Quantifying the Effects of Landscape Fragmentation on Biodiversity at Multiple Scales: Community Assembly, Community Diversity, and Population Genetic Diversity

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Abstract

We observe the continued human alteration to natural landscapes around us, fragmenting and isolating populations, yet it remains a challenge to identify the evolutionary processes that are involved and make predictions on the impacts that fragmentation has on community assembly and disassembly processes. These predictions are made increasingly difficult as these impacts are species dependent. In this dissertation I use phylogenetic and genomic tools to quantify the impacts of fragmentation on biodiversity at multiple organizational scales. For this work I have collaborated with researchers to use a combination of techniques, for example, species traits, the relatedness of species to compare species assemblages, and DNA as a tool to be able to infer population level differences. My goal is to quantify the impacts of fragmentation on biodiversity at different scales and identify evolutionary processes that are influencing insular, or seemingly isolated, populations and communities. Further, in my chosen study system of Craters of the Moon National Monument and Preserve (CRMO) in Idaho, I, and my collaborators, can ask and answer questions related to the assembly of communities and the disassembly of communities in fragmented populations. With this work we can inform conservation and restoration efforts, particularly in isolated populations. Thus, science communication and scientific literacy are integral to the scientific process.

In **Chapter 1**, I focus on community level processes, using phylogenies as a tool to quantify the relatedness of species and a trait of interest. Using the community of vascular plants, we compare those species found in insular communities to the species in a larger pool that could potentially inhabit the isolated habitats to test for the impact of a range of factors on the membership of a species in a community. To this end, we use both traditional metrics and a new machine learning approach. With the traditional metrics we inferred neutral processes as important for shaping the insular communities at CRMO. However, with a proposed novel approach we inferred the joint influence of neutral and filtering processes.

In **Chapter 2**, the focus is on the species level impact of fragmentation. Populations of an individual species may be impacted by changes in isolation brought on my fragmentation and may also become isolated genetically. I, along with my collaborators, use DNA as a tool to infer population level changes in a species of crab spider, *Mecaphesa celer*. This allows us to infer potential impacts to gene flow among separated populations. From this first genome-wide assessment of *M. celer* at CRMO we do not detect clustering or genetic structure between the isolated populations, so genetically it is as if the spiders are one population. This means high amounts of gene flow exist between the isolated habitats and potentially the neighboring areas as well.

In **Chapter 3**, I describe a community outreach series called Science After Hours that I created and coordinated. I describe its impacts and provide information on the replication of a similar program. As scientists our knowledge is worthless if not shared, as learning does not occur in a vacuum. Sharing our work allows for informed actions and decisions. Science communication is an imperative, integral role for researchers and few low risk, small time commitment opportunities exist. This program filled a need in the Moscow, ID and Pullman, WA community and brought together stakeholders from the community, local businesses, and researchers.

Through this work we were able to quantify the impacts of fragmentation on biodiversity at different scales and identify evolutionary processes that are influencing insular, or seemingly isolated, populations and communities at CRMO. Neutral and filtering processes dominate the community assembly process for the vascular plant communities and high amounts of gene flow in *M. celer* indicate little population structure in the species. By creating a science outreach series, I, along with other researchers in the Moscow and Pullman community were able to fulfill one aspect of our role as a scientist and share the importance of our work.

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Dedication

For their unconditional love and support, my parents (Debbie and Clif), and my sister (Kelsey). To my partner in life David Arnold, I am so thankful we ended up in McCall, ID, together. And for Zoey "Toes" Peterson for always helping me to smile.

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Statement of Contribution

In chapter 1: KP conceived and designed the study, compiled the dataset, and led writing. Collaborators contributed to design of the study, analysis of the data, and with writing inputs. Field assistants conducted fieldwork to collect samples with KP.

In chapter 2: KP conceived and designed the study, performed field and laboratory work to compile the data set, and led writing. Collaborators contributed to design of the study, assisted with genomics laboratory work, and with writing inputs. Field assistants conducted fieldwork to collect samples with KP.

In chapter 3: KP designed the program and wrote the study.

Chapter 1: Phylogenetic Diversity and Community Assembly in a Naturally Fragmented System

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Abstract

We sought to assess effects of fragmentation and quantify the contribution of ecological processes to community assembly by measuring species richness, phylogenetic, and phenotypic diversity of species found in local and regional plant communities. Specifically, our fragmented system is Craters of the Moon National Monument and Preserve, Idaho, USA. CRMO is characterized by vegetated islands, kipukas, that are isolated in a matrix of lava. We used floristic surveys of vascular plants in 19 kipukas to create a local species list to compare traditional dispersion metrics, mean pairwise distance and mean nearest taxon distance (MPD and MNTD), to a regional species list with phenotypic and phylogenetic data. We combined phylogenetic and functional trait data in a novel machine-learning model selection approach, Community Assembly Model Inference (CAMI), to infer probability associated with different models of community assembly given the data. Finally, we used linear regression to explore whether the geography of kipukas explained estimated support for community assembly models. Using traditional metrics of MPD and MNTD neutral processes received the most support when comparing kipuka species to regional species. Individually no kipukas showed significant support for overdispersion. Rather, five kipukas showed significant support for phylogenetic clustering using MPD and two kipukas using MNTD. Using CAMI, we inferred neutral and filtering models structured the kipuka plant community for our trait of interest. Finally, we found as species richness in kipukas increases, model support for competition decreases and lower elevation kipukas show more support for habitat filtering models. While traditional phylogenetic community approaches suggest neutral assembly dynamics, recently developed approaches utilizing machine learning and model choice revealed joint influences of assembly processes to form the kipuka plant communities. Understanding ecological processes at play in naturally fragmented systems will aid in guiding our understanding of how fragmentation impacts future changes in landscapes.

Introduction

With the continued anthropogenic alteration of natural landscapes, there is a persistent and pressing need to investigate the consequences of habitat fragmentation and how these consequences affect

biodiversity in ecological communities. Specifically, there is a need to understand the effects of fragmentation on phylogenetic and functional trait diversity (Debinski & Holt, 2000; Ewers & Didham, 2006) as they have the power to elucidate past ecological processes that have impacted the community (Cavender-Bares, Kozak, Fine, & Kembel, 2009). Understanding the processes involved in community formation can provide insight into what ecological pressures are influencing community assembly and ultimately the biodiversity we observe (Faith, 1992). By studying recently formed, naturally fragmented landscapes we can explore the ecological processes that are involved in the early construction of species assemblages, the coexistence of species, and importantly the maintenance of diversity. Thus, if we understand the natural ecological processes at play in response to fragmented landscapes, we can use this information to guide our understanding of how future ecosystems may respond to fragmentation, either natural or human-caused. Additionally, we can explore the impact of fragmentation on phylogenetic and phenotypic diversity.

Previous work has characterized species richness and phylogenetic diversity in fragmented systems, and sometimes both components are explored (e.g., Helm, Hanski, & Pärtel, 2006; Santos, Arroyo-Rodriguez, Moreno, & Tabarelli, 2010). In these and other studies, however, the fragmentation process is often implemented experimentally or due to human impacts on a system (Arroyo-Rodríguez et al., 2012; Laurance, Laurance, Andrade, Fearnside, Harms, Vicentini, & Luizão, 2010). Furthermore, functional trait diversity of fragmented systems is rarely explored alongside phylogenetic information (but see Ribeiro, Colli, Batista, & Soares, 2017), even though the traits important for existing in a community and local environment can be very telling of the processes that led to the assembly of the current community (de Bello et al., 2009; Kraft, Cornwell, Webb, & Ackerly, 2007; McGill, Enquist, Weiher, & Westoby, 2006; Weiher & Keddy, 1999). Research has thus far focused on frequency of traits, e.g., relative abundance of reproductive strategy and how overall functional diversity is reduced with fragmentation (Girão, Lopes, Tabarelli, & Bruna, 2007), rather than the impact of the functional trait variation present. Exploring the effect(s) of fragmentation on phylogenetic and functional trait diversity in a naturally fragmented system will help establish what ecological pressures fragmentation evokes, for example possible increased competition, and how biodiversity is impacted by fragmentation.

The phylogenetic diversity of a community captures information about the amount of evolutionary history shared among the species within a community, which is oftentimes used as a proxy for functional trait differences among species within that particular community (Webb, Ackerly, McPeek, & Donoghue, 2002). Phylogenies overall are assumed to reflect morphological, ecological, genetic, and physiological differences that have accumulated between lineages (Gerhold, Cahill, Winter,

Bartish, & Prinzing, 2015). Phylogenies are thus useful in understanding processes that have influenced, and may continue to influence, multiple aspects of diversity within a community (Brooks & McLennan, 1991; Webb, 2000; Tucker et al., 2017; Owen, Gumbs, Gray, & Faith, 2019). For example, community phylogenetic approaches have been used to understand ecological processes important for the assembly of alpine plant communities (Marx et al., 2017), as plants in alpine environments are exposed to harsh conditions requiring a suite of functional traits that may be best represented using a phylogeny.

