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ABSTRACT:

Disturbance often increases local-scale (α) diversity by suppressing dominant competitors. However, widespread disturbances may also reduce biotic heterogeneity (β diversity) by making the identities and abundances of species more similar among patches. Landscape-scale (γ) diversity may also decline if disturbance-sensitive species are lost. California's vernal pool plant communities are species-rich due in part to two scales of β diversity: (1) within pools, as species composition changes with depth (referred to here as *vertical β diversity*), (2) between pools, in response to dispersal limitation and variation in pool attributes (referred to here as *horizontal β diversity*). We asked how grazing by livestock, a common management practice, affects vernal pool plant diversity at multiple hierarchical spatial scales. In terms of abundance-weighted diversity, grazing increased diversity at the α and γ scales without influencing β diversity. In terms of species richness, increases in α diversity with grazing lead to small decreases in β diversity as species occupancy increased. This had a dampened effect on species richness at the γ scale without any loss of disturbance-sensitive species. We conclude that grazing increases species richness and evenness (α) by reducing competitive dominance, without large disruptiions to ~~ng~~ the critical spatial heterogeneity (β) that generates high landscape-level diversity (γ).

Key Words:

Beta diversity, disturbance, spatial scale, wetlands, grazing

INTRODUCTION:

As global biodiversity loss continues to occur at an unprecedented rate, the maintenance of plant diversity at regional and local scales is a key target in restoration and land management (Turnbull et al. 2016). Management-driven ~~changes to~~ disturbance regimes, such as livestock grazing and prescribed burning, are known to increase plant diversity in many contexts, particularly at local ($<1m^2$) scales (Stohlgren et al. 1999, Marty 2015, Bovee 2017). However, many studies have found that disturbance effects on biodiversity are scale-dependent, in which the magnitude or direction of the response depends on the area of observation (Crawley & Harral 2001, Hill & Hamer 2004, Hillebrand et al. 2008, Socolar et al. 2016, Chase et al. 2018). This scale-dependence may reflect interactions between disturbance and multiple drivers of species coexistence. At local (α) scales, disturbance may increase species diversity through changes to competitive dynamics, while at larger scales, it may disrupt environmental gradients and other processes that drive community heterogeneity (β diversity) and maintain overall site level (γ) diversity (Olff & Ritchie 1998, Adler 2001, Socolar et al. 2016).

Grazing by livestock is the most extensive anthropogenic land use worldwide (Diaz 2007, Ellis & Ramankutty, 2008). Livestock grazing has been shown to have strong and scale-dependent effects on plant diversity (Adler et al., 2001; Osem et al., 2002; Stahlheber & D'Antonio, 2013). Experimental grazing treatments at moderate stocking rates can increase plant diversity in both mesic grasslands (Koerner & Collins, 2014) and arid grasslands (Souther et al. 2019) . While grazing can maintain local (α) diversity by suppressing competitively dominant species such as tall grasses (Hobbs & Huenneke 1979, Porensky et al. 2013, Stahlheber & D'Antonio, 2013), it could simultaneously reduce landscape (γ) diversity by selecting for a smaller pool of species that tolerant to grazing (Olff & Ritchie 1998). Grazing may also directly affect heterogeneity (β diversity) by decreasing the underlying spatial gradients of such physical drivers as topography, soil texture, nutrients, or hydrology (Adler et al. 2001, Augustine and Frank 2001, Olofsson et al. 2007, Golodets et al. 2011), or by accelerating seed dispersal (Cosyns et al. 2005, Chuong et al 2016). While many studies have focused on changes to species richness, changes in the relative abundances of species are ~~far more frequent, are quicker to respond to changes~~quicker to respond to disturbances, are more frequently observed, and are critical drivers of ecosystem function (Chapin III et al. 2000). Thus, it is important to consider disturbance effects on both species richness and abundance-weighted diversity measures (Hillebrand et al. 2017).

In California grasslands, grazing is currently a widespread management practice for livestock cultivation, wildfire reduction, and exotic species control. Revlatively little is known about the natural history of this ecosystem prior to the arrival of the Spanish in the 1700s, but it has been suggested that these grasslands were grazed by ungulates such as Tule elk and possibly small granivores. The Eurasian exotic annual grasses were introduced to improve pasture lands and now dominate the uplands, leaving only small patches of native plant communities (Stromberg et. al 2007). There is growing interest in the use of livestock grazing to promote diversity in these ecosystems, where light to moderate stocking rates generally select against perennials, taller plants, and graminoids, and promotes small-statured fobs ~~Grazing by cattle has often been shown to promote the local diversity of forbs within the matrix of dominant Eurasian exotic annual grasses~~ (Stahlheber & D'Antonio, 2013). Grazing is also a key management tool for the seasonally flooded depressions within grasslands known as vernal pools, which are among the Californian bioregion's most important and critically threatened reservoirs of endemic plant diversity (Bartolome 2007**)**. In these pools, inundation prevents the encroachment of non-native invasive upland grasses and forbs and selects for native species that are adapted to longer hydroperiods.

Livestock grazing at low to moderate rates is believed to be beneficial in California vernal pool complexes because it ~~increases the local (α) diversity of native and endemic forbs by suppressing~~ can suppress the ~~exotic~~ dominant species that ~~encroach on the edges of pools~~outcompete locally rare species, particularly in the edges around the pools. ~~(Marty 2005, 2015).~~ In addition to the direct effects of defoliation, livestock has been shown to increase the availability and duration of standing water in the pools, which reduces the competitively dominant species that cannot withstand prolonged moisture. It has been suggested that livestock can increase standing water (1) in local (<1m^2) patches within pools, as hoofprint trampling create pockets of lower, wet habitat (Barry 1995), and (2) at the scale of the whole pool, as trampling can lead to changes to soil compaction and/or water holding capacity (Marty 2005, 2015). The net effects of these biotic and abiotic grazing impacts in vernal pools have therefore been shown to maintain local (α) diversity within pools.

However, substantial turnover (β) diversity also exists in vernal pool complexes. Within a vernal pool, spatial variation is driven by vertical zonation from the inundated pool bottom to the upland edge (here called vertical β diversity). There is also considerable spatial variation among pools within a pasture (horizontal β diversity), driven by differences in pool size, depth, shape, soil, and dispersal limitation (Gerhardt & Collinge 2003, Gosejehan 2017, Kneitel 2016). The physical effects of grazing may have particularly strong outcomes on β diversity in this system because the endemic plants are highly adapted to subtle changes in hydrology and soil characteristics.

Because ungrazed vernal pool systems are rare, previous studies of grazing effects have necessarily relied on the use of small exclosures within otherwise grazed lands. Thus, the effects of grazing on whole-landscape (γ) diversity and on the spatial distinctiveness of communities both within pools (vertical β diversity) and among pools (horizontal β diversity) have not been well studied. We took advantage of a highly unusual opportunity to study a vernal pool complex divided into closely adjacent grazed and long-term ungrazed pastures. This 458-ha complex hosts 42 native plant species including 11 endemic species.

Hypotheses:

We hypothesized that (1) we would find higher local (α) diversity in grazed than ungrazed pools in agreement with previous studies. However, (2) we hypothesized that we would find lower vertical β diversity among the habitat zones within grazed pools as livestock trampling disrupts the gradual natural gradient that creates the transition zone. Finally, we hypothesized that (3) we would find lower horizontal β diversity among pools, and lower γ diversity at the whole pasture level, because of selection for similar grazing-tolerant species across pools.

METHODS:

Site selection:

Our study took place at Rancho Seco (38.34˚ N, -121.11˚ W), a 458.10-ha conservation site in Northern California. Rancho Seco is located on a high-terrace alluvial formation that hosts

Northern Hardpan Vernal Pools on Redding Gravelly Loam and Corning Complex soils (USGS SoilWeb) (Figure 1). The climate is Mediterranean with an average annual precipitation of 526.2 mm per water year (1 Oct – 30 Sep, CIMIS Weather Station, 21-year avg. 1997-2018, Fair Oaks, CA). Annual plants germinate with the first significant fall rains (generally Oct.-Nov.) and flower as the rainy season ends (Apr.-May), and seeds are dormant through the dry summers. Our study included the last 2 years of a multi-year drought: ~~water years of~~ 2014-15 (39.06 cm, 75.27% of 21-year avg.), the slightly wetter year of 2015-2016 (43.60 cm, 82.83% of 21-year avg.), and the extremely wet year of 2016-2017 (93.06 cm, 176.84% of 21-year avg.) (based on the Oct 1-Sep 30th water year, CIMIS Weather Station, 1997-2018, Fair Oaks, CA). Pool standing water depths vary greatly both between pools and within pools between years. The pools at our site ranged from water depths of 0.00 to 38.00 cm over the three years of our study. The site includes a 20.9 ha pasture, where grazing has been in place for 150 years, and the current regime is 1 cow-calf unit (1 Animal Unit (AU) per 2.4 ha (0.31 AU Year/ha). While typical stocking rate varies greatly by region (Herrero-Jáuregui & Oesterheld 2017), this stocking density is within the typical carrying capacity range for ~~annual~~ grasslands in this region (1 animal unit per 2.43-4.86 ha per year) (George et al. 2016), and similar to other conservation grazing stocking densities in vernal pool landscapes (Marty 2015). In montane vernal pool landscapes, this stocking rate may be higher (1 AU/1.68 ha) (Merriam 2017). This site also includes an adjacent ungrazed ~~area~~ pasture of 24.35 ha from which cattle were removed 40 years ago when a fence was built to delineate property management boundaries.

Commented [JSM1]: I added in the depths since reviewer 1 requested it. I also played with including the total days of inundation but I got nervous that reviewer 2 would get too hung up on it (when really there just isn't room in this paper to go into it in detail). What do you think?

In winter 2014, we selected 14 pools each from the grazed and ungrazed areas that spanned two soil types, Corning Complex and Redding Gravelly Loam, (USGS SoilWeb) and a range of pool characteristics affecting plant communities, including, size, shape and slope around the pool perimeter (Gerhardt and Collinge 2003). We matched each grazed pool with an ungrazed pool with as many similar key characteristics as possible (Appendix A).

We were interested in the effects of grazing at the pasture scale in addition to the local (<1 m^2) and pool (4-6800 m^2) scale. To achieve this, ~~our grazing treatment was applied~~we chose a site in which grazing was applied at the pasture level rather than in a spatially random pattern. We therefore expected to see some spatial autocorrelation across the whole site driven by vegetation differences between the grazed and ungrazed pastures. Within grazing treatments, however, we also wanted to ensure that the similarity between any set of pools (horizontal β diversity) that we observed were not simply due to their spatial proximity. To determine whether spatial autocorrelation needed to be accounted for in our analyses, we conducted a partial Mantel test using spatial coordinates of each pool centroid. After accounting for grazing treatment, we found no significant spatial pattern in community composition~~, suggesting that horizontal β diversity is not driven by spatial proximity within treatments~~ (Mantel statistic based on Pearson's product-moment correlation = 0.09, P = 0.10; Appendix B**)**. Thus, we can rely on our multivariate analyses to assess differences in plant composition that are not confounded by spatial proximity.

