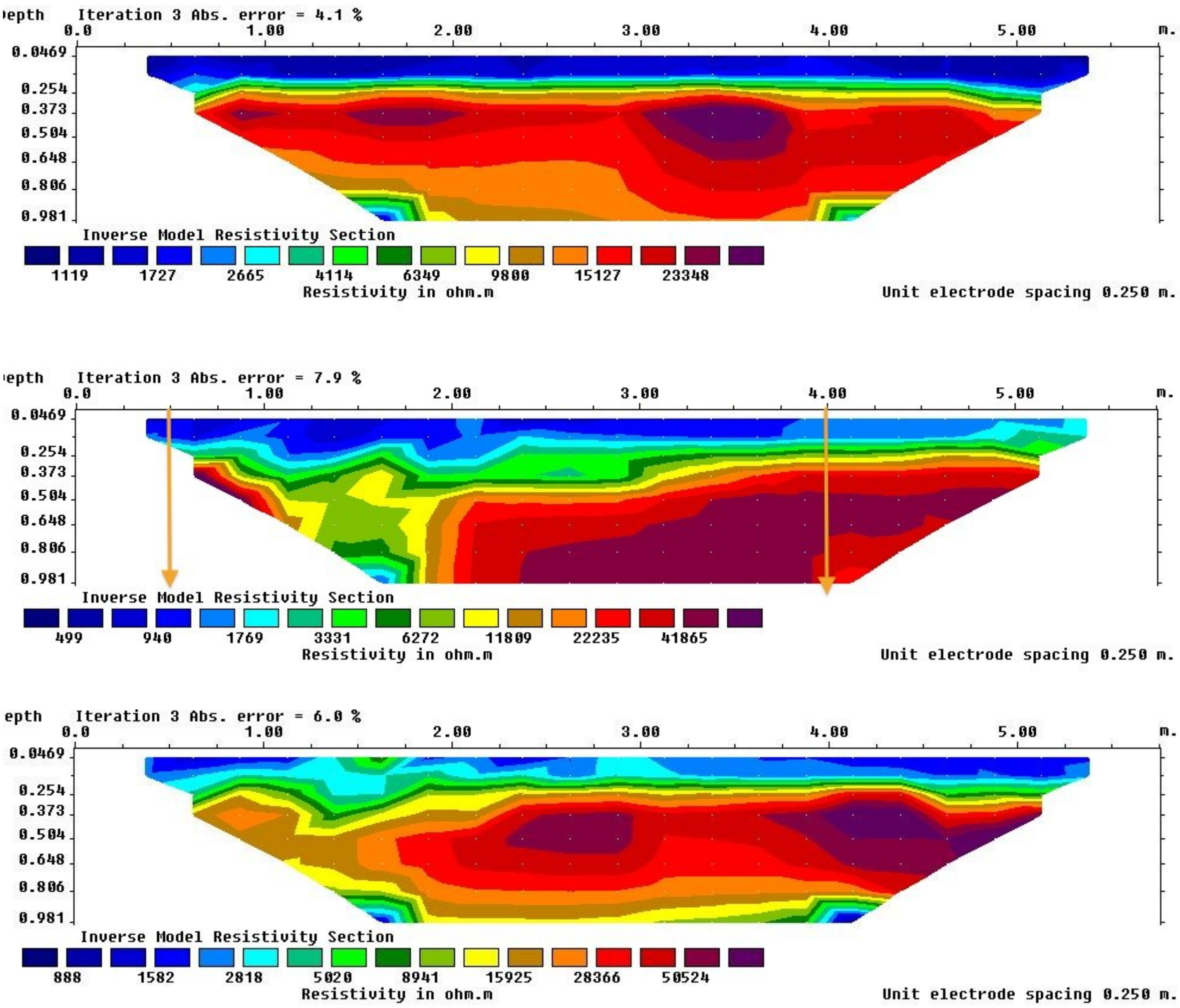

Figure 15. Patch three geoelectric resistivity profile. Note that color-coded resistivity keys follow different scales for each image. Orange arrows delineate avens patch edges.

	Mann-Whitney U	**P-value**	**In patch mean**	**In patch Std. Dev.**	**Out of patch mean**	**Out of patch Std. Dev.**
Depth 1	25.00	<0.0005	1331.56	256.843	2318.918	778.82
Depth 2	56.00	<0.0005	12686.478	10588.95	35250.54	14359.8
Depth 3	178.00	0.967	32543.56	16600.12	43490.86	51009.199

Figure 16. Patch three statistical results.