In the field of community ecology, dispersion metrics calculated from phylogenetic distances between species are often used to infer local ecological processes that have contributed to community structure (Webb et al. 2002; Kraft et al., 2007; Webb, Ackerly, & & Kembel, 2008; Kembel, Cowan, Helmus, Cornwell, Morlon, Ackerly, Blomberg, & Webb, 2010). The non-neutral processes inferred are generally habitat filtering (Bazzaz, 1991), which is inferred when species within a community are phylogenetically closely related, and competitive exclusion (Macarthur & Levins, 1967), which is inferred from a community of species encompassing high phylogenetic variation (Webb et al., 2008). The justification for these inferences relies on the assumption that most functional traits, especially those important in surviving habitat conditions or local competition for resources, are conserved so that closely related species tend to share similar functional traits. Thus, if many species require similar functional traits to survive in an environment, we then expect these species to be more closely related to one another than by chance, i.e., would observe low phylogenetic dispersion. Likewise, if species are competing for a similar niche space, species with traits that are dissimilar are those that exist in the community because they have not outcompeted one another, resulting in species that are not as closely related, and subsequently large phylogenetic dispersion is observed.

In addition to phylogenetic information, morphological, physiological, behavioral, or ecological traits can also be incorporated directly to understand community assembly processes (Cornwell, Schwilk, & Ackerly, 2006; Kraft et al., 2007; Kraft, Godoy, & Levine, 2015). Traits are often assumed to correlate with phylogenetic information, but this is not always the case (Mazel et al., 2018) and thus sometimes using the traits themselves, rather than the phylogeny as a proxy, can provide a more accurate depiction of community assembly processes (Kraft et al., 2007; de Bello, Thuiller, Leps, Cholder, Clement, Macek, Sebastia, Lavorel, 2009). Specifically, functional trait diversity can, perhaps more directly, provide information about how competition between members in a community might promote or hinder their coexistence (Macarthur & Levins, 1967; McGill et al., 2006; Weiher & Keddy, 1999). Thus, incorporating both phylogenetic and functional trait diversity within a single community can help infer the processes that have led to the assembly of that community, and

ultimately what contributes to the maintenance or loss of biodiversity (Webb, 2000; Cadotte, Albert, & Walker, 2013).

Utilizing both traits and phylogenies presents challenges, as incorporating both traditional metrics in community ecology is not straightforward. Additionally, the use of phylogenetic dispersion metrics to infer processes of community assembly has presented its own concerns. One of which is the assumption that functional traits important for assembly are conserved across, or correlated with, the phylogeny as this does not always hold (Cavender-Bares et al., 2009; (Mayfield & Levine, 2010) However, limiting analyses to functional traits does not necessarily solve the problem because then the phylogenetic information is not incorporated, meaning information inherent in evolutionary relationships is not accounted for. Additionally, a conclusion based on hypothesis testing and interpretation of processes when a significance threshold is passed is arguably problematic for biological inferences when we know the inference itself exists on a continuum, rather than on a binary threshold (i.e., yes/no). Therefore, we also use an alternative approach Community Assembly Model Inference (CAMI; (Ruffley, Peterson, Week, Harmon, & Tank, 2019). This approach attempts to address the aforementioned problems by inferring a model of community assembly using both phylogenetic information and information on a single continuous trait. The advantages of this approach include the avoidance of assumptions as to how traits evolved along a phylogeny and the uncertainty in the community assembly inferences to be quantified, avoiding a significance threshold for inference. In utilizing this new approach, along with traditional dispersion metric approaches, we seek to learn more about the ecological processes at play in naturally fragmented systems by incorporating phylogenetic information and functional traits together.

We ultimately combine the phylogenetic and functional trait data for use in CAMI, a novel machine-learning model selection approach (Ruffley et al., 2019), to infer the probability associated with different models of community assembly given the data. With CAMI, we also go one step further than testing for non-neutrality by quantifying the strength of proposed non-neutral models associated with inferred processes of community assembly. Finally, with the probabilities associated with the predicted models and their relationship to island meta-data, such as area and proximity to the outer edge of lava flow, we can further quantify the effect of fragmentation on assembly processes. With this information we can ask whether these methods, hypothesis testing with dispersion metrics and CAMI, are corroborative of each other and whether simultaneously considering phylogenetic and trait information changes the inferences made by dispersion metrics that consider the two methods alone. This work investigates phylogenetic and functional diversity within a naturally fragmented system and ultimately, we assess the effects of fragmentation on kipuka plant communities at Craters of the

Moon National Monument and Preserve by (1) measuring species richness, phylogenetic, and phenotypic diversity of species found in the kipuka community and those found in the greater shrub-steppe region, and (2) quantifying the contribution of different ecological processes to the assembly of communities in the fragmented landscape with both phylogenetic and ecological information. Given the harsh landscape and the isolation of the kipukas, we predict that the assembly of the plant communities in kipukas will be shaped by non-neutral processes, predominantly by environmental conditions and less so by competitive interactions due to the combination of climatic extremes in the availability of water, temperature variation, and high wind experienced in the region.

Methods

Study system

Craters of the Moon National Monument and Preserve (CRMO) located in south central Idaho, USA is a naturally fragmented system ideal to explore these questions because the lava-flow islands of vegetation within the preserve have been formed relatively recently, within the last 15 thousand years. The islands are young in age, and there are many of them, thus offering many replicates to detect the impacts of natural fragmentation. Additionally, within CRMO, the plants that exist in the lava-flow islands experience harsh environmental conditions that have further shaped the assembly of species within the communities. Between 15 thousand years ago (kya) and as recently as 2 kya, the eruptive periods at CRMO have resulted in 60 overlapping flows that encompass nearly 1,900 km^2 (Kuntz, Champion, Spiker, Lefebvre, & McBroome, 1982; National Park Service, 2011). After each eruption, islands of vegetation surrounded by lava flows were formed. These vegetation-filled lava-flow islands are known as kipukas, a Hawaiian term used for an area of older land that is completely surrounded by an area of younger lava flows (Vandergast & Gillespie, 2004). There are over 500 kipukas at CRMO creating a vegetated archipelago of islands within an "ocean" of basaltic lava. The size of the kipukas ranges from substantially less than one km^2 up to a privately owned kipuka that is over 341 km^2 (National Park Service, 2018). The plant communities at CRMO differ depending on successional stage and location, for example whether on lava flows, in cinder areas, or within kipukas.

Plant communities in kipukas are dominated by shrubs like sagebrush (*Artemisia tridentata*) and perennial bunchgrasses such as Idaho Fescue (*Festuca idahoensis*) (Link, Mast, & Hill, 2006). Shrubs and perennial bunchgrasses dominate the shrub steppe ecoregion, which covers about 6,450,000 km^2 of western North America (Daubenmire, 1970; Link et al., 2006; Rickard & Vaughan, 1988). Typical of the semi-arid shrub steppe ecosystem, the dry climate of CRMO is characterized by a combination of high temperature, low precipitation, and strong winds. Air temperatures approach 30° C in summer

months and the surface of the lava can reach 77° C whereas in the winter the air temperature can get as low as -17° C (Western Regional Climate Center, n.d.; NPS Contributors, 1991). Average annual precipitation ranges throughout the monument from southern portions to northern portions accumulating 38 – 51 cm respectively and most of the precipitation comes in the form of snow (NPS Contributors, 1991). Strong daily afternoon winds are between 24 and 48 km/hr (National Park Service, 2016). Individually, these harsh conditions, and the combination of them, limit the possible plant diversity that could persist at CRMO to those species that can deal with these physiological stresses.

For this study we used data from floristic surveys of vascular plants in 19 kipukas at CRMO. We used the collections, along with a Flora of the shrub-steppe ecoregion, to describe the phylogenetic diversity in and around the naturally fragmented landscape. We used an existing phylogeny of Spermatophyta (Smith & Brown, 2018) to construct a community-wide phylogeny of the species in the kipukas and around the region. With these regional and kipuka phylogenies, we used traditional dispersion metrics and hypothesis testing (Webb et al., 2008; Webb et al., 2002) to infer processes of community assembly in the kipukas. As we are interested in the effects of fragmentation on plant communities, we focused on plants collected within kipukas and not on the lava fields.

Plant traits are important for resource acquisition, seed dispersal, reproductive systems, and might be specific adaptations to low water availability. Adaptations include for example, modifications to increase photosynthesis efficiency (e.g., relative abundance of CAM, C3, and C4 species (Cavagnaro, 1988), a reduction in size of stomata (Sundberg, 1985), and an overall decrease in height to minimize conduit diameter for water transport as a wider diameter makes the species more vulnerable to conduction-blocking embolisms from drought or cold (Olson et al., 2018). We chose the functional trait of maximum vegetative height to generate phenotypic dispersion metrics as height is a proxy for resource allocation and competitive ability in plants (William K Cornwell et al., 2014; Weiher & Keddy, 1999; Westoby, 1998). Additionally, it is consistently noted in species descriptions and as such, the amount of missing data would be minimal (Cornwell et al., 2014).