Vegetation Sampling:

We followed established sampling methods for vernal pools that stratify based on vertical habitat zones and randomly sample within each zone (Marty 2005, ~~Solomneshch 2007,~~ Gerhardt & Collinge, 2007~~, Bartolome 2007~~). In early spring 2015, after the pools dried down and before ~~native~~ forb taxa were identifiable, we delineated three vertical habitat zones (inundated, transition, and upland) by recording slope and water marks that indicated differences in inundation time. Two water lines were visible in each pool—one distinct line marking suggesting constant inundation throughout the season, and another, fainter line suggesting more variable inundation. We delineated the lowest point in the pool up to the inner line as the ‘inundated’ zone and the area between the two lines as the ‘transition’ zone. We delineated the ‘upland zone’ as the area within 5-m of the transition zone, beyond which we expect little interaction with the vernal pool ecosystem (Marty 2005). Biweekly from March-May, we visited each pool and tracked the phenology of forb species. When we determined that a pool had reached ‘peak flowering’ in which the majority of forbs were blooming and identifiable, we placed quadrats in ~~three~~ randomly chosen locations within each zone. Each quadrat was 50x50 cm, divided into 100 5 x 5 cm squares. We recorded the number of cells in which each species occurred. Each year, new locations were randomly chosen for the quadrats within each habitat zone in each pool. Due to the short phenological sampling window, we were limited to three quadrats per zone in each pool (9 quadrats per pool, 216 quadrats/year total). Our sampling replication was not strong enough to detect grazing-related differences in turnover between the three quadrats within zones (q0: F(1,82): 2016: $p<0.53$, 2017: $p<0.25$, 2018: $p<0.42$, q2: F(1,82): 2016: $p<0.73$, 2017: $p<0.80$, 2018: $p<0.35$). We therefore did not consider β diversity differences between individual quadrats. Instead, we averaged the individual quadrats in order to obtain a measure of diversity at the zone-level for each pool.

Commented [JSM2]: Here is where we ran the beta diversity test between quadrats and found no differences in turnover related to grazing. Is it too strange to include these results in the methods? It does seem like the best placement because then it flows right into the breakdown of how we measured alpha, beta, and gamma. What do you think?

Data analysis

We defined α_1 as the diversity contained in individual zones, β_1 as the vertical turnover between habitat zones within each pool, α_2 as the diversity of a whole pool, β_2 as horizontal turnover between pools within each pasture, and γ as the total diversity at the pasture level (Figure 2).

We calculated α, β, and γ using linearized diversity metrics referred to as 'Hill numbers' that permit variable emphasis to be placed on common versus rare species (Hill 1973, Jost, 2006, 2007). These indices (denoted by ^{q}D) decompose species diversity into independent "effective number of species" and "effective number of samples" components (α and β, respectively; Hill 1973; Jost 2006, 2007). In our experiment, $\gamma_{treatment} = \alpha_{pool} * \beta_{pool}$ and $\alpha_{pool} = \alpha_{sample} * \beta_{sample}$. When calculated at "order 0 (q=0)", α and γ are species richness and β is defined by species presence or absence (Jaccard dissimilarity), which gives equal weight to common and rare species. When calculated at order 2 (q=2, where α is Simpson's diversity index) they reflect species richness weighted by squared abundance, which gives low weight to rare species (Jost 2007, Cook et al. 2018). We used orders 0 and 2, omitting the intermediate "Order 1" (q=1, where α is Shannon-Weaver diversity). This emphasized the limiting cases where rare species have the most (order 0) and the least (order 2) influence on diversity metrics.

We obtained p-values for differences between our test statistic and a null distribution generated by shuffling treatment labels (grazed/ungrazed) within each hierarchical level of interest (Legendre & Legendre, 2012). For tests at the zone and pool scales (α_1, α_2; β_1) we used a permutation F-test (permutation ANOVA) to shuffle grazed/ungrazed labels. For tests at the landscape scale (β_2, γ) with a single observation of diversity, we used a standard permutation test of differences in group means that randomizes treatment labels (grazed/ungrazed) within a year and calculates the difference in diversity. The fraction of observations that have an absolute difference greater than the observed difference are used to calculate P-values. (Manly, 2006). All significance tests were based on 9999 permutations.

To test for effects of grazing on species composition as opposed to diversity at the α and γ scale, we used two-way permutational multivariate analysis of variance (PERMANOVA). To test for the compositional differences in β diversity between the grazed and ungrazed treatments, we used permutational tests for homogeneity of multivariate dispersion (PermDISP, Anderson 2001). Both tests were based on Bray Curtis (abundance-weighted) similarity. To visualize the effects identified by PERMANOVA and PERMDISP in two dimensions we used non-dimensional scaling (NMDS). We projected abundances of the 10 most common species onto the NMDS plots to visualize their contributions to grazing effects.

To further identify the specific species that were driving grazing effects, we calculated the mean relative abundance of each species summed over all three years. We compared these abundances between the grazing treatments using two-sample t-tests and the Benjamni-Hochberg correction for multiple comparisons (Benjamini and Hochberg 1995, Waite and Campbell 2006). We also calculated relative cover of native and exotic species (Appendix C). All analyses were completed in R statistical software v3.6, and all scripts are available on GitHub online repository (Michaels 2020).

RESULTS:

Grazing increases α *diversity* ~~*both*~~ *within zones* ~~*and across the whole pool:*~~

Grazing was associated with significant increases in α_1 diversity at the smallest spatial scale, that of ~~individual quadrats within~~ vertical habitat zones (Figure 3). Measured at order 0, this effect

Commented [JSM3]:

Commented [JSM4]: Removed the language about quadrats to be more consistent with what we actually did--- we averaged the quadrats by vertical habitat zone.

occurred in all three years for the upland and transition zones. Measured at order 2, it occurred in 2016 for all three zones, and in 2017 for the transition zone only (Table 1).

Communities within vertical habitat zones varied in their compositional response to grazing. In both grazing treatments, the upland zones had the lowest species richness and lowest diversity weighted by abundance (Table 1). In the upland zones, grazing did not have consistent effects on the key dominant species—for example, grazing increased the cover of *Avena fatua* while decreasing the cover of *Bromus diandrus* (Appendix D-4). In the inundated zones, grazing reduced the cover of the two key dominant ~~dominant species, the exotic~~ forbs ~~*Leontodon saxatalis*~~ ~~and the native forb~~ *Lasthenia fremontii* and *Leontodon saxatalis* (Appendix D-2). The position of the transition zones on the margins between inundated and upland habitats gave rise to the highest average species richness in both grazing treatments. Grazing-related increases in diversity were associated with decreases in the cover of key dominants, including two f~~exotic~~ ~~f~~orbs, *Erodium botrys* and *Leontodon saxatalis,* and two ~~exotic~~ grasses, *Avena fatua* and *Briza minor* (Appendix D-3).

Grazing increases α diversity across the whole pool:

The increases in diversity that were associated with grazing within each zone were maintained at the scale of whole pools (α_2) with an average of 4 more species in grazed pools in all three years (order 0 α_2 2015: $p=0.01$, 2016: $p<0.01$, 2017: $p=0.04$) (Figure 3a). This suggests that at least some of the increases in species diversity were due to species additions to each pool (increase in α_2), mostly through additions to the transition and upland zones (Table 1). We also found a trend toward increased richness weighted by abundance at the whole-pool level (Figure 3b), although this effect was only significant in 2016 (order 2 α_2, 2016: $p<0.01$, Table 1**)**. This increase was commonly associated with decreases in the cover of key dominants. Grazing significantly reduced the relative abundance of 5 of the 10 most common species at the whole-pool level, including three ~~exotic~~ grasses (*Avena fatua, Bromus diandrus*, and *Briza minor*) and two forbs ~~,~~ ~~one exotic forb~~ (*Lasthenia fremontii and* *Leontodon saxatalis*~~) and one native forb (*Lasthenia fremontii*~~). The largest observed change in composition was grazing reductions in the abundance of the ~~exotic~~ forb *Leontodon saxatalis* (Grazed relative abundance: 11.90%, Ungrazed relative abundance: 19.12%), which increased presence of more locally rare species, particularly forb and legume taxa such as Ranunculus bonariensis and Psilocarphus brevissimus (Appendix D-1).

Grazing does not affect pool zonation (vertical β diversity)

Consistent with other studies and our hypotheses, we demonstrated that the vertical habitat zones within vernal pools host distinct plant species assemblages; β_1 was significantly greater than 0 whether measured at order 0 or order 2 (Figure 3a, Table 1). Vertical habitat zone, structured by the topographical gradient between upland and pool bottom, was by far the strongest controller of species composition within pools (PERMANOVA, F(1, 26) = 77.36, $p<0.001$) (Figure 4a). Contrary to our expectations, the distinction between the vertical habitat zones (vertical β_1 diversity) did not differ between grazed and ungrazed pools whether measured at order 0 or order 2 (Table 1), or when it was measured as compositional turnover between zones (Figure 4a).

Grazing decreases variation in species richness between pools (horizontal β diversity)

As expected, we found that plant diversity was structured by variation among pools (horizontal β diversity) within each pasture ~~within our site~~ (Average β_2 (order 0) =1.93, Average β_2 (order 2) =1.32, Table 1). For species richness (order=0), grazing decreased this horizontal β_2 diversity between pools in two years (2015: β_2, p = 0.042, 2016: β_2, p = 0.034, Table 1, Figure 3b), driven by richness changes in the upland zone in 2015, and in the transition zone in 2016 and 2017 (Appendix E). However, grazing did not alter β_2 diversity across pools when considering the strongly abundance-weighted metric (order 2) (Table 1, Figure 3a), or compositional turnover (Figure 4b).

Grazing increases species evenness, but not richness at the pasture (γ) scale

We identified a total of 61 species at our site over the three-year study period (Appendix D-1). The grazed pasture was compositionally distinct from the ungrazed pasture (PERMANOVA, (1, 26)=13.55, $p<0.001$, Figure 4b). Grazing was not associated with a significant increase in species richness (order=0) at the pasture (γ)scale (Table 1, Figure 3a), but it did cause a significant increase in abundance-weighted (order=2) plant diversity in 2016 and 2017 (2016: γ, $p = 0.002$, 2017: γ, $p = 0.020$, Table 1, Figure 3b). The divergent results between species richness and abundance-weighted diversity metrics demonstrate that the compositional differences were primarily driven by reductions in the proportional abundances of the most common species, rather than any large changes in species identity, or addition or loss of species at the pasture level.

DISCUSSION:

Taking advantage of a rare set of grazed and adjacent ungrazed vernal pool grasslands, we asked whether managed grazing disturbance could increase diversity at pool (α_1, α_2) scales while leading to decreases in diversity at the pasture (γ) scale, mediated by reductions in the grazing intolerant rare species that contribute to β diversity both within (β_1) and between (β_2) pools. Our findings suggest that at the pasture (γ) level, compositional differences were primarily driven by reductions in the proportional abundances of the most common species, rather than any large changes in species identity, or addition or loss of species at the pasture level.