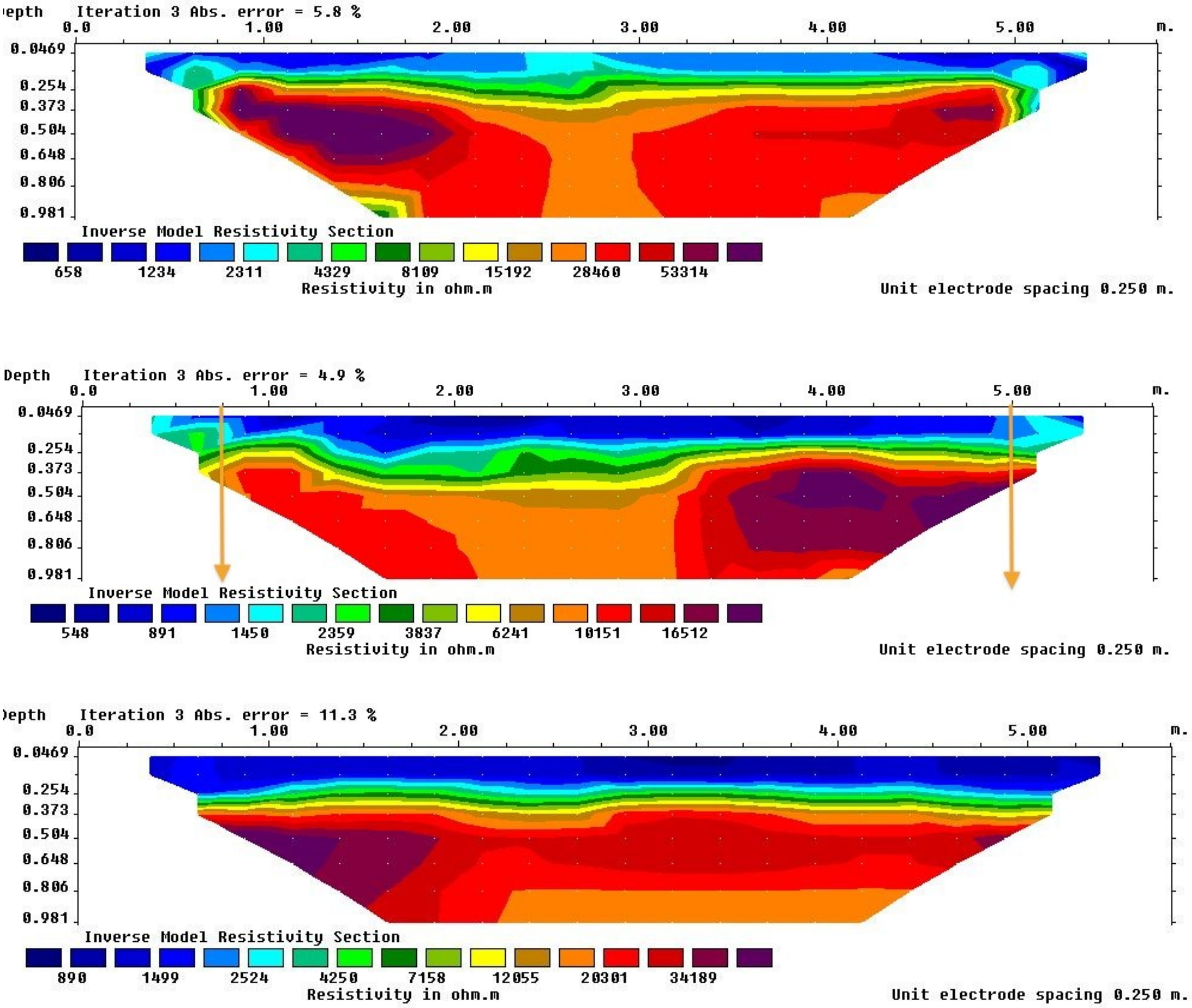

Figure 17. Patch four geoelectric resistivity profile. Note that color-coded resistivity keys follow different scales for each image. Orange arrows delineate avens patch edges.

	Mann-Whitney U	**P-value**	**In patch mean**	**In patch Std. Dev.**	**Out of patch mean**	**Out of patch Std. Dev.**
Depth 1	92.000	<0.0005	983.608	231.997	1614.652	988.16
Depth 2	156.00	<0.0005	7532.15	4784.839	19580.331	15891.377
Depth 3	227.000	0.013	10145.81	7465.75	23200.119	19212.198

Figure 18. Patch four statistical results.