Sampling

We obtained a permit for collection from the National Park Service and conducted floristic surveys in 27 kipukas at CRMO in May - July 2016 and May 2017 (Figure 1.1). Kipukas were accessed by foot and surveys targeted smaller kipukas that were generally less than 0.02 km^2 in size where we were confident that the habitat could be thoroughly inventoried by two people in the field by searching within the lava boundary of the kipuka. For each species encountered in a given kipuka we collected

two or three representatives in florescence. Collected plants were pressed, brought back to the University of Idaho for identification, and are stored in the Stillinger Herbarium and publicly available online (www.pnwherbaria.org). The surveys resulted in a total of 66 species, which we use here as the kipuka community species list, and thus used in the kipuka community phylogeny. Nineteen of the 27 kipukas contained nine or more species and were used for subsequent analysis and categorized as northern, central, or southern kipukas (as indicated in Figure 1.1). We chose that cutoff to keep as many kipukas as possible in our dataset to maximize statistical power while balancing the fact that communities with less than 10 species tend to have error rates in model identification of over 30% (see Ruffley et al. 2019). Identifying and using a comprehensive regional pool is important as this determines the species located within the region that could disperse into the communities of interest. Plant species located up to 17 km away have been demonstrated to have a role in the colonization process after the large-scale destruction of an ecosystem has occurred (Kirmer et al., 2008). For the present study a regional species pool was compiled by using the kipuka community list and adding the 621 other species listed on existing checklists for vascular plants at CRMO (Popovich, 2006) and the shrub-steppe ecoregion (Link et al., 2006), resulting in a regional pool, and the regional community phylogeny, consisting of 687 species (Appendix S1; Appendices and all input data and scripts for each analysis, along with the output data, can be found in https://github.com/ruffleymr/Peterson_Data and data is in a permanent Dryad repository https://doi.org/10.5061/dryad.dncjsxm13.). Thus, the kipuka phylogeny is a subset of the regional phylogeny.

Community phylogenetics

We constructed two community phylogenies: one from the species list stemming from all of the kipukas sampled, and one for the regional species pool. This was accomplished by using the drop.tip and keep.tip functions in the R package “ape”, “phytools”, and also the grepl function (Paradis, Claude, & Strimmer, 2004; Revell, 2012). The complete regional species pool included all vascular plant species documented within CRMO and the shrub-steppe ecoregion, as these species are potentially able to colonize the kipukas and thereby play an important role in the colonization process of the kipuka community (Kirmer et al., 2008). We chose to prune from an existing seed plant megaphylogeny (Smith & Brown, 2018) to create a single kipuka phylogeny, as opposed to creating individual community phylogenies for each kipuka, as the approach we chose has been shown to result in a more consistent estimate of evolutionary relationships and distances between taxa (Erickson et al., 2014). We constructed the regional phylogeny in a similar way, by dropping species not included in the regional checklists from the seed plant megaphylogeny (Smith & Brown, 2018).

This subsampling of the megaphylogeny has the advantage of having no impact on the branch lengths already estimated and recent studies suggest these are reliable trees for community phylogenetic inference (Li et al., 2019). The megaphylogeny we used, which consists of 79,881 vascular plant species with molecular data available from GenBank, is the largest dated phylogeny currently available for seed plants and has broad taxon sampling (Jantzen et al., 2019).

If a species was present in the community but absent in the megaphylogeny, a "replacement" species that is a close relative in the same genus with a similar ecological distribution present in the megaphylogeny was retained in the phylogeny (Qian & Jin, 2016). We acknowledge using replacement species could impact our calculation for community dispersion, though this is unlikely to be significant as a majority of the species relationships are rather distant (Jantzen et al., 2019). Species present in the kipuka and regional communities but for which the genus was not represented in the megaphylogeny and/or no suitable replacement was available (e.g., only one species was present in the megaphylogeny and there were multiple species in the regional species list) were not included in the community phylogenies. The resulting two community phylogenetic trees, after dropping species not present in the checklists and adding replacements, contained 65 and 641 species for the kipukas and regional pool of CRMO, respectively (Figures 1.2 and 1.3).

Functional trait

Maximum vegetative height data for all species in the kipuka and regional communities were gathered using a combination of herbarium records, species descriptions, and Floras (e.g., (Hitchcock & Cronquist, 2018). Maximum vegetative height values were log transformed because the data were strongly right skewed. Though it made the data more normal, log transformation was performed primarily for ease of biological interpretation of maximum vegetative height. Notably, a very small number of tree species in the kipukas have very large maximum height values compared to the rest of the species in the kipukas thereby inflating the impact the maximum vegetative height of these species has on the analyses of ecological process. Transforming the data allows us to consider the differences in height at a small scale as equally important as the large differences in height presented by the species of trees within the kipukas.

Community dispersion metrics

We measured the amount of phylogenetic dispersion among species in the kipuka community and tested for significance of the difference between the observed patterns and neutrality by calculating the standardized effect sizes of two different dispersion metrics (Webb, 2000; Webb et al., 2002) using the R package 'picante' (Kembel et al., 2010). First, we calculated mean pairwise distance

(MPD) between all species in the kipuka community phylogeny. We also calculated the mean nearest taxon distance (MNTD) as the mean distance separating each species in a community from its closest relative, this metric captures how clumped the species in the community are on the phylogenetic tree and the prevalence of short-branched clusters of species separated by longer branches. We then compared the observed values to the null expectations of these metrics that were produced by generating 1,000 replicate metrics. Each of these replicates were made from shuffling the species present in the regional community randomly, resampling the same number of species, and then recalculating the metrics.

If the observed values for MPD or MNTD are significantly under-dispersed or clustered, the test statistic fell in the lower 2.5% of the values obtained in the null distribution (p-value < 0.025). A community assembly process of habitat filtering is inferred in this case because the species in the local community are more closely related than is expected by chance (Gotelli & Colwell, 2001; Kembel et al., 2010; Webb et al., 2008; Webb et al., 2002; Webb, 2000). Alternatively, if the observed metrics are significantly over-dispersed, meaning the test statistic fell within the upper 97.5% of the null distribution (p-value > 0.0975). In this case, a community assembly process of competitive exclusion is inferred because the species in the local community are more distantly related than you would expect by chance. As these tests are done separately, if neither metric fell in either tail of the null distribution, a neutral process of community assembly was inferred. Though if one metric, either MPD or MNTD was found to be significant and the other not significant, we still considered the significant result.

MPD and MNTD can be calculated using phylogenetic branch lengths, the number of nodal distances, or phenotypic/functional trait differences (Gotelli & Colwell, 2001; Kembel et al., 2010; Webb, 2000; Webb et al., 2008, 2002). Thus, we measured the phenotypic dispersion the same way we calculated the phylogenetic dispersion metrics. We calculated each metric, mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), then performed 1,000 random shuffles of the regional and local communities to get the null distribution and to see if the observed metrics fell within either tail. We first ran a comparison between the kipuka and regional communities and then also looked at the kipukas separately by further pruning the phylogeny to represent only species present in a given kipuka. We then repeated this process for each of the remaining kipukas individually.

CAMI

To integrate phenotypic and phylogenetic data while inferring community assembly processes, we used a novel simulation software and inference procedure for community assembly models

implemented in the R package 'CAMI' (Ruffley et al., 2019). This approach works by first simulating many datasets of phylogenetic and phenotypic data under various community assembly processes such as habitat filtering, competitive exclusion, and neutrality. We then use a set of summary statistics that capture information in the phylogeny and traits to compare the simulations with the observed data. Approximate model selection and parameter estimation methods of random forests (RF; Breiman, 2001) and Approximate Bayesian Computation (ABC; Csilléry, Blum, Gaggiotti, & François, 2010) are then used for inference. The simulations used in model selection and the parameter estimation must match the empirical data conditions as much as possible, as described below.

To establish what model under which to simulate data, we first determined the model of trait evolution that best fits the regional phylogeny and regional trait information prior to simulation of phylogenetic and phenotypic data in CAMI. We fit the empirical data to two models of trait evolution, Brownian Motion (BM; Felsenstein, 1985) and Ornstein Uhlenbeck (OU; Butler & King, 2004; Hansen, 1997) using the fitcontinuous() function in the R package 'Geiger' (Pennell, Eastman, Slater, Brown, Uyeda, Fitzjohn, Alfaro, Harmon, 2014). BM models mimic the process of evolutionary drift over macroevolutionary time, t, with a single parameter, σ^2, that controls the rate of phenotypic change through time such that the expected distribution of trait values should be normal with the variance $\sigma^2 t$. OU does the same, only it includes a selective regime in which traits are "pulled" toward a phenotypic optimum at a rate of α. Using AIC, the best fitting model was found to be OU, which meant both parameters σ^2 and α needed to be estimated. To fit an OU model, we maximized the likelihood of the parameters of the OU model given the kipuka data. However, OU model parameters are notoriously hard to estimate as σ^2 and α are confounded and data can be fit using various combinations of these parameters where the likelihood always gets better with an increasing α and smaller σ^2, though increasing α values become more and more unrealistic the larger they get (Uyeda & Harmon, 2014). Therefore, we fit several OU models to the empirical data, varying the bounds of α from 0.01 to 1, to determine at what values of σ^2 and α the likelihood stopped getting dramatically better. This was at an estimated σ^2 of 0.92 with a corresponding estimate of α at 0.2; we used these estimates to simulate the trait data in CAMI (Appendix S2).