These findings are consistent with literature which suggests that disturbance can increase plant α diversity if competitively dominant species are selected against, freeing up niche space for less competitive species. This pattern has been found across several types of disturbance, including grazing (Hobbes and Huenneke 1979, Stalheber and D'Antonio 2012, Porensky et al. 2013), fire (Safford and Harrison 2003, Keeley 2006, Marty 2015b, Burkle et al. 2015), flooding (Price et al. 2011), and anthropogenic changes (Mackey and Currie 2001). In our vernal pool site, moderate grazing (0.31 AU Year/ha) had the effect of reducing the dominant forbs which play a particularly important role in suppressing locally-rare forbs because of their similar functional traits (Gerhardt and Collinge 2007). This likely led to the increased distribution of more locally rare taxa , increasing their presence in the habitat-zone (α_1) and pool (α_2) scale plots. In addition, these locally rare taxa may have been more readily dispersed by livestock across the landscape. While rare vernal pool taxa such as *Ranunculus bonariensis* and *Psilocarphus brevissimus* are known to exhibit considerable dispersal limitation and strong site fidelity (Solomneshch 2007, Jain 1978), grazing has been shown to disperse seeds in CA grasslands through mud, fur, and dung (Chuong et al 2015), and could have a disproportionate effect in a system that has very high dispersal limitation without grazing.

We hypothesized that grazing would reduce the distinction between habitat zones (vertical β_1 diversity) by disrupting the subtle topographical gradient that creates this structure in the absence of grazing (Adler 2001). However, we found that grazing was not a strong enough driver to reduce the compositional distinction between the habitat zones. Our results suggest that disturbance may have only minor effects on plant heterogeneity (β diversity) in systems in which this heterogeneity is maintained by strong environmental gradients. It is important to note that our method, which sampled the center of each habitat zone, may not have picked up on some more fine-scale ‘blurring’ of the edges of habitat zones.

We also expected to find lower turnover (horizontal β_2 diversity) among grazed pools, and lower γ diversity of the whole grazed pool complex, driven by selection for similar grazing-tolerant species across pools. We found that grazing did make pools more similar to one another in species richness (decreased horizontal β_2); however, this occurred by increasing the occupancy of rare species within our samples, not by changing the total number of species at the pasture scale (γ). Socolar et al (2016) similarly suggested that increases in site occupancy by rare species can cause β diversity to decline, with positive or neutral outcomes on γ.

Our findings add an important caveat that local species richness increases may not be reflected at larger scales of observation, reiterating the importance of measuring species abundance as a measure of diversity change and heterogeneity. Species evenness often responds more quickly to environmental disturbance than richness, since species can persist in very low abundances after disturbance even as their role in ecosystem function has been greatly reduced (Hillebrand 2008, 2017). We also found that reductions in between-pool variation (horizontal β diversity) were reflected in species richness but not evenness, as the more consistent presence of locally rare species in the grazed samples drove down the dissimilarity between these samples. Li et al. (2016) similarly found divergent patterns in β diversity measured using species identity and abundance-weighted metrics in abandoned agricultural fields. In these fields, as the dominant species became more similar while the rare species were unaffected, only the abundance-weighted metrics revealed trends towards convergence in these fields. The divergent pattern of species richness and evenness has been demonstrated in several plant communities and is considered to be a major challenge to effective conservation monitoring and management Hillebrand 2008, 2017).

A major advantage of our study was our ability to look at the effects of grazing on vegetation at multiple hierarchical scales. Our study expanded the scope of small scale ($<1m^2$) observational studies to address grazing effects at the whole-pool (α_2) scale, or spatial scales of 10-600m^2, as well as the pasture scale (γ), which are less studied in the grassland literature (Johnson and Cushman 2007). We showed that both local and site level analyses are necessary in order to fully understand grazing effects in vernal pool ecosystems. It is interesting to note that similar scale-driven pattern has been found in montane vernal pools, despite the fact that montane vernal pools are ~~driven~~ influenced by a different set of biotic and abiotic constraints and lack strong competition from exotic dominant species (Bovee et al. 2017). In our system, a manager measuring increases in species richness at only the local scale might incorrectly conclude that species were being added to the overall system by grazing. This demonstrates the importance of measuring disturbance responses using multiple scales as scientists and managers monitor the effects of global biodiversity loss.

Finally, our study underscores the importance of context-dependence when measuring plant diversity responses to disturbance. We found that grazing affected habitat zones within vernal pools differently, most likely due to the fact that each zone is uniquely affected by a balance between the biotic constraints of competition and the abiotic constraints of inundation (Adler et al. 2001, Collinge 2003, Gerhardt and Collinge 2007, Gosejehan 2017). We also found that the years which had the strongest diversity response to grazing were also the years with the highest overall diversity, suggesting that in years in which diversity is low due to abiotic conditions such as drought, the plant community response to grazing may be dampened. These results stress the importance of developing studies which stratify across key habitat types rather than selecting locations at random, as well as the importance of monitoring over multiple years, in order to optimally detect diversity responses to disturbance.

Beta (β) diversity can shed light on the patterns and processes that lead to the scale-dependent outcomes of disturbance (Socolar 2016), and is particularly important in ecosystems where diversity is maintained by a high level of heterogeneity. Our findings demonstrated that increases in species richness at the local (α) scale can be dampened at the landscape scale (γ) through decreases in β diversity, even when these β decreases are not driven by species loss. Additionally, our findings underscore the value of utilizing available statistical techniques that can place different weights on species abundance when measuring heterogeneity. This study demonstrates how incorporating β-diversity can improve our understanding of local and landscape-scale diversity in response to managed disturbance and inform conservation decision making.

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LITERATURE CITED:

Adler, P., Raff, D., & Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, *128*(4), 465–479.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Australian Ecology*, *26* (2001), 32–46.

Augustine, D. J., & Frank, D. A. (2001). Effects of Migratory Grazers on Spatial Heterogeneity of Soil Nitrogen Properties in a Grassland Ecosystem. *Ecology*, *82*(11), 15.

Bartolome, J. W., J. Barry, T. Griggs, and P. Hopkinson. (2007). *Terrestrial vegetation of California*. (T. K.-W. M. G. Barbour and A. A. Schoenherr, Ed.) (Third edit). Berkeley, California: University of California Press.

Benjamini, Y. and Hochberg, Y. (1995); Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series*,57(1)

Bovee, K. M., Merriam, K. E., & Gosejohan, M. C. (2017). Livestock grazing affects vernal pool specialists more than habitat generalists in montane vernal pools. *Applied Vegetation Science*, 1–10.

Burkle, L. A., Myers, J. A., & Belote, R. T. (2015). Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. *Ecosphere*, *6*(10), 202.

Chase, J., McGill, B., McGlinn, D. J., May, F., Blowes, S. A., Xiao, X., Gotelli, N. J. (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology letters*, 21(11) 1737-1751.

Chapin III, F., Zavaleta, E., Eviner, V. *et al.* Consequences of changing biodiversity. *Nature*, 405, 234–242 (2000).

Chuong, J., Huxley, J., Spotswood, E. N., Nichols, L., Mariotte, P., & Suding, K. N. (2016). Cattle as Dispersal Vectors of Invasive and Introduced Plants in a California Annual Grassland. *Rangeland Ecology & Management*, *69*(1), 52–58.

Cook, S. C., Housley, L., Back, J. A., & King, R. S. (2018). Freshwater eutrophication drives sharp reductions in temporal beta diversity. *Ecology*, *99*(1), 47–56.

Cosyns, E., Claerbout, S., Lamoot, I., & Hoffmann, M. (2005). Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. *Plant Ecology*, *178*(2), 149–162.

Crawley, M. J. & J.E. Harral (2001). Scale Dependence in Plant Biodiversity. *Science*, *291*(5505), 864–868.

Díaz, Sandra, Sandra Lavorel, Sue McIntyre, Valeria Falczuk, Fernando Casanoves, Daniel G. Milchunas, Christina Skarpe, et al. 2007. “Plant Trait Responses to Grazing: A Global Synthesis.” *Global Change Biology* 13 (2): 313–41.

~~gerh~~Gerhardt, F., & Collinge, S. K. (2003). Exotic plant invasions of vernal pools in the Central Valley of California, USA: Exotic plant invasions of vernal pools. Journal of Biogeography, 30(7), 1043–1052.

Gerhardt, F., & Collinge, S. K. (2007). Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. *Ecological Applications*, *17*(3), 922–933.

George, M.R., W. Frost, and N. McDougald. 2016. Grazing Management. In: M.R. George (ed.). Ecology and Management of Annual Rangelands. Davis, CA: Department of Plant Science. Pgs 157-189.

Golodets, C., Kigel, J., & Sternberg, M. (2011). Plant diversity partitioning in grazed Mediterranean grassland at multiple spatial and temporal scales: Diversity partitioning in grazed grasslands. Journal of Applied Ecology, 48(5), 1260–1268.

Harrison, S, Inouye, B. D., & Safford, H. D. (2003). Ecological Heterogeneity in the Effects of Grazing and Fire on Grassland Diversity. *Conservation Biology*, *17*(3), 837–845.

Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, *54*(2), 427–432.

Hill, J. K., & Hamer, K. C. (2004). Determining impacts of habitat modification on diversity of tropical forest fauna: The importance of spatial scale: Diversity in tropical forests. *Journal of Applied Ecology*, *41*(4), 744–754.

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, *89* (6), 1510–1520.

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B., & Ryabov, A. B. (2017). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. Journal of Applied Ecology, 55(1), 169–184.

Hobbs, R. J., & Huenneke, L. F. (1979). Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology*, 14.

Jain, S. K. 1978. Local dispersal of Limnanthes nutlets: an experiment with artificial vernal pools. Can. J. Bot. 56: 1995-1997.

Johnson, B. E., & Cushman, J. H. (2007). Influence of a Large Herbivore Reintroduction on Plant Invasions and Community Composition in a California Grassland. *Conservation Biology*, *21*(2), 515–526.

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439.

Keeley, J. E. (2006). Fire Management Impacts on Invasive Plants in the Western United States. *Conservation Biology*, *20*(2), 375–384.

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*(1), 98–109.

Kneitel, J. M. (2016). Climate-driven habitat size determines the latitudinal diversity gradient in temporary ponds. *Ecology*, *97*(4), 961–968.

Legendre, P., & Legendre, L. F. J. (2012). *Numerical Ecology*. Third Edition. Elsevier Science. ISBN: 978-0-444-53869-7

Li, S., Cadotte, M. W., Meiners, S. J., Pu, Z., Fukami, T., & Jiang, L. (2016). Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. Ecology Letters, 19(9), 1101–1109.

Mackey, R.L. & D.J. Currie. The diversity–disturbance relationship: Is it generally strong and peaked? Ecology, 82 (2001), pp. 3479-3492

Manly, B. F. J. (2006). *Randomization, Bootstrap and Monte Carlo Methods in Biology, Third Edition.* Chapman and Hall/CRC.

Marty, J. T. (2005). Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology*, *19*(5), 1626–1632.

Marty, J. T. (2015). Loss of biodiversity and hydrologic function in seasonal wetlands persists over 10 years of livestock grazing removal. *Restoration Ecology*, *23*(5), 548–554.

Michaels, Julia, Manuscript1, (2020), GitHub repository, https://github.com/JuliaMichaels/Mansucript1_Jmichaels

Myers, J.A., Chase, J.M., Crandall, R.M. and I. Jiménez (2015). Disturbance Alters Beta-Diversity but Not the Relative Importance of Community Assembly Mechanisms. *Journal of Ecology* 103 (5): 1291–99.