We simulated 10,000 community assembly datasets for each assembly model, for competitive exclusion, habitat filtering, and neutral, all under an OU model of trait evolution with the above estimated parameters. The other parameters such as the strength of filtering/competition t and the phylogenetic parameters, the speciation rate λ and the extinction rate μ, were drawn from their default uniform prior distributions as implemented in CAMI. The resulting simulated data, along with the

empirical data, were summarized into 30 different summary statistics (Appendix S3) to be used for model selection in RF and parameter estimation in ABC.

For community assembly model selection, we constructed a classification forest consisting of 1,000 decision trees using the 30,000 simulated datasets and the 30 summary statistics. RF works by using many decision trees to partition out the variation in the summary statistics and uses these differences to distinguish between the three community assembly models. As the decision trees are being constructed, they are also simultaneously being validated by a portion of the data that is withheld from the construction. This enables the calculation of the out-of-bag (OOB) error rate, or the proportion of misclassified simulations. This OOB error rate details how accurate the classifier is overall and also for each model, as some models are easier to distinguish than others. The resulting classification forest was then used to determine which model of community assembly structured the kipuka plant communities at CRMO. Here, we inferred the probability of each community assembly model for each of the 19 kipukas surveyed.

We performed parameter estimation using ABC following Ruffley et al. (2019). For ABC, we scaled the summary statistics by their standard deviation and then used the top 10 informative summary statistics from the RF classifier to estimate the posterior probability of t, the strength of habitat filtering (Appendix S4). We only considered the simulations under the community assembly model that best fit the data given the RF model selection, (i.e., the habitat filtering simulations). From those, we accepted 100 simulations from the posterior distribution for the parameter t. We used these estimates to generate 95% high density confidence intervals (Kruschke, 2011).

Factors influencing community assembly

To understand whether the model probabilities were explained by the fragmented nature of the kipukas, we constructed linear regression models using the lm() function in R 3.6.1 and tested whether any significant relationship existed. Specifically, we tested for whether any of the following independent variables; species richness, area of kipuka, distance to the edge of lava flow (isolation), and kipuka elevation, explained the variation in support for community assembly models associated with the 19 kipukas in our study (dependent variable). One may expect the combination of isolation and area, or isolation and elevation to better capture “fragmentation” than just one of the variables alone. Thus, we also tested whether the interaction between any of these variables resulted in a significant relationship with model support. This analysis aimed to understand whether these metrics of fragmentation explained variation in the ecological processes inferred from the phylogenetic and functional trait data.

Results

Kipuka community diversity and biogeographical attributes

The 66 plant species collected in the 19 kipukas sampled at CRMO represent 24 families and 51 genera. Species richness ranged from nine to 20 species per kipuka. The phylogenies created using an existing seed plant megaphylogeny consisted of 65 and 641 species in the kipuka and in the regional community phylogenies, respectively. Mean maximum vegetative height was 126 cm for the regional community and 77 cm for the kipuka community (Table 1.1). There was no missing data for the height data for species used in the analysis.

The mean area of kipukas sampled was 13,670 m^2, mean kipuka isolation, that is the distance from the edge of a kipuka to the outer lava flow, was 348.5 m, and mean kipuka elevation was 1574 m.

Community dispersion metrics

The observed values of MPD and MNTD for the kipuka community as a whole (all 66 species observed in kipukas) suggest that neutral processes are dominant as neither dispersion metric was significantly under- or over-dispersed (Appendix S5). Although not significant, the lower rank of the standardized effect size of the observed MPD (156 out of the 1,000 randomizations) shows a tendency to the lower 25% of values (p-value 0.156) and thus towards an under-dispersion or clustering signal. The rank of the standardized effect size of the observed MNTD tends toward the middle of randomizations and thus for neutral processes (406 out of 1,000). The standardized effect sizes (SES) are calculated by standardizing the raw phenotypic and phylogenetic dispersion metrics relative to the total variation observed. The empirically calculated SES is then considered the test statistic when compared to a null distribution of SES and the p-value is where that test statistic falls within the null distribution. In Figure 1.4 the p-values reported in each cell are as follows, for example, kipuka A received a SES rank of 10 out of 1,000 randomizations for phylogenetic data using the MPD metric and has a p- value of 0.01 listed and thus significant support for clustering. In sum, neither process of habitat filtering, nor competitive exclusion were inferred with these traditional phylogenetic dispersion metrics.

When considered individually across kipukas, none of the 19 kipukas showed significant support for over-dispersion with either the MPD or MNTD metric using phylogenetic data (Figure 1.4). Using the MPD metric based on phylogenetic data, five kipukas showed significant support for phylogenetic clustering and with the MNTD metric based on phylogenetic data, two kipukas showed significant support for phylogenetic clustering. Two kipukas (G and P) showed significant support for clustering

with each metric, MPD and MNTD. Thus, we found more individual kipukas at CRMO to be phylogenetically clustered than over-dispersed.

Among the remaining fourteen kipukas that did not significantly support either clustering or over-dispersion using the MPD metric and phylogenetic data, eleven trended towards phylogenetic clustering ($p = 0.5 – 0.25$), and only one (kipuka S) trended towards over-dispersion ($p = 0.75 – 0.95$). Using the MNTD metric and phylogenetic data nine kipukas trended towards clustering. None of the kipukas had significant support for over-dispersion based on the phylogenetic MNTD metric.

Regarding phenotypic dispersion based on maximum vegetative height and the MPD metric, no kipuka showed significant support for either clustering or over-dispersion using MPD. Six kipukas had ranks above 50 but less than 250, indicating a trend towards phenotypic clustering. Only two kipukas tended towards over-dispersion indicating possible competition (kipukas I and G had ranks above 750 but below 950). Nine kipukas trended towards clustering.

Selection of community assembly model

In general, most kipukas had very similar summary statistics, many with an expected amount of deviation given the varying species' pools across kipukas (Appendix S6). Notably, the variance of vegetative height amongst kipuka species was almost always, except in four kipukas, smaller than that of the regional species pool trait variance. This is somewhat indicative of environmental filtering because the trait variance is decreased in the local community. Specifically, for the sampled kipukas, Blomberg's K, which measures phylogenetic signal, showed there was weak evidence for a phylogenetic signal of the trait maximum vegetative height as the value was generally very low (mean = 0.27, Appendix S5).

The classification forest constructed using RF had an overall error rate of 20.23%, meaning that about 20% of the time the classifier is misclassifying simulations into the wrong model of community assembly. More specifically though, with an error rate of 3.1%, the competitive exclusion model was found to have the lowest classification error rate. The other two models, habitat filtering and neutral assembly, had higher error rates of 34% and 25%, respectively, indicating these two models are harder to distinguish from one another but both are easily distinguished from the competition assembly model. Using the classification forest, we were able to infer which model of community assembly structured the kipuka plant community at CRMO by our trait of interest, maximum vegetative height (Figure 1.5). In general, the competition model had the least support with an average probability of 11% across all kipukas, while the neutral and the filtering models on average had probabilities of 43% and 46%, respectively.

When estimating the t parameter, which in this case is the strength of filtering, we simulated under a range of values from one to 60. Counterintuitively, the values closer to 1 indicate strong filtering, while larger values indicate weak filtering. When the values are smaller, the filtering effect is stronger because species are heavily penalized for phenotypes dissimilar to the optimum. The average median estimate of t across the kipuka communities was 30.82, ranging from 16.23 to 39.34 (Appendix S7). The 90% high density confidence intervals for the t posterior distribution for each of the communities was quite broad, with many of the confidence intervals spanning a majority of the prior distribution.

Factors influencing community assembly

Of all the linear regression models tested to evaluate the effect of kipuka properties on the support for community assembly models, few resulted in significant relationships ($\alpha = 0.05$). The only models with significant prediction ability were species richness predicting model support for competition, as well as species richness predicting model support for the neutral model (Figure 1.6, Appendix S8). Specifically, as species richness for a kipuka increased, the model support for competition decreases (p-value 0.018) and the model support for the neutral model of assembly increased (p-value 0.019). Likewise, elevation was nearly a significant predictor of the model support for habitat filtering (p-value 0.052), where low elevation kipukas showed higher support for the habitat filtering model (Figure 1.6). All other models, including those with interaction terms and multiple predictors did not increase the predictability of any of the response variables.

Discussion

While traditional phylogenetic community approaches based on trait and phylogenetic dispersion suggest neutral assembly dynamics, overall, we do find some support for phylogenetic clustering, and ultimately habitat filtering. Importantly, we find that recently developed approaches utilizing machine learning and model choice in assembly reveal there are joint influences of both neutral dynamics, involving colonization and drift, as well as non-neutral dynamics such as habitat filtering influencing the kipuka plant communities. In combination these two processes together could be interpreted as mild filtering pressure on the species in the community that are generally under neutral processes. Likewise, we explored the relationships between model support for the various community assembly models, and various factors of fragmentation. Together these analyses allow us to describe the phylogenetic and functional trait diversity across the kipukas and interpret the influence of fragmentation.

Phylogenetic and Functional Trait Diversity

Using traditional dispersion metrics alone, such as MPD and MNTD, and hypothesis testing, our analyses mainly support the role of neutral processes forming the community as very few kipukas resulted in significantly over or under-dispersed phylogenetic or functional trait metrics. Under a neutral model of assembly all species present in a regional community pool have an equal probability of colonizing and persisting in that local community (Hubbell, 2001; Rosindell, Hubbell, He, Harmon, & Etienne, 2012). This neutrality implies that species differences (e.g., in traits) do not impact their presence or absence in the local community. Species neutrality a main component of the foundational Theory of Island Biogeography (MacArthur & Wilson 1967), whereas most island systems are a result of who can colonize the open habitat. This may be the case for the kipukas, given their very young age (~15 kya) and the harsh habitat that mimics true island dynamics. Support for neutral processes of community assembly have been found in a variety of isolated and/or fragmented organismal systems including aquatic bacteria communities in tree holes in the same area (Woodcock et al., 2007), farmland birds that exist in a fragmented agricultural landscape (Henckel, Meynard, Devictor, Mouquet, & Bretagnolle, 2019), and cichlids in Lake Tanganyika (Janzen et al., 2017).

Given that no phylogenetic signal, or Blomberg's K in this case, for our trait of interest was estimated to be of 0.27 across all kipukas, the approaches above were not completely reliable. This is because the use of phylogenetic and functional trait dispersion metrics for community assembly relies on high phylogenetic signal in the trait(s) of interest. Rather an approach that does not assume phylogenetic signal in traits, such as CAMI, is justifiable to use (Cavender-Bares et al., 2009; Kraft et al., 2007). In CAMI, in all models of community assembly the species in the regional pool have an equal probability of colonizing a community thus, support for neutral and filtering suggests that the trait of maximum vegetative height reflects a barrier for some species inhabiting the kipukas. Perhaps the true functional trait barrier is the height of the plants, or perhaps it is related to the shared resource allocation that the plant trait height is a proxy for. Either way, there is evidence that there is an environmental limitation or barrier to some species existing in the kipukas.

Support for multiple process of community assembly could mean processes of community assembly are operating at different scales. For example, previous work has found multiple mechanisms of community assembly operating in early plant communities (Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2018). Assembly from the regional pool to local communities was mostly neutral, and within communities, non-random assembly occurred related to various traits important in a plant species ability to disperse, establish, and persist in a local community. Additionally, others have found that different community assembly processes operate at different life stages of plants (Hu,

Feeley, & Yu, 2016). It is important to note that all environments, or each individual kipuka in this case, may not select for the same variant in traits (Lowe & McPeek, 2014). The kipuka community as a whole is then comprised of a set of species that are expressing different traits based on selective pressures at different scales (e.g., spatial, temporal, and phenological) (Lowe & McPeek, 2014; Hu et al., 2016; Marteinsdóttir et al., 2018). Support for both neutral and filtering processes operating in the assembly of the kipuka communities at CRMO may highlight processes impacting at different scales, different life stages, and the differences in selective pressures between kipukas. We may be observing and measuring the initial impacts of fragmentation on the kipuka communities and the long-term effects of these processes over a macroevolutionary timescale might not yet be realized.

Various traits in plants are important for resource acquisition, seed dispersal, and specific adaptations to the stress of low water availability exist. One of these, a reduction in overall plant height to minimize the diameter of vascular tissue to decrease occurrence of embolisms (Olson et al., 2018) would be particularly beneficial in habitats that experience temperature and precipitation extremes, such as at CRMO. We chose the single trait of plant height because of its impact on overall water movement in a plant, as susceptibility to stress due to low water availability and cold would impact a plants ability to persist at CRMO. Water stress in plants has been shown to be an important primary filter in restricting which species present in a regional pool were available to establish via community assembly (Luzuriaga, Sánchez, Maestre, & Escudero, 2012). Future studies including several ecologically relevant traits could reveal a more complete picture of the role of phenotypic variation across species in constraining or promoting the assembly of fragmented communities. Although one quantitative trait can be used at a time in CAMI, multiple analyses could be done to compare across traits.

Qualitative traits, for example seed dispersal mechanisms may vary between plants found within the local kipuka community and those in the regional community (Lowe & McPeek, 2014). Perhaps gravity seed dispersal is more prevalent for the kipuka species than for the regional species, however this was outside of the scope of the present study.

In our efforts to measure the strength of filtering through the t parameter, we find that we do not have much confidence to estimate this parameter with our current techniques and data. The data are limited by small communities, and we know small communities lead to a lack of power in estimating this parameter (Ruffley et al. 2019). However, we also know that these data support both filtering and neutral models of assembly, which could also be why estimating a parameter only from the filtering model is unsuccessful.

The topography of the kipukas at CRMO could in part explain the support for filtering with our trait of interest, maximum vegetative height, in these fragmented plant communities. In addition to the influence of vegetative height on water conduction in vascular tissue and sensitivity to environmental stressors, susceptibility to wind damage can also determine species presence and persistence in a community. Most of the kipukas are bowl shaped with the outer lava flow forming a higher, almost ridge-like edge and the vegetation within. It might be additionally disadvantageous for plants to be taller than the ridge around the kipuka as high winds could be damaging to the plant. Plants do have the ability to acclimate to wind at multiple scales from cellular to the entire organism, but root or stem failure is still possible (Gardiner et al. 2016). Increased susceptibility and negative impacts of wind damage has been found to be exacerbated when surrounding areas lack vegetation (e.g., denuded) such as those of the lava matrix at CRMO (Laurance & Curran, 2008). Thus, plants with a maximum vegetative height shorter than the lava boundary would be able to withstand the strong winds experienced at CRMO better as they are partially protected within the "bowl" shape.

A Fragmented Landscape

Within the fragmented landscape of kipukas at CRMO, the trait of maximum vegetative height may be particularly influential in the ability of a species to establish and thrive in the kipukas as height may be especially costly in this environment due to environmental stressors caused by fluctuations of temperature and precipitation that occur. How wind acts as a selective force for plants is of interest in other fragmented landscapes as well, as abiotic factors greatly influence the successful establishment and persistence of a species within a community. The fact that lower elevation kipukas show more support for habitat filtering models compared to the kipuka community as a whole is interesting and could be due to a finer scale filtering pressure along an elevational gradient, in addition to the already mentioned environmental stresses operating on the community as whole.

The impacts of fragmentation can be hard to measure at the phylogenetic scale which broadly characterizes diversity at a macroevolutionary scale. One way to obtain a finer perspective of local diversity within and between kipukas at CRMO for future work could be to incorporate genetic sequencing of individuals from each species collected. Producing species specific population genetic data would then allow for quantification of diversity within species and comparisons among species. This proposed population genetic approach would allow us to quantify contemporary migration (i.e., dispersal) occurring within the local community between kipukas. Although outside of the scope of the present study, leaf tissue samples were obtained (and stored in silica) from each individual species collected and these could be used in the future in such a proposed population genetic study.

The fragmented landscape at CRMO is a particularly useful system in which to ask questions related to functional trait diversity and phylogenetic diversity due to the lava matrix in which the archipelago of kipukas is situated. Although this system is naturally fragmented, the intervening matrix in many ways is similar to anthropogenic alterations of landscape occurring elsewhere (e.g., asphalt, concrete). By understanding the ecological processes at play in natural fragmented systems and traits that may impact community assembly we can then use this information to guide our conservation and restoration efforts in future fragmented ecosystems.

Conclusion

With the continued alteration to natural landscapes, there is a persistent and pressing need to investigate the consequences of habitat fragmentation and how these consequences may impact phylogenetic and functional trait diversity. The incorporation of both phylogenetic and functional trait diversity within a single community can help infer the processes that have led to the assembly and formation of that community, and ultimately what contributes to the maintenance or loss of biodiversity. Using a new approach that infers a model of community assembly using both phylogenetic and trait information, along with measuring the strength of the inferred ecological process, we find that for the kipuka plant community at CRMO dual processes of neutrality and filtering based on maximum vegetative height have contributed to community formation. Additionally, we find there is evidence that environmental pressures are indeed prohibiting some species from inhabiting some or all of the kipukas, and these pressures may be more severe at lower elevations. When data for more than one trait are available, multiple CAMI analyses could be performed to compare the role of different traits and their impact on community formation. This type of comparative trait-based analysis could help to predict how community assembly might respond to changes such as fragmentation.

Table 1.1 Summary of vegetative height data for the regional community (n=641 species) and the kipuka community (n=65 species) and the biogeographical factors of kipukas that were included in the analyses.

	Regional Community	Kipuka Community
Mean (range) minimum vegetative height (cm)	45 (0.3 –4054)	23 (1.3–100)
Mean (range) maximum vegetative height (cm)	126 (1.5 – 9144)	77 (6 – 300)
Kipuka mean area (m^2)	1.37 (700 –114,100)	
Kipuka mean isolation (m)	348.5 (17.65 – 2137)	
Kipuka mean elevation (m)	1574 (1358 – 1678)	

Figure 1.1 Map of Craters of the Moon National Monument and Preserve, Idaho, USA. Colored outline of map inlays corresponds to organizational scheme of northern, central, and southern regions (yellow, blue, and gray, respectively). The 19 locations of kipukas with vascular plants surveyed are referenced with a letter. Photo at top right is of kipuka "A."