Olff, Han, and Mark E. Ritchie. 1998. Effects of Herbivores on Grassland Plant Diversity. *Trends in Ecology & Evolution* 13 (7): 261–65.

Olofsson, J., de Mazancourt, C., & Crawley, M. J. (2007). Contrasting effects of rabbit exclusion on nutrient availability and primary production in grasslands at different time scales. *Oecologia*, *150*(4), 582–589.

Porensky, L. M., Wittman, S. E., Riginos, C., & Young, T. P. (2013). Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. Oecologia, 173(2), 591–602.

Price, J. N., Berney, P. J., Ryder, D., Whalley, R. D. B., & Gross, C. L. (2011). Disturbance governs dominance of an invasive forb in a temporary wetland. *Oecologia*, *167*(3), 759–769.

Pyke, C. R., & Marty, J. (2005). Cattle Grazing Mediates Climate Change Impacts on Ephemeral Wetlands. *Conservation Biology*, *19*(5), 1619–1625.

Safford, H. D., & Harrison, S. (2004). Fire Effects on Plant Diversity in Serpentine vs. Sandstone Chaparral. *Ecology*, *85*(2), 539–548.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology and Evolution*, *31*(1), 67–80.

Solomeshch, A.I., Barbour, M.G., Holland, R.F. 2007. Vernal Pools. In: Barbour M.G., T. Keeler-Wolf and A. A. Shoenherr (eds.). Terrestrial Vegetation of California, Third Edition. University of California Press, Berkeley.)

Souther, S., Loeser, M., Crews, T. E., & Sisk, T. (2019). Complex response of vegetation to grazing suggests need for coordinated, landscape-level approaches to grazing management. *Global Ecology and Conservation*, *20*,

Stohlgren, T. J., Schell, L. D., & Vanden Heuvel, B. (1999). How Grazing and Soil Quality Affect Native and Exotic Plant Diversity in Rocky Mountain Grasslands. *Ecological Applications*, *9*(1), 45–64.

Stahlheber, K.A., & D’Antonio, C. M. (2013). Using livestock to manage plant composition: A meta-analysis of grazing in California Mediterranean grasslands. *Biological Conservation*, *157*, 300–308.

Stromberg MR, Corbin JD, D'Antonio CM. 2007. California Grasslands: Ecology and Management. Berkeley: Univ. Calif. Press

Turnbull, L. A., Isbell, F., Purves, D. W., Loreau, M., & Hector, A. (2016). Understanding the value of plant diversity for ecosystem functioning through niche theory. Proceedings of the Royal Society B: Biological Sciences, 283(1844), 20160536.

Waite, T.A. and Campbell, L.G. (2006). Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13(4), 439-442.

~~Adler, P., Raff, D., & Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, *128*(4), 465–479. https://doi.org/10.1007/s004420100737~~

TABLES:

	Order = 0 (Species Richness)						**Order = 2 (Abundance-Weighted Inverse Simpson Index)**				
	Scale	**Year**	**Not Grazed**	**Grazed**	**p-value**		**Scale**	**Year**	**Not Grazed**	**Grazed**	**p-value**
α_1	all zones avg.	**2015**	**10.74**	**13.12**	**0.0005**	α_1	all zones avg.	2015	4.38	5.17	0.0603
	inundated		11.57	12.57	0.3570		inundated		4.44	5.41	0.1950
	transition		12.36	15.71	**0.0010**		transition		5.19	6.08	0.2720
	upland		8.36	11.07	**0.0020**		upland		3.50	4.01	0.2390
	all zones avg.	**2016**	**11.36**	**14.19**	**0.0008**		all zones avg.	**2016**	**4.17**	**5.99**	**0.0000**
	inundated		13.07	12.71	0.7750		inundated		4.88	6.53	**0.0010**
	transition		13.07	18.50	**0.0000**		transition		4.05	6.95	**0.0000**
	upland		8.21	10.79	**0.0030**		upland		3.58	4.48	**0.0000**
	all zones avg.	**2017**	**12.21**	**13.76**	**0.0492**		all zones avg.	**2017**	**4.82**	**5.71**	**0.0074**
	inundated		13.36	12.71	0.5480		inundated		5.83	6.06	0.6800
	transition		14.21	17.43	0.0800		transition		4.40	6.29	**0.0050**
	upland		9.64	11.93	**0.0030**		upland		4.23	4.78	0.0900
β_1	btwn. zones	2015	1.97	1.96	0.9376	β_1	btwn. zones	2015	1.82	1.73	0.5429
		2016	1.95	1.94	0.9143			2016	1.72	1.92	0.1692
		2017	2.10	2.13	0.5976			2017	2.10	2.06	0.7499
α_2	whole pool	**2015**	**21.21**	**25.64**	**0.0060**	α_2	whole pool	2015	7.99	8.89	0.3293
		2016	**22.29**	**27.43**	**0.0024**			**2016**	**7.31**	**11.47**	**0.0000**
		2017	**25.64**	**29.36**	**0.0416**			2017	10.18	11.84	0.1140
β_2	btwn. pools	**2015**	**2.12**	**1.72**	**0.0419**	β_2	btwn. pools	2015	1.16	1.36	0.0782
		2016	**2.06**	**1.75**	**0.0340**			2016	1.21	1.27	0.6743
		2017	1.91	1.74	0.2836			2017	1.35	1.56	0.0581
γ_2	pasture	2015	45.00	44.00	0.8958	γ_2	pasture	2015	9.26	12.11	0.1147
		2016	46.00	48.00	0.4613			**2016**	**8.88**	**14.61**	**0.0015**
		2017	49.00	51.00	0.6806			**2017**	**13.75**	**18.46**	**0.0204**

Table 1: Average diversity of samples taken at each scale as measured by Hill numbers at order=0 (Species richness) and order=2 (Inverse Simpson aka abundance-weighted diversity). Bolded p-values indicate significant differences in diversity between the grazing exclusion and grazing treatments.

FIGURE LEGENDS:

Figure 1: Map of Rancho Seco pools. Long-term ungrazed pools are in yellow (n=14) and located in the ungrazed pasture within the fenced area. Long-term continuously grazed pools are in green (n=14) and located in the grazed pasture on the outside of the fenced area. Dark grey=permanent lake, light gray=Redding Gravelly Loam soil, white=Corning soil.

Figure 2: Diversity partitioning in vernal pools at two spatial scales. (a) Within-pool diversity: α_1=diversity within habitat zones, β_1= vertical turnover between habitat zones; (b) Between-pool diversity: α_2= all habitat zones in pool averaged, β_2=horizontal turnover between pools, γ=whole pasture diversity.

Figure 3: (a) Avg. species richness and (b) Inverse Simpson at all three spatial scales: Zone (α_1), Pool (α_2) and Pasture (γ) for 2015-2017 averaged. The slopes between the points are proportional to the β diversity between hierarchical levels. Standard error bars represent differences across years. Differences across years are available in Table 1. Stars indicate permutated p-values based on 999 permutations ***=p<0.001, **=p<0.01).

Figure 4: (a) Plant community composition within grazed and ungrazed pools.

NMDS by habitat zone for all three years combined (2015-2017) with 95% confidence ellipses displayed. The ten species with the highest abundance avg. over all three years of the study are projected. Species codes available in Appendix D. Coordinates were generated on the same NMDS axes before plotting in separate figures for clarity. PERMANOVA results suggest that community composition did vary significantly by grazing (Grazing: F(1, 238)=13.55, p<0.001), but that the size of this effect was small in comparison to habitat zone (Zone: F(2, 238)=77.36, p<0.001). Year was also significant (Year: F(2,238)=11.40, p<0.001) as well as interaction effects (Grazing*Zone: F(2,238)=6.16, p<0.001), (Grazing*Year: F(2,238)=1.75, p<0.001), (Zone*Year: F(2,238)=4.67, p<0.001).

(b) Differences in community composition between grazed and ungrazed pools for years 2015-2017 combined. Non-metric multidimensional scaling (NMDS) by pool (all habitat zones combined) for all three years combined (2015-2017) with 95% confidence ellipses displayed. The distance between any two points represents the difference in community composition (Bray-

Curtis dissimilarity index). The ten species with the highest abundance averaged over all three years of the study are projected. Species codes available in Appendix D. PERMANOVA results suggest that community composition did vary significantly by grazing (Grazing: F(1, 251)=7.87, p<0.001, Year: F(2, 251)=6.62, p<0.001, Grazing*Year: F(2, 251)=1.02, p=0.41. The size of the ellipses represents pool-to-pool dispersion in species composition. PERMDISP results for each individual year suggest that community dispersion (β_2 diversity among pools within pastures) did not vary significantly by grazing treatment (2015:p=1.00, 2016:p=0.68, 2017:p=.063).

FIGURES:

Figure 1:

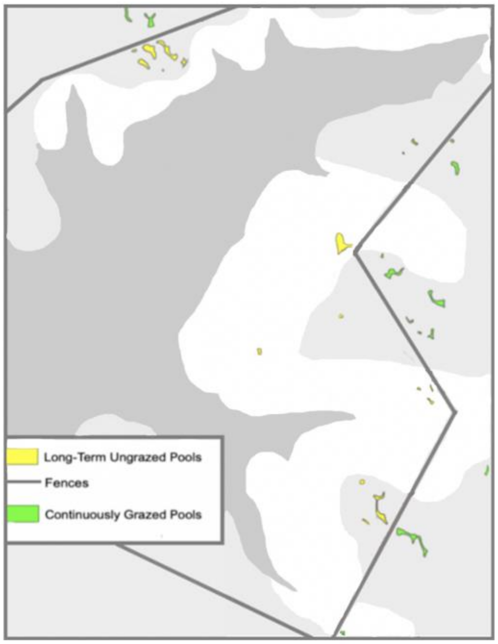

Long-Term Ungrazed Pools
Fences
Continuously Grazed Pools

Figure 2:

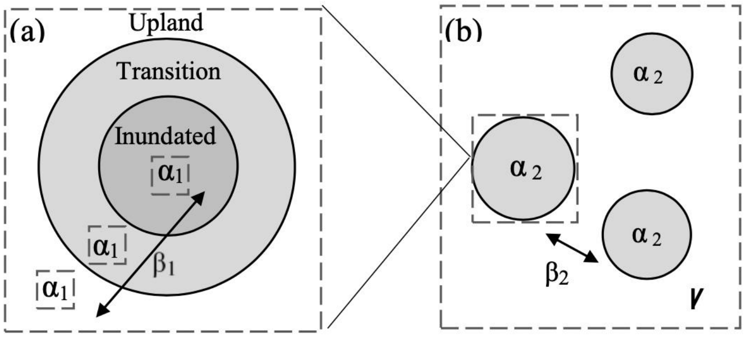
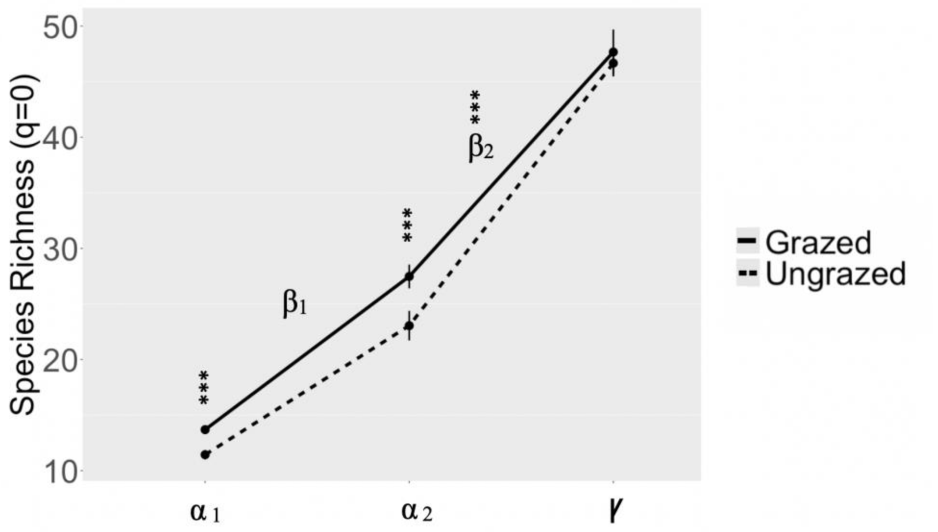

(a)
Upland
Transition
Inundated
α_1
α_1
α_1
β_1
(b)
α_2
α_2
α_2
β_2
γ

Figure 3:

(a)


Species Richness (q=0)
50
40
30
20
10
***
***
***
β_2
β_1
α_1
α_2
γ
Grazed
Ungrazed

(b)

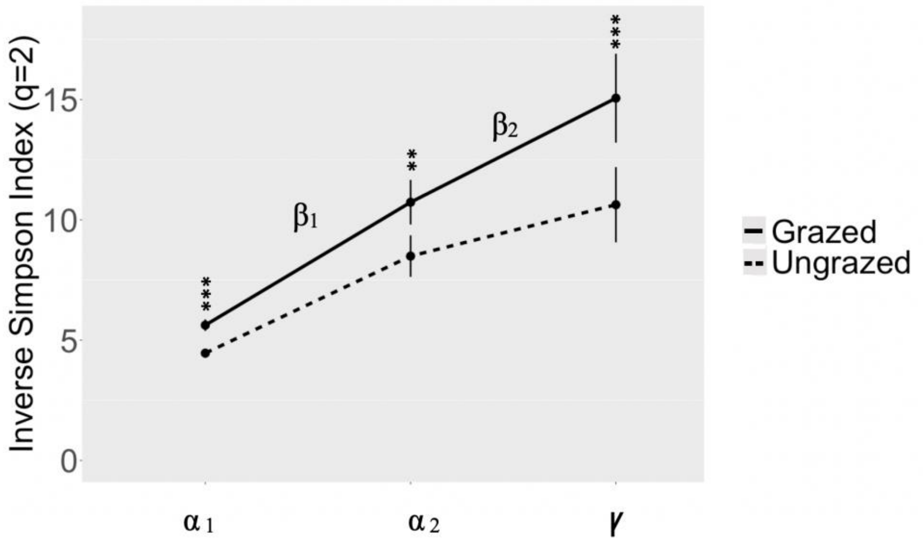
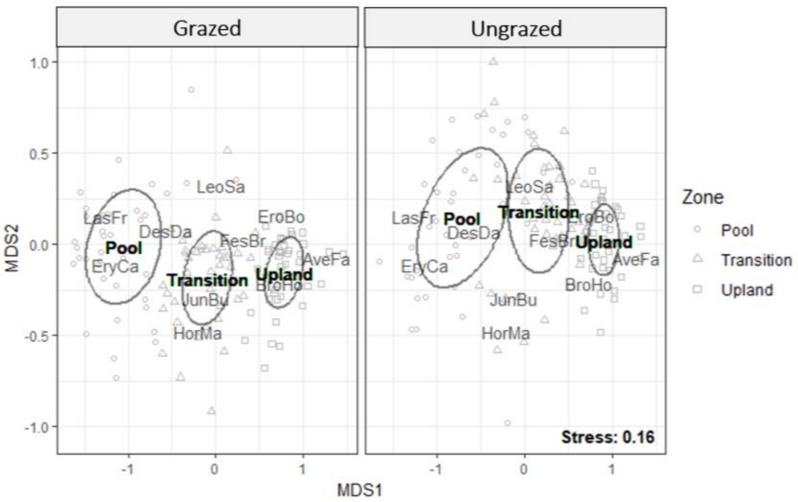
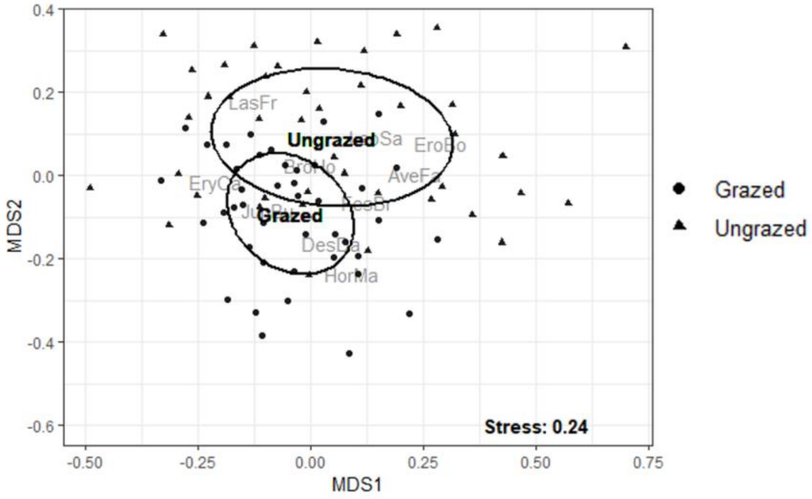

Inverse Simpson Index (q=2)
15
10
5
0
***
**
***
β_1
β_2
α_1
α_2
γ
Grazed
Ungrazed

Figure 4:

(a)



(b)



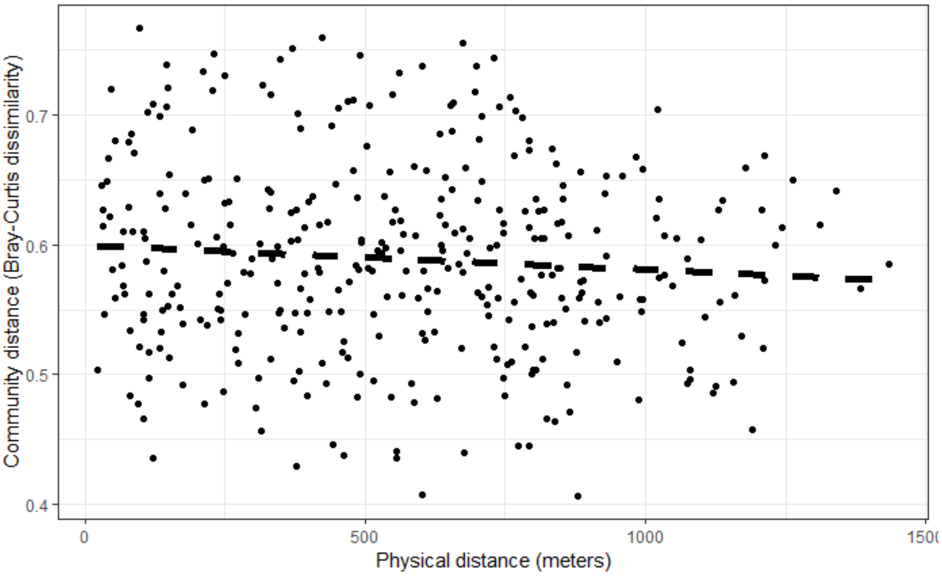
APPENDICES:

Appendix A:

Pair #	Treatment	Soil Type	Size (m^2)	Shape	Topography (distance from edge of the pool to the pool bottom, and % of pool perimeter with slope (not flat)
1	Grazed	C	16.30	Oval	Flat (<0.15 m)
1	Ungrazed	C	10.82	Oval	Flat (<0.15 m)
2	Grazed	C	24.05	Oval	0.3-0.61 m slope, 25% of perimeter
2	Ungrazed	C	11.17	Oval	Flat (<0.15 m)
3	Grazed	C	35.54	Oval	Flat (<0.15 m)
3	Ungrazed	C	29.00	Oval with segments	Flat (<0.15 m)
4	Grazed	C	79.33	Oval with segments	0.3 m, 50% of perimeter
4	Ungrazed	C	70.80	Oval with segments	0.91-1.22 m, 50% of perimeter
5	Grazed	C	154.25	Long, thin	0.3-0.61 m, 50% perimeter
5	Ungrazed	C	47.60	Long, thin	0.61-0.91 m, 50% of perimeter
6	Grazed	C	168.86	Oval	0.61-0.91 m, 50% of perimeter
6	Ungrazed	C	62.80	Oval	0.61-0.91 m, 50% of perimeter
7	Grazed	C	206.57	Oval with segments	0.61-0.91 m, 75% of perimeter
7	Ungrazed	C	166.34	Misc: long oval	0.91-1.22 m, 50% of perimeter
8	Grazed	C	239.30	Oval with segments	0.3-0.61 m, 100% of perimeter
8	Ungrazed	C	332.25	Long, thin	0.61-0.91 m, 50% of perimeter
9	Grazed	C	249.81	Oval with segments	0.61-0.91 m, 50% of perimeter
9	Ungrazed	C	336.93	Oval with segments	3-4 ft, 50% of perimeter
10	Grazed	RGL	13.90	Oval	Flat (<0.15 m)
10	Ungrazed	RGL	64.01	Oval	Flat (<0.15 m)
11	Grazed	RGL	14.63	Oval	0.61-0.91 m, 25% of perimeter
11	Ungrazed	RGL	26.19	Oval	0.61-0.91 m, 25% of perimeter
12	Grazed	RGL	29.30	Long, thin	Flat (<0.15 m)
12	Ungrazed	RGL	59.99	Long, thin	0.61-0.91 m, 25% of perimeter
13	Grazed	RGL	45.30	Oval with segments	0.3-0.61 m slope, 25% of perimeter
13	Ungrazed	RGL	9.83	Oval	0.3-0.61 m, 50% perimeter
14	Grazed	RGL	474.06	Oval with segments	0.61-1.22 m, 75% of perimeter
14	Ungrazed	RGL	610.00	Misc; Oval	3-4 ft, 75% of perimeter

Appendix A: Pool characteristics. Each group of grazed/ungrazed pools was balanced by identifying ‘pairs’ of pools based on similarities in: soil type (Corning (C) and Redding Gravelly Loam (RGL)) and whenever possible, size, shape, and topography (measured as the slope height surrounding the pool edges). When pairing based on size, pools were considered comparable in size if they were within 150m2 in size. At the site, pools ranged from 4.00m2-6839.19 m2 at the site, chosen pools ranged from 9.83 m2-610.00 m2 . The pools chosen for this study (within 150m2 in size, pools ranged from 4.00m2-6839.19 m2 at the site, chosen pools ranged from 9.83 m2-610.00 m2), shape, and topography (measured as the slope height surrounding the pool edges). If the pool had variation in slope (flat in some areas, steep in other areas), the % of the perimeter that was not flat is listed. Soil compaction within each pool was recorded using a penetrometer, but was not used to pair because of fine-scale variability within the pools.

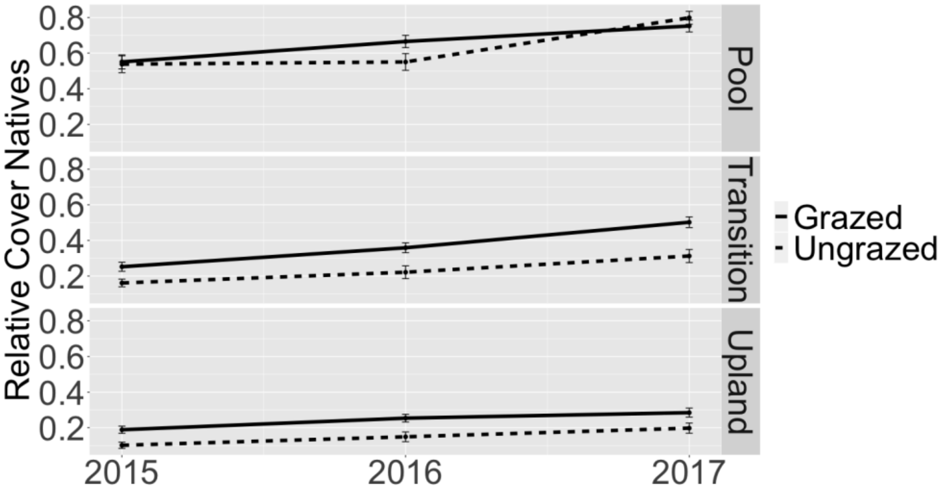
Appendix B:



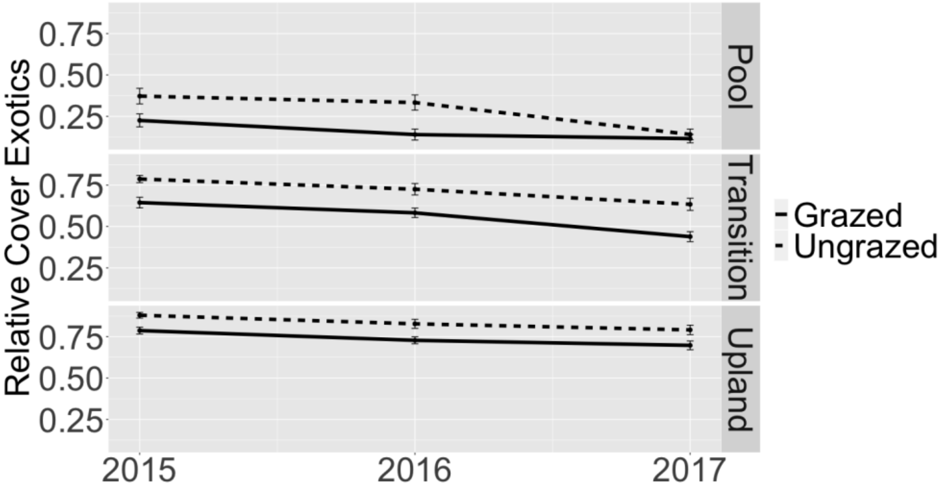
Appendix B: Community distance between pool samples (Bray-Curtis dissimilarity) vs. physical distance between pool centroids (meters). A partial Mantel test showed no significant evidence of spatial autocorrelation in communities within each of the two grazing treatments (Mantel statistic based on Pearson's product-moment correlation = 0.09, P = 0.10). Mantel statistic calculated using 999 permutations.

Appendix C:

(a)



(b)



Appendix C: (a) Native cover by habitat zone, year, and grazing. ANOVA (Grazing: F(2,746)=112.73, p<0.00, Zone:F(2,756)=130.51, p<0.00, Zone*Grazing: F(2,746)=1.23, p=0.29, Grazing*Year: F(4,746)=5.83, p<0.00). Standard error bars represent differences across replicates. (b) Exotic cover by habitat zone, year, and grazing. ANOVA (Grazing: F(2,746)=71.83, p<0.00, Zone: F(2,756)=511.36, p<0.00, Year: F(2,756)=33.28, p<0.00, Zone*Grazing: F(2,746)=1.53, p=0.22., Grazing*Year: F(4,746)=0.66, p=0.52). Standard error bars represent differences across replicates.

Appendix D-1: All zones combined

Species Code	Species	Status	Origin	Mean Ungrazed % Rel. Abun.	SE	Mean Grazed % Rel. Abun.	SE	p-value	Corrected p-value	
LeoSa	Leontodon saxatilis	Exotic	Forb	19.123	1.180	11.904	0.835	1.63E-09	9.61E-08	↓
EroBo	Erodium botrys	Exotic	Forb	13.545	1.345	9.957	0.951	0.00783	0.328847	
AveFa	Avena fatua	Exotic	Grass	8.672	0.925	4.267	0.654	2.38E-06	0.000128	↓
FesBr	Festuca bromoides	Exotic	Grass	8.507	1.051	11.142	0.743	0.012338	0.481187	
BroHo	Bromus hordeaceous	Exotic	Grass	6.307	0.895	6.331	0.633	0.977905	0.977905	
LasFr	Lasthenia fremontii	Native	Forb	5.705	0.801	2.882	0.566	0.000454	0.021809	↓
DesDa	Deschampsia danthanoides	Native	Grass	3.963	0.743	3.826	0.525	0.852893	0.977905	
EryCa	Eryngium castrense	Native	Forb	3.475	0.591	5.628	0.418	0.000288	0.014124	↑
BroDi	Bromus diandrus	Exotic	Grass	3.213	0.643	0.507	0.455	3.18E-05	0.001655	↓
BriMi	Briza minor	Exotic	Grass	2.405	0.275	0.834	0.195	1.93E-08	1.12E-06	↓
JunCa	Juncus capitatus	Exotic	Rush	2.137	0.361	0.610	0.255	2.71E-05	0.001438	↓
HorMa	Hordeum marinum	Exotic	Grass	1.721	0.675	4.369	0.477	9.73E-05	0.004961	↑
GraEb	Gratiola 39bracteate	Native	Forb	1.720	0.339	1.120	0.240	0.076902	0.977905	
JunBu	Juncus bufonius	Native	Rush	1.532	0.580	4.693	0.410	7.31E-08	4.17E-06	↑
PlaSt	Plagiobothrys stipitatus	Native	Forb	1.332	0.369	1.529	0.261	0.593633	0.977905	
PogZi	Pogogyne zizyphoroides	Native	Forb	1.158	0.245	0.918	0.173	0.32615	0.977905	
EleMa	Eleocharis macrostachya	Native	Grass	1.134	0.487	2.832	0.344	0.000521	0.024484	↑
RanBo	Ranunculus bonariensis	Native	Forb	1.052	0.403	2.540	0.285	0.000247	0.012343	↑
ElyCa	Elymus caput-medusae	Exotic	Grass	0.940	0.417	1.678	0.295	0.07708	0.977905	
LayFr	Layia fremontii	Native	Forb	0.907	0.309	0.611	0.218	0.337475	0.977905	
FesPe	Festuca perennis	Exotic	Grass	0.904	0.322	0.501	0.228	0.211562	0.977905	
DowBi	Downingia bicornuta	Native	Forb	0.721	0.313	1.402	0.221	0.029713	0.977905	
PsiBre	Psilocarphus brevissimus	Native	Forb	0.705	0.432	3.403	0.305	8.56E-10	5.22E-08	↑
DowOr	Downingia ornatissima	Native	Forb	0.534	0.175	0.227	0.124	0.080201	0.977905	

NavLe	Navarretia leucocephala	Native	Forb	0.516	0.459	2.942	0.324	1.94E-07	1.07E-05	↑
CasCa	Castilleja campestris	Native	Forb	0.507	0.172	0.646	0.122	0.421152	0.977905	
CenSp	Centromadia spp.	Native	Forb	0.475	0.129	0.692	0.091	0.09371	0.977905	
JunPa	Juncus patens	Native	Rush	0.445	0.275	0.596	0.194	0.581654	0.977905	
DowCu	Downingia cuspidata	Native	Forb	0.375	0.197	0.454	0.140	0.688438	0.977905	
CinQu	Cicendia quadrangularis	Native	Forb	0.361	0.084	0.089	0.060	0.001358	0.062462	↓
BroMi	Brodiaea minor	Native	Forb	0.351	0.123	1.009	0.087	1.27E-07	7.1E-06	
TriHy	Triphysaria eriantha	Native	Forb	0.330	0.154	0.122	0.109	0.175398	0.977905	
PlaLe	Plagiobothrys leptocladus	Native	Forb	0.290	0.125	0.012	0.088	0.026813	0.965265	
LupBi	Lupinus bicolor	Native	Forb	0.274	0.121	0.368	0.085	0.437871	0.977905	
AloSa	Alopecurus saccatus	Native	Grass	0.270	0.105	0.100	0.074	0.105125	0.977905	
LytHy	Lythrum hyssopifolia	Exotic	Forb	0.244	0.270	1.911	0.191	1.58E-09	9.51E-08	
HypRa	Hypochaeris radicata	Exotic	Forb	0.186	0.128	0.010	0.091	0.171341	0.977905	
AcmAm	Acmispon americanus	Native	Forb	0.181	0.145	0.245	0.102	0.655903	0.977905	
JunBa	Juncus balticus	Native	Rush	0.150	0.127	0.217	0.090	0.598859	0.977905	
TriEr	Trifolium hirtum	Native	Forb	0.131	0.085	0.059	0.060	0.396663	0.977905	
CroSe	Croton setigerus	Native	Forb	0.127	0.053	0.214	0.038	0.101744	0.977905	
TriLa	Triteleia hyacinthina	Native	Forb	0.111	0.042	0.064	0.030	0.266637	0.977905	
TriLa	Triteleia laxa	Native	Forb	0.111	0.042	0.064	0.030	0.266637	0.977905	
NavMe	Navarretia Mersii	Native	Forb	0.109	0.108	0.138	0.076	0.790748	0.977905	
BleNa	Blennosperma nanum	Native	Forb	0.106	0.080	0.002	0.056	0.191535	0.977905	
CasAt	Castilleja attenuata	Native	Forb	0.094	0.041	0.028	0.029	0.109761	0.977905	
EleAr	Eleocharis acicularis	Native	Forb	0.057	0.054	**0.000**	0.038	0.288787	0.977905	
TriHi	Trifolium hirtum	Exotic	Forb	0.051	0.095	0.336	0.067	0.002879	0.126684	
TriDe	Trifolium depauperatum	Native	Forb	0.047	0.106	0.317	0.075	0.011184	0.447354	↑
CotCo	Cotula coronopifolia	Exotic	Forb	0.040	0.164	0.384	0.116	0.036638	0.977905	↑
PilAm	Pilularia americana	Native	Fern	0.030	0.028	0.017	0.020	0.626658	0.977905	
AirCa	Aira caryophella	Exotic	Grass	0.017	0.036	0.052	0.025	0.336445	0.977905	
EscLo	Eschscholzia lobii	Native	Forb	0.009	0.005	**0.000**	0.004	0.074684	0.977905	