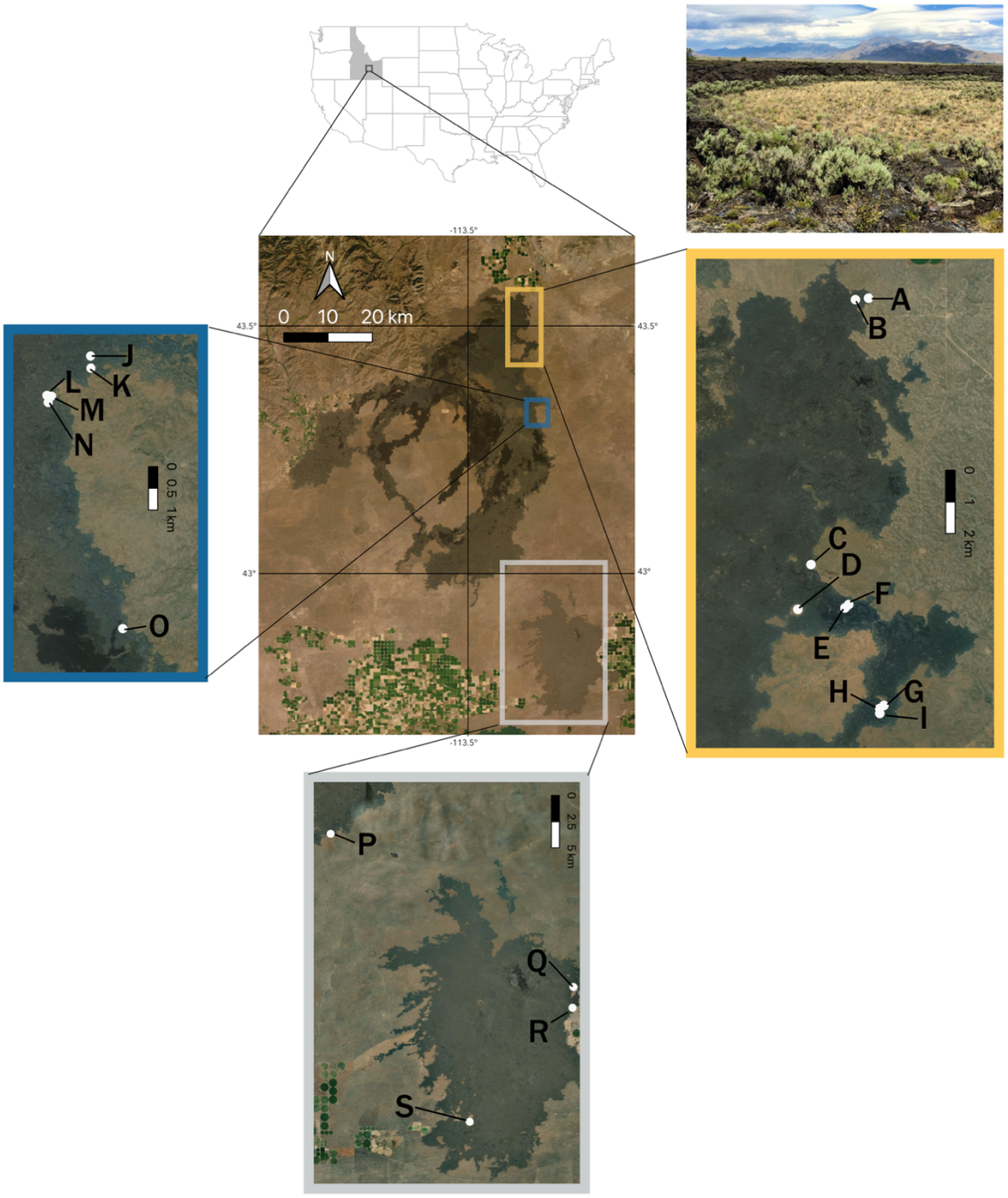


Figure 1.2 Local community phylogeny of species found in the kipukas sampled at Craters of the Moon National Monument and Preserve, Idaho, USA. Colors shading taxon names correspond to Family listed at right.

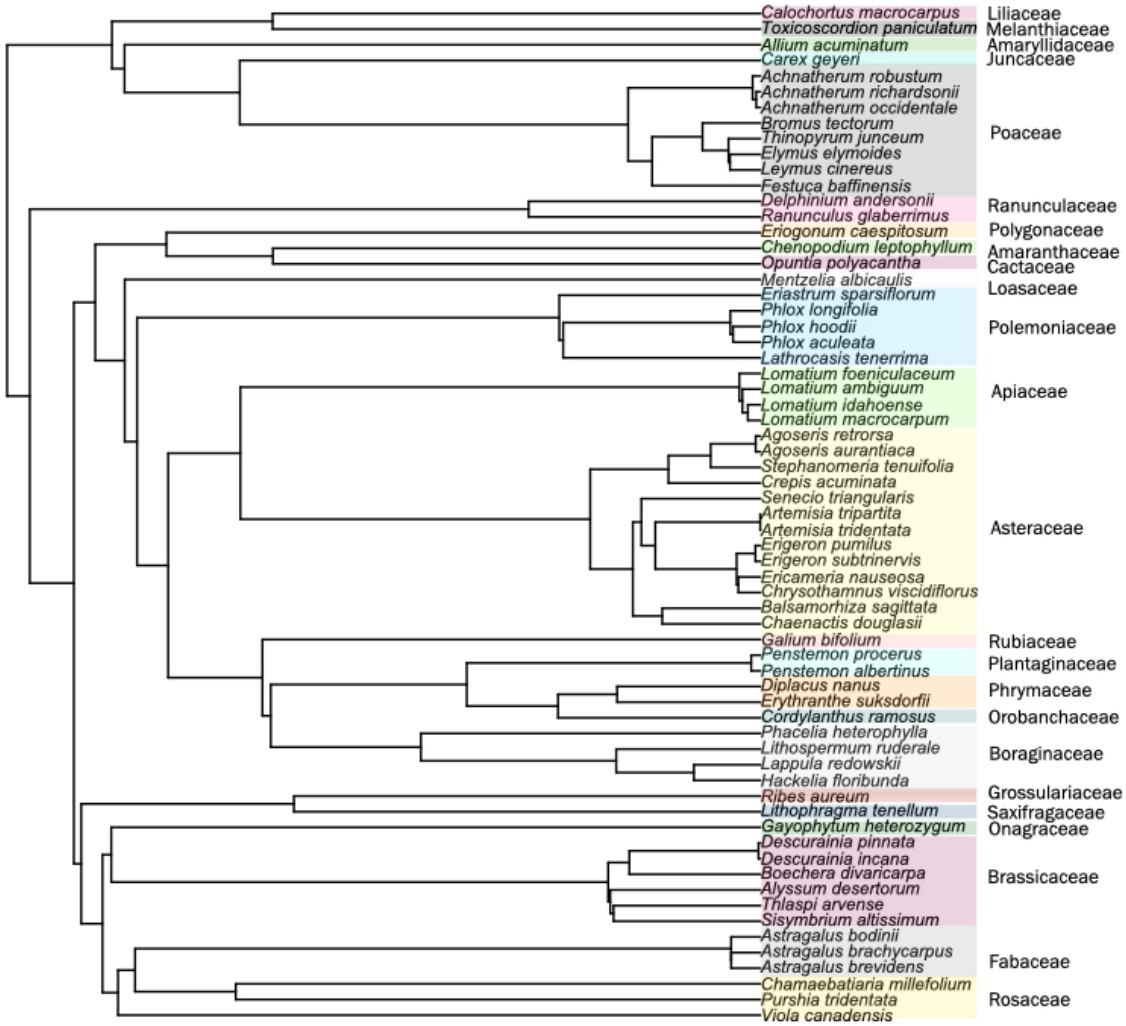


Figure 1.3 Regional community phylogeny of species found in the shrub-steppe ecosystem. The bars surrounding the phylogeny loosely indicate Family grouping.