BroAp	Brodiaea appendiculata	Native	Forb	0.008	0.007	0.005	0.005	0.689794	0.977905
GerDi	Geranium dissectum	Exotic	Forb	0.004	0.004	**0.000**	0.003	0.317952	0.977905
LasGl	Lasthenia glaberrima	Native	Forb	0.004	0.102	0.280	0.072	0.007109	0.305693
TriDu	Trifolium dubium	Exotic	Forb	0.003	0.080	0.210	0.057	0.009759	0.400122
TriVa	Trifolium variegatum	Native	Forb	0.002	0.141	0.341	0.100	0.016866	0.640919
HolVi	Holocarpha virgata	Native	Forb	**0.000**	0.007	0.007	0.005	0.317952	0.977905
ChlPo	Chlorogalum pomeridianum	Native	Forb	**0.000**	0.009	0.013	0.007	0.175884	0.977905
GlyDe	Glyceria declinata	Exotic	Grass	**0.000**	0.113	0.261	0.080	0.020808	0.769913

Appendix D-2: Inundated zone

Species Code	**Species**	**Status**	**Origin**	**Mean Ungrazed % Rel. Abun.**	**SE**	**Mean Grazed % Rel. Abun.**	**SE**	**p-value**	**Corrected p-value**	
LeoSa	Leontodon saxatilis	Exotic	Forb	18.604	2.154	7.897	1.523	1.34E-06	0.0001	↓
LasFr	Lasthenia fremontii	Native	Forb	15.914	2.008	7.393	1.420	3.39E-05	0.0016	↓
EryCa	Eryngium castrense	Native	Forb	9.360	1.230	12.640	0.870	0.00821	0.3284	
DesDa	Deschampsia danthanoides	Native	Grass	7.700	1.624	6.458	1.149	0.445482	0.8185	
GraEb	Gratiola ebracteata	Native	Forb	4.036	0.840	2.005	0.594	0.016527	0.6445	
PlaSt	Plagiobothrys stipitatus	Native	Forb	3.814	1.026	4.170	0.725	0.728324	0.8185	
PogZi	Pogogyne zizyphoroides	Native	Forb	2.705	0.612	1.640	0.433	0.083197	0.8185	
RanBo	Ranunculus bonariensis	Native	Forb	2.393	1.025	6.035	0.725	0.000473	0.0208	↑
FesBr	Festuca bromoides	Exotic	Grass	2.329	0.783	1.186	0.553	0.145639	0.8185	
EleMa	Eleocharis macrostachya	Native	Grass	2.304	0.982	5.725	0.695	0.000601	0.0258	
JunCa	Juncus capitatus	Exotic	Rush	2.222	0.589	0.419	0.417	0.002609	0.1070	
DowBi	Downingia bicornuta	Native	Forb	2.139	0.877	4.148	0.620	0.022911	0.8185	
PsiBre	Psilocarphus brevissimus	Native	Forb	1.939	1.082	9.389	0.765	7.8E-11	0.0000	↓
JunBu	Juncus bufonius	Native	Rush	1.901	0.697	1.446	0.493	0.514533	0.8185	
BriMi	Briza minor	Exotic	Grass	1.632	0.398	0.365	0.281	0.001767	0.0742	↓
NavLe	Navarretia leucocephala	Native	Forb	1.458	1.232	8.076	0.871	2.92E-07	0.0000	↑
EroBo	Erodium botrys	Exotic	Forb	1.420	0.645	0.025	0.456	0.032487	0.8185	
CasCa	Castilleja campestris	Native	Forb	1.400	0.487	1.829	0.344	0.378511	0.8185	

DowOr	Downingia ornatissima	Native	Forb	1.358	0.499	0.571	0.353	0.11625	0.8185	
JunPa	Juncus patens	Native	Rush	1.239	0.514	0.267	0.364	0.060779	0.8185	
DowCu	Downingia cuspidata	Native	Forb	1.126	0.580	1.339	0.410	0.713445	0.8185	
LayFr	Layia fremontii	Native	Forb	1.013	0.465	0.115	0.329	0.055579	0.8185	
CenSp	Centromadia spp.	Native	Forb	0.786	0.285	0.866	0.201	0.777097	0.8185	
HorMa	Hordeum marinum	Exotic	Grass	0.757	0.593	1.893	0.419	0.056979	0.8185	
AveFa	Avena fatua	Exotic	Grass	0.743	0.296	0.230	0.209	0.084629	0.8185	
PlaLe	Plagiobothrys leptocladus	Native	Forb	0.641	0.330	0.000	0.233	0.054472	0.8185	
AcmAm	Acmispon americanus	Native	Forb	0.528	0.374	0.012	0.264	0.169572	0.8185	
TriHy	Triphysaria eriantha	Native	Forb	0.527	0.443	0.000	0.313	0.236075	0.8185	
AloSa	Alopecurus saccatus	Native	Grass	0.468	0.235	0.210	0.166	0.272872	0.8185	
BroMi	Brodiaea minor	Native	Forb	0.419	0.183	0.803	0.130	0.037152	0.8185	
CinQu	Cicendia quadrangularis	Native	Forb	0.396	0.183	0.072	0.129	0.078397	0.8185	
FesPe	Festuca perennis	Exotic	Grass	0.337	0.282	0.455	0.199	0.675933	0.8185	
LytHy	Lythrum hyssopifolia	Exotic	Forb	0.337	0.480	2.204	0.340	0.000152	0.0069	↑
NavMe	Navarretia Mersii	Native	Forb	0.328	0.321	0.414	0.227	0.789997	0.8185	
JunBa	Juncus balticus	Native	Rush	0.312	0.218	0.090	0.154	0.309407	0.8185	
CroSe	Croton setigerus	Native	Forb	0.150	0.098	0.021	0.070	0.192903	0.8185	
CotCo	Cotula coronopifolia	Exotic	Forb	0.115	0.454	0.807	0.321	0.129099	0.8185	
PilAm	Pilularia americana	Native	Fern	0.090	0.083	0.050	0.059	0.626459	0.8185	
BroHo	Bromus hordeaceous	Native	Forb	0.071	0.065	0.027	0.046	0.507264	0.8185	
TriLa	Triteleia hyacinthina	Native	Forb	0.063	0.049	0.042	0.035	0.67275	0.8185	
TriLa	Triteleia laxa	Native	Forb	0.063	0.049	0.042	0.035	0.67275	0.8185	
BroAp	Brodieae appendiculata	Native	Forb	0.023	0.018	0.000	0.013	0.197321	0.8185	
TriDe	Trifolium depauperatum	Native	Forb	0.014	0.019	0.018	0.014	0.818482	0.8185	
LupBi	Lupinus bicolor	Native	Forb	0.010	0.010	0.000	0.007	0.319242	0.8185	
AirCa	Aira caryophella	Exotic	Grass	0.006	0.006	0.000	0.004	0.319242	0.8185	
TriHi	Trifolium hirtum	Exotic	Forb	0.009	0.009	0.000	0.007	0.319242	0.7293	
LasGl	Lasthenia glaberrima	Native	Forb	0.000	0.285	0.676	0.202	0.019192	0.8185	
TriVa	Trifolium variegatum	Native	Forb	0.000	0.010	0.010	0.007	0.319242	0.8185	
GlyDe	Glyceria declinata	Exotic	Grass	0.000	0.328	0.715	0.232	0.031029	0.0001	↑

Appendix D-3: Transition Zone

Species Code	Species	Status	Origin	Mean Ungrazed % Rel. Abun.	SE	Mean Grazed % Rel. Abun.	SE	P-value	Corrected p-value	
LeoSa	Leontodon saxatilis	Exotic	Forb	30.541	1.945	18.306	1.375	1.61E-09	8.71E-08	↓
EroBo	Erodium botrys	Exotic	Forb	12.486	1.747	5.730	1.235	0.000151	0.007244	↓
FesBr	Festuca bromoides	Exotic	Grass	10.139	1.746	13.089	1.235	0.092435	0.914349	
BroHo	Bromus hordeaceous	Native	Forb	5.755	1.266	2.386	0.896	0.008517	0.349209	
BriMi	Briza minor	Exotic	Grass	4.601	0.596	1.712	0.421	2.55E-06	0.00013	↓
HorMa	Hordeum marinum	Exotic	Grass	4.260	1.757	9.980	1.243	0.00131	0.060244	
DesDa	Deschampsia danthanoides	Native	Grass	4.186	1.287	4.007	0.910	0.889165	0.914349	
JunCa	Juncus capitatus	Exotic	Rush	4.043	0.870	1.382	0.615	0.002493	0.112189	
AveFa	Avena fatua	Exotic	Grass	3.987	0.718	0.508	0.508	3.49E-06	0.000175	↓
JunBu	Juncus bufonius	Native	Rush	2.676	1.340	10.051	0.947	1.08E-07	5.74E-06	↑
LayFr	Layia fremontii	Native	Forb	1.428	0.757	1.718	0.535	0.702509	0.914349	
LasFr	Lasthenia fremontii	Native	Forb	1.198	0.512	1.253	0.362	0.914349	0.914349	
GraEb	Gratiola ebracteata	Native	Forb	1.125	0.497	1.355	0.351	0.642878	0.914349	
EleMa	Eleocharis macrostachya	Native	Grass	1.097	1.014	2.770	0.717	0.100348	0.914349	
FesPe	Festuca perennis	Exotic	Grass	1.084	0.484	0.698	0.342	0.425327	0.914349	
EryCa	Eryngium castrense	Native	Forb	1.064	0.613	3.400	0.434	0.000183	0.008617	↑
PogZi	Pogogyne zizyphoroides	Native	Forb	0.747	0.355	1.113	0.251	0.303673	0.914349	
RanBo	Ranunculus bonariensis	Native	Forb	0.700	0.490	1.584	0.346	0.07249	0.914349	
CinQu	Cicendia quadrangularis	Native	Forb	0.624	0.159	0.184	0.112	0.006287	0.268015	
CenSp	Centromadia spp.	Native	Forb	0.622	0.215	0.850	0.152	0.290308	0.914349	
HypRa	Hypochaeris radicata	Exotic	Forb	0.557	0.384	0.029	0.271	0.171724	0.914349	
BroMi	Brodiaea minor	Native	Forb	0.465	0.278	1.752	0.197	6.81E-06	0.000334	↑
LytHy	Lythrum hyssopifolia	Exotic	Forb	0.395	0.617	3.474	0.436	1.73E-06	9.01E-05	↑
TriEr	Trifolium hirtum	Native	Forb	0.392	0.247	0.121	0.174	0.273461	0.914349	
AloSa	Alopecurus saccatus	Native	Grass	0.342	0.206	0.091	0.146	0.226083	0.914349	
BleNa	Blennosperma nanum	Native	Forb	0.319	0.238	0.006	0.168	0.192212	0.914349	
CasAt	Castilleja attenuata	Native	Forb	0.268	0.117	0.046	0.083	0.059742	0.914349	