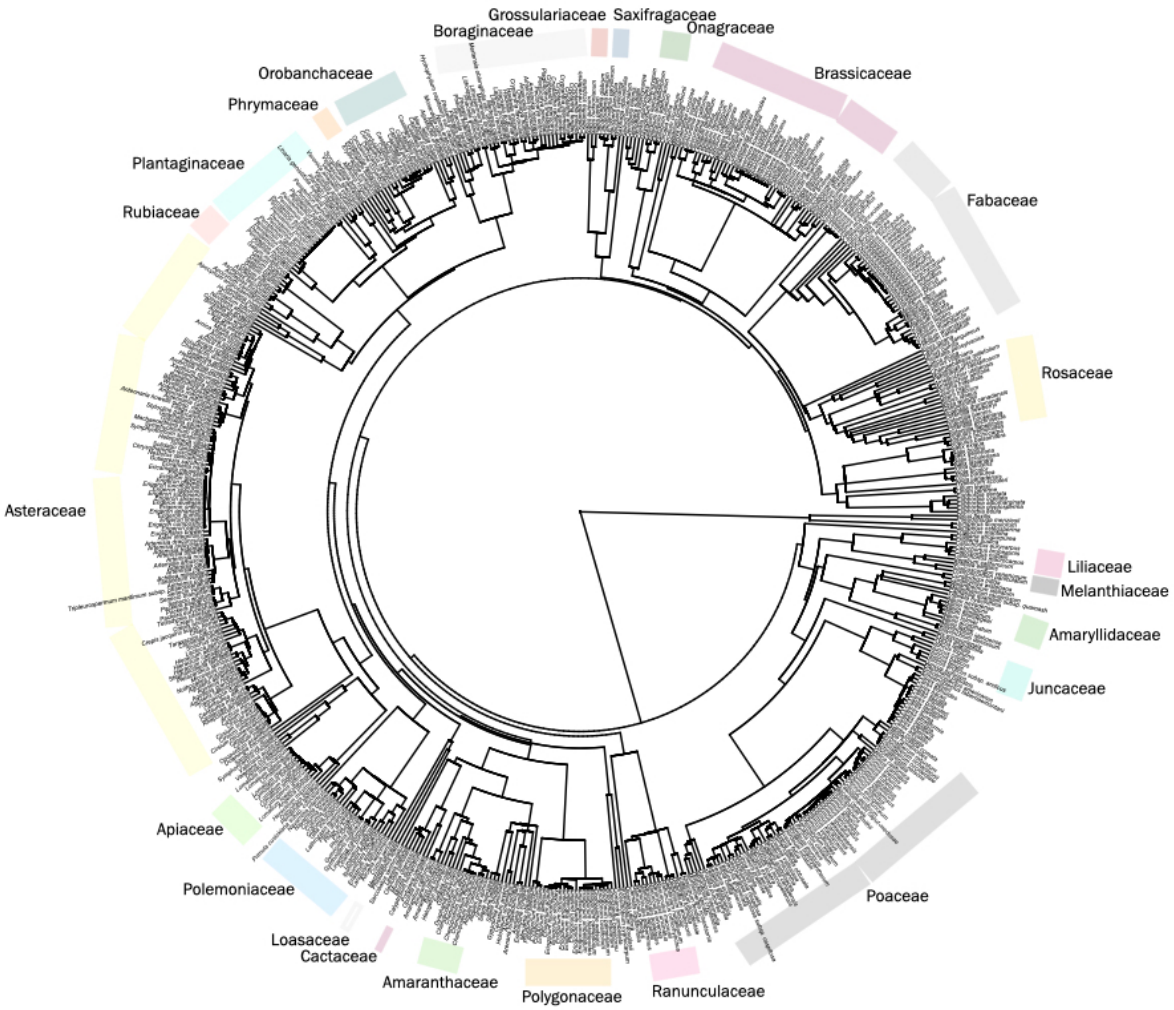


Figure 1.4 Heatmap of p-values for the 19 kipukas sampled at Craters of the Moon National Monument and Preserve, Idaho, USA for each phylogenetic and phenotypic diversity metric. The header of each column is the test that the p-value in the cells refers to (mean pairwise distance, MPD and mean nearest taxon distance, MNTD). Colored squares at the left of the heatmap denote the kipuka letter and region (northern, central, and southern) as indicated in Figure 1.1. Darker gray colors represent lower p-values and lighter gray colors represent higher p-values. The standardized p-value is noted in each cell. Additionally, a black circle within an individual cell represents a p-value of less than 0.025 indicating significant support for phylogenetic or phenotypic clustering. A p-value of more than 0.975 would indicate significant support for over-dispersion.

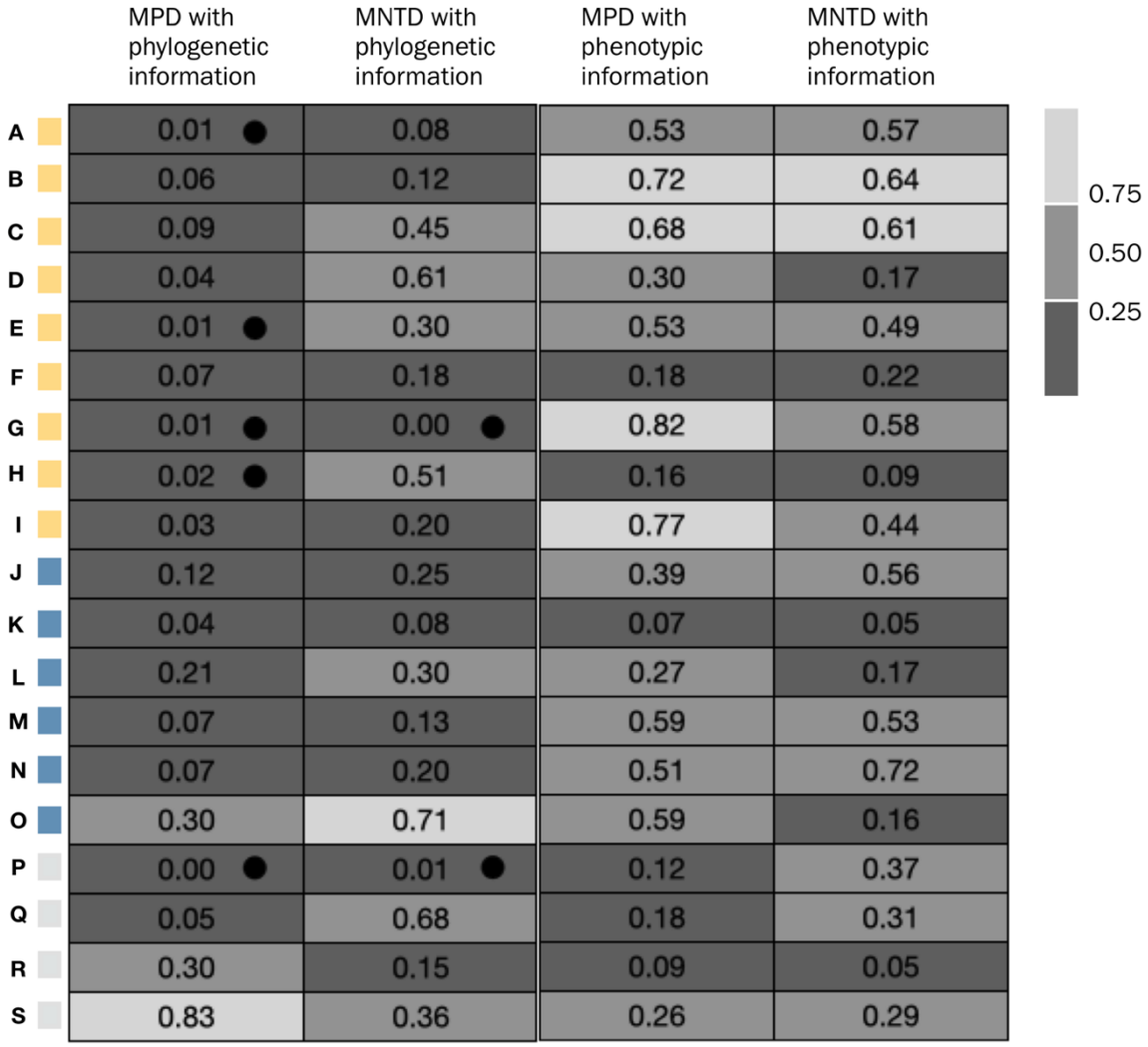


Figure 1.5 Stacked bar plot of percent model support values for the 19 kipukas. Model support values indicated at left. Colored squares at bottom denote kipuka region (northern, central, and southern as indicated in Figure 1.1) at Craters of the Moon National Monument and Preserve, Idaho, USA. Shade of bar denotes community assembly model.