DowOr	Downingia ornatissima	Native	Forb	0.243	0.135	0.110	0.095	0.324626	0.914349
PlaGr	Plagiobothrys greeneii	Native	Forb	0.228	0.173	0.031	0.122	0.258073	0.914349
PlaSt	Plagiobothrys stipitatus	Native	Forb	0.183	0.155	0.417	0.110	0.131212	0.914349
PsiBre	Psilocarphus brevissimus	Native	Forb	0.177	0.255	0.819	0.181	0.013047	0.508842
EleAr	Eleocharis acicularis	Native	Forb	0.057	0.054	0.000	0.038	0.288787	0.914349
TriLa	Triteleia hyacinthina	Native	Forb	0.149	0.100	0.034	0.070	0.251136	0.914349
JunBa	Juncus balticus	Native	Rush	0.137	0.312	0.560	0.220	0.176877	0.452198
TriDe	Trifolium depauperatum	Native	Forb	0.127	0.311	0.925	0.220	0.011305	0.914349
CasCa	Castilleja campestris	Native	Forb	0.123	0.069	0.109	0.049	0.841202	0.914349
CroSe	Croton setigerus	Native	Forb	0.111	0.052	0.047	0.037	0.220245	0.914349
TriHy	Triphysaria eriantha	Native	Forb	0.106	0.050	0.080	0.035	0.598492	0.914349
TriHi	Trifolium hirtum	Exotic	Forb	0.101	0.131	0.235	0.093	0.306282	0.914349
JunPa	Juncus patens	Native	Rush	0.095	0.634	1.522	0.448	0.026023	0.268015
NavLe	Navarretia leucocephala	Native	Forb	0.089	0.239	0.751	0.169	0.006381	0.914349
BroDi	Bromus diandrus	Exotic	Grass	0.074	0.060	0.000	0.042	0.213838	0.914349
ElyCa	Elymus caput-medusae	Exotic	Grass	0.065	0.492	0.509	0.348	0.368631	0.914349
AirCa	Aira caryophella	Exotic	Grass	0.047	0.034	0.000	0.024	0.17342	0.914349
DowBi	Downingia bicornuta	Native	Forb	0.022	0.027	0.058	0.019	0.185853	0.914349
AcmAm	Acmispon americanus	Native	Forb	0.014	0.092	0.125	0.065	0.232751	0.914349
LasGl	Lasthenia glaberrima	Native	Forb	0.011	0.105	0.163	0.074	0.148351	0.914349
LupBi	Lupinus bicolor	Native	Forb	0.009	0.020	0.029	0.014	0.31121	0.914349
TriVa	Trifolium variegatum	Native	Forb	0.005	0.391	0.843	0.277	0.034359	0.914349
CotCo	Cotula coronopifolia	Exotic	Forb	0.005	0.187	0.344	0.133	0.072505	0.914349
GlyDe	Glyceria declinata	Exotic	Grass	0.000	0.069	0.069	0.049	0.319242	0.914349
DowCu	Downingia cuspidata	Native	Forb	0.000	0.012	0.024	0.009	0.052141	0.914349
TriDu	Trifolium dubium	Exotic	Forb	0.000	0.050	0.110	0.035	0.030797	0.914349

Appendix D-4: Upland Zone

Species Code	**Species**	**Status**	**Origin**	**Mean Ungrazed**	**SE**	**Mean Grazed**	**SE**	**p-value**	**Corrected p-value**

				% Rel. Abun.		% Rel. Abun.				
EroBo	Erodium botrys	Exotic	Forb	26.729	2.793	24.116	1.975	0.350372	0.92506	
AveFa	Avena fatua	Exotic	Grass	21.286	2.112	12.063	1.493	1.91E-05	0.000765	↑
BroHo	Bromus hordeaceous	Native	Forb	13.094	1.917	16.581	1.356	0.070204	0.92506	
FesBr	Festuca bromoides	Exotic	Grass	13.052	2.121	19.151	1.500	0.004381	0.153325	
BroDi	Bromus diandrus	Exotic	Grass	9.565	1.801	1.521	1.273	1.66E-05	0.000681	↓
LeoSa	Leontodon saxatilis	Exotic	Forb	8.224	1.297	9.509	0.917	0.322895	0.92506	
ElyCa	Elymus caput-medusae	Exotic	Grass	2.754	1.093	4.527	0.773	0.106263	0.92506	
FesPe	Festuca perennis	Exotic	Grass	1.290	0.787	0.350	0.557	0.234643	0.92506	
BriMi	Briza minor	Exotic	Grass	0.983	0.323	0.426	0.228	0.085821	0.92506	
LupBi	Lupinus bicolor	Native	Forb	0.803	0.349	1.074	0.247	0.438464	0.92506	
TriEr	Triphysaria eriantha	Native	Forb	0.358	0.120	0.286	0.085	0.544306	0.92506	
LayFr	Layia fremontii	Native	Forb	0.279	0.228	0.000	0.161	0.222131	0.92506	
BroMi	Brodiaea minor	Native	Forb	0.169	0.136	0.471	0.096	0.027357	0.92506	
HorMa	Hordeum marinum	Exotic	Grass	0.145	0.475	1.233	0.336	0.023554	0.875434	
JunCa	Juncus capitatus	Exotic	Rush	0.145	0.084	0.028	0.059	0.162816	0.777277	
TriLa	Triteleia hyacinthina	Native	Forb	0.120	0.062	0.114	0.044	0.92506	0.92506	
TriLa	Triteleia laxa	Native	Forb	0.120	0.062	0.114	0.044	0.92506	0.92506	
CroSe	Croton setigerus	Native	Forb	0.120	0.107	0.573	0.076	4.02E-05	0.001569	↑
RanBo	Ranunculus bonariensis	Native	Forb	0.064	0.045	0.000	0.032	0.158784	0.92506	
CinQu	Cicendia quadrangularis	Native	Forb	0.062	0.063	0.013	0.045	0.433355	0.92506	
TriHi	Trifolium hirtum	Exotic	Forb	0.043	0.249	0.773	0.176	0.003987	0.143548	
EscLo	Eschscholzia lobii	Native	Forb	0.028	0.015	0.000	0.011	0.074606	0.92506	
PogZi	Pogogyne zizyphoroides	Native	Forb	0.023	0.020	0.000	0.014	0.261866	0.92506	
JunBu	Juncus bufonius	Native	Rush	0.021	0.620	2.583	0.438	6.5E-05	0.002468	↑
CenSp	Centromadia spp.	Native	Forb	0.019	0.140	0.360	0.099	0.015839	0.538526	
GerDi	Geranium dissectum	Exotic	Forb	0.013	0.013	0.000	0.009	0.319242	0.92506	
CasAt	Castilleja attenuata	Native	Forb	0.012	0.031	0.038	0.022	0.401352	0.92506	
TriDu	Trifolium dubium	Exotic	Forb	0.008	0.233	0.522	0.164	0.029138	0.903284	
LasFr	Lasthenia fremontii	Native	Forb	0.004	0.004	0.000	0.003	0.319242	0.92506	
DesDa	Deschampsia danthanoides	Native	Grass	0.004	0.580	1.011	0.410	0.084948	0.92506	

AcmAm	Acmispon americanus	Native	Forb	0.000	0.197	0.599	0.139	0.002878	0.106475
TriEr	Trifolium hirtum	Exotic	Forb	0.000	0.056	0.056	0.039	0.319242	0.92506
HolVi	Holocarpha virgata	Native	Forb	0.000	0.020	0.020	0.014	0.319242	0.92506
EryCa	Eryngium castrense	Native	Forb	0.000	0.483	0.843	0.341	0.083383	0.92506
LytHy	Lythrum hyssopifolia	Exotic	Forb	0.000	0.030	0.054	0.021	0.073327	0.92506
PlaGr	Plagiobothrys greeneii	Native	Forb	0.000	0.006	0.006	0.004	0.319242	0.92506
TriDe	Trifolium depauperatum	Native	Forb	0.000	0.007	0.007	0.005	0.319242	0.92506
BroEl	Brodieae elegans	Native	Forb	0.000	0.011	0.015	0.008	0.161618	0.92506
TriVa	Trifolium variegatum	Native	Forb	0.000	0.155	0.169	0.109	0.276065	0.92506
ChlPo	Chlorogalum Pomeridianum	Native	Forb	0.000	0.028	0.038	0.020	0.176553	0.92506
AirCa	Aira caryophella	Exotic	Grass	0.000	0.101	0.156	0.072	0.126703	0.92506

Appendix D: All species identified (1) at the study site and (2-4) within each habitat zone from 2015-2016, ranked by mean relative abundance in the ungrazed area across all three years (2015-2017). Raw p-values as well as corrected p-values (Benjamini-Hochberg procedure for correction for multiple comparisons between years) are displayed. Species that differed significantly in the grazed and ungrazed pastures are highlighted in grey, and species with significant p-values after the Hochberg correction are given arrows which represent the direction of change in abundance in the grazed management area compared to the ungrazed area.

	Year	Habitat zone	Mean β_2 diversity (Grazed)	Mean β_2 diversity (Ungrazed)	Difference	p-value
Species Richness (q=0)	2015	Pool	2.55	3.02	-0.48	0.189
	2016	Pool	2.48	2.75	-0.27	0.251
	2017	Pool	2.43	2.68	-0.25	0.506
	2015	Transition	2.42	2.52	-0.11	0.764
	2016	**Transition**	**2.22**	**2.94**	**-0.72**	**0.005**
	2017	**Transition**	**2.58**	**3.18**	**-0.6**	**0.049**
	2015	**Upland**	**1.72**	**2.27**	**-0.56**	**0.042**
	2016	Upland	2.41	2.11	0.3	0.301
	2017	Upland	2.28	2.44	-0.16	0.544
Inverse Simpson (q=2)	2015	Pool	2.3	1.74	0.56	0.122
	2016	Pool	2.12	1.85	0.27	0.593
	2017	Pool	2.19	2.21	-0.02	0.939
	2015	Transition	1.46	1.34	0.12	0.198
	2016	Transition	1.32	1.39	-0.07	0.586
	2017	**Transition**	**2.14**	**1.46**	**0.67**	**0.030**
	2015	Upland	1.12	1.25	-0.13	0.562
	2016	Upland	1.22	1.42	-0.2	0.152
	2017	Upland	1.54	1.36	0.18	0.320

Appendix E: Habitat zones driving the differences in horizontal turnover (β_2 diversity) between grazing treatments. Hill numbers at q=0 (Species Richness) and q=2 (Inverse Simpson Index).

~~(Golodets et al., 2011)(Golodets et al., 2011)~~

~~(Souther et al., 2019)Adler, P., Raff, D., & Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, *128*(4), 465–479. https://doi.org/10.1007/s004420100737~~

~~Jost, L. (2006). Entropy and di v ersity. *Oikos*, *113*, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x~~

~~Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1890/06-1736.1~~

~~Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*(1), 98–109. https://doi.org/10.1890/13-0526.1~~

~~Manly, B. F. J. (2006). *Randomization, Bootstrap and Monte Carlo Methods in Biology, Third Edition.* Chapman and Hall/CRC.~~

~~Osem, Y., Perevolotsky, A. V. I., & Kigel, J. (2002). *Grazing effect on diversity of annual plant communities in a semi-arid rangeland: Interactions with small-scale spatial and temporal variation in primary productivity*. 936–946.~~