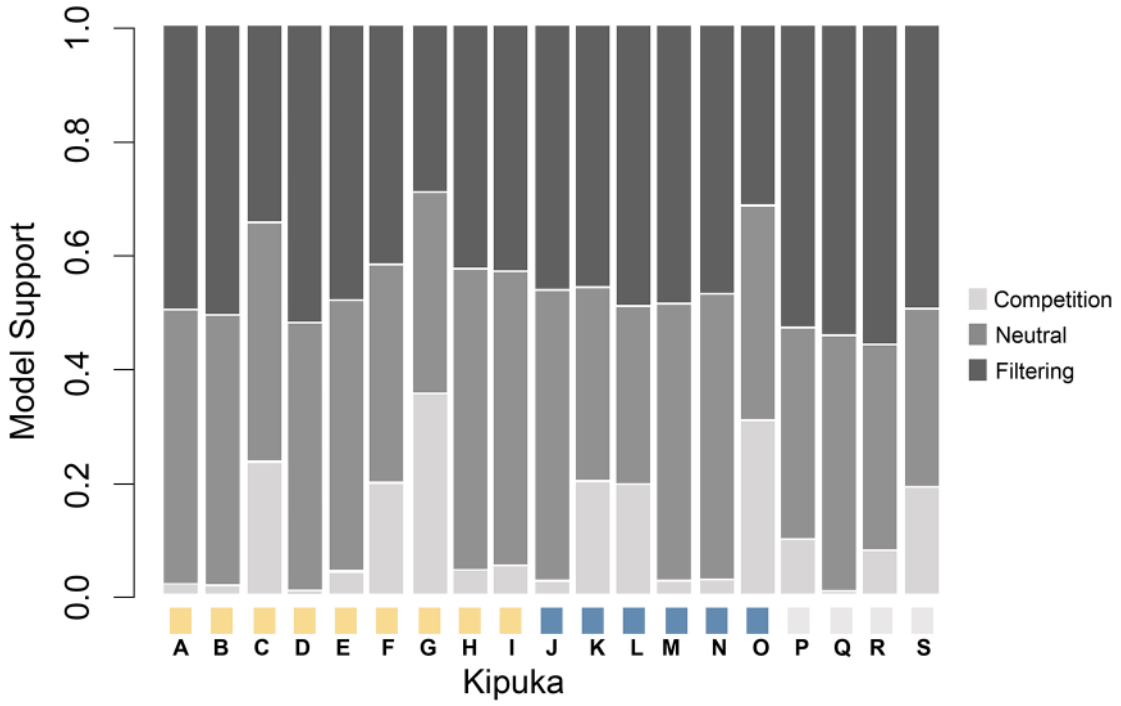
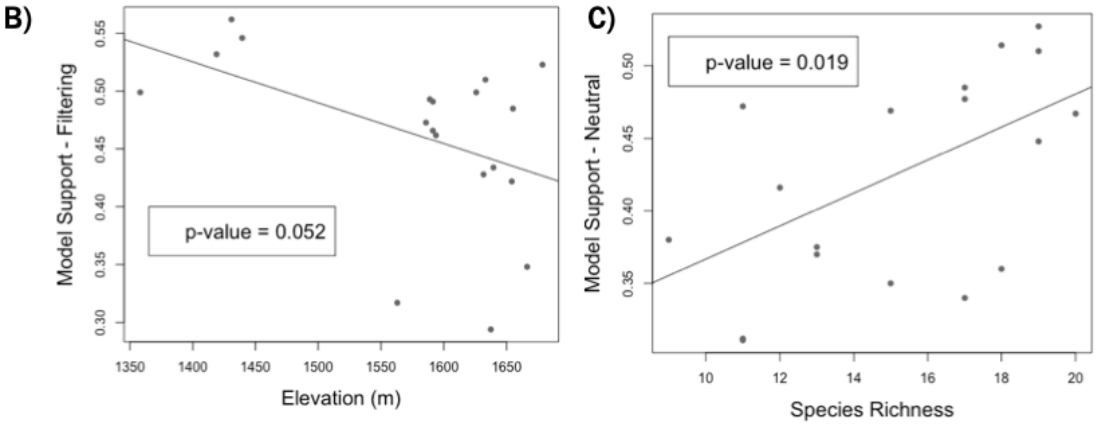


Figure 1.6 Significant linear regression model results ($\alpha = 0.05$). Top panel A) includes significant (**) results for the model support (dependent variable) and factor of kipuka (independent variable). Split panels demonstrate B) nearly significant (*) relationship negative relationship between elevation and model support for filtering and C) significant (**) positive relationship between species richness and model support for neutrality. The rest of the linear regression model results can be found in Appendix S8.

A)

Model	Intercepts	Regression Coefficient	Adjusted R^2	P-value
Competition Model Support ~ Species Richness	0.375494	-0.017366	0.244	0.01832
Neutral Model Support ~ Species Richness	0.25298	0.01138	0.2381	0.01971



Chapter 2: Panmixia in Spiders (*Mecaphesa celer*) Despite Fragmented Habitat at Craters of the Moon in Idaho

Peterson, K., Hendricks, S., Hohenlohe, P., and C.E. Parent. "Panmixia in Spiders (*Mecaphesa celer*) Despite Fragmented Habitat at Craters of the Moon in Idaho." Forthcoming in *Ecological Entomology*.

Abstract

A fragmented landscape, which contains a patchwork of vegetated hospitable areas and a barren intervening matrix, may reduce gene flow in a population and over time result in an increase in population structure. We tested this prediction in crab spiders (*Mecaphesa celer* (Hentz, 1847)) inhabiting isolated habitat patches in the lava matrix of Craters of the Moon National Monument and Preserve (CRMO), Idaho, USA. Using reduced-representation genomic sequencing, we did not find evidence of population structure due to a reduction in gene flow among habitat patches. Instead, our results show strong evidence of panmixia likely due to abundant juvenile dispersal and possible connectivity to outer regions surrounding the lava flows despite the species' habitat specificity.

Introduction

The natural world is becoming more fragmented, isolated, and altered. The many ecological processes of fragmented populations are complex (Young & Clarke, 2000). In some cases, detrimental effects may arise as isolation of populations and landscape fragmentation increases due to an intervening matrix that may be inhospitable and/or limit dispersal. Reduced dispersal ability of organisms, and ultimately decreased gene flow between fragmented populations, can result in increased population structure and decreases in the effective population size (Hedrick & Gilpin, 1997; Whitlock & Barton, 1997). The decreases in gene flow and effective population size can lead to genetic drift in the population and an overall decrease in genetic diversity (Frankham, 2015). Additionally, these populations may be unable to then purge detrimental alleles and others may become fixed. These impacts make it difficult for such a population to respond to environmental changes. Observing patterns of gene flow after natural landscape fragmentation, such that can occur with lava flows, can help identify potential parallel threats associated with anthropogenic fragmentation of landscapes (e.g., urbanization, asphalt). However, little is known how the process of fragmentation in a landscape, in combination with both passive dispersal and a high chance of landing in inhospitable habitat, may impact species on a fine, genetic scale.

Although dispersal distances in spiders can vary widely depending on species, habitat, and climatic variables, some spiders can travel great distances, as Darwin noted small spiders descending from the

air aboard the Beagle when it was at least 95 km away from land (Darwin, 1860). Crab spiders (Araneae: Thomisidae) aerially disperse by relying on their fine fibers to catch air currents in a passive behavior known as ballooning (Homann, 1934). These ambush predators, in particular spiders within the Genus *Mecapehsa*, exploit vegetation as hunting habitat to prey on pollinators (Nentwig, 1986). Some species use camouflage to match the inflorescence(s), can change color, and also can interfere with insect visual signals thereby increasing pollinator visits to the inflorescence(s) they occupy (Heiling, Herberstein, & Chittka, 2003). In this present study, the species *Mecaphesa celer* were most often observed and collected on the inflorescences of Arrowleaf Balsamroot (*Balsamorhiza sagitatta*) and foliage of the shrub Big Sagebrush (*Artemisia tridentata)*. Given that *M. celer* are more restricted to vegetative hunting areas and exhibit passive dispersal, fragmentation by a low-quality intervening matrix may exacerbate this restriction of movement resulting in decreased dispersal and, over time, an increase in observed population structure.

Previous work on arthropods in naturally fragmented areas, and particularly those separated by lava flows, has found population structure at small scales, both temporal and spatial (Vandergast, Gillespie, & Roderick, 2004; Goodman, Welter, & Roderick, 2012). For example, the long-jawed-orb-weavers, *Tetragnatha* spp., on Hawaii, which disperse by passive ballooning, show geographic population structure in a fragmented landscape of lava and forest fragments (Vandergast et al., 2004). The evolutionary impacts of forest fragmentation measured in the genetic analysis of the spiders occurred within approximately the last 150 years. In a Hawaiian planthopper (*Nesosydne chambersi*), a sap feeding specialist, genetic structure was found to be strongly associated with geographical location across lava substrates that ranged from 200-3000 years in age (Goodman et al., 2012). While genetic structure has been observed in populations of arthropods within the geologically fragmented landscape of Hawaii, it has yet to be studied whether similar patterns are observed in arthropods in an analogous lava-fragmented system in the continental United States such as Craters of the Moon National Monument and Preserve (CRMO).

CRMO, located in south central Idaho, USA (Figure 2.1), is an ideal system to explore patterns of gene flow in fragmented landscapes because, like with the Hawaii forest fragments, naturally produced islands of vegetation have been created between the sequential, inhospitable surrounding lava flows. There are over 500 of these lava-flow islands at CRMO, thus offering many replicates to detect the impacts of natural fragmentation on population structure. Between 15 thousand years ago (kya) and as recently as 2 kya, the eruptive periods at CRMO have resulted in 60 overlapping flows that encompass nearly 1,900 km^2 (Kuntz et al., 1982; National Park Service, 2011). After each eruption, islands of vegetation surrounded by lava flows were formed. These vegetation-filled lava-

flow islands are known as *kipukas*, a Hawaiian term used for an area of older land that is completely surrounded by an area of younger lava flows (Vandergast & Gillespie, 2004). The kipukas at CRMO create a vegetated archipelago of islands within an "ocean" of basaltic lava. The size of the kipukas ranges from substantially less than one km^2 up to over 341 km^2 (National Park Service, 2018). This patchwork landscape is home to a diverse community of plants and animals, some of which are endemic to lava fields and/or sagebrush steppe habitat.

Although the geology, flora, and some of the 2,000 documented species of wildlife including charismatic megafauna such as pika and pronghorn within CRMO have been studied, invertebrates overall remain poorly studied (Camp, Shipley, Varner, & Waterhouse, 2020; Cohn, 2010; Kuntz, Champion, Spiker, & Lefebvre, 1986; Kuntz et al., 1982; Popovich, 2006). One arthropod of interest found at CRMO, the Lava tube beetle (*Glacicavicola bathyscioides*), is found only in lava tubes in the western United States (Peck, 1981) and to date one survey of insects has occurred (Horning & Barr, 1970). Therefore, abundance estimates and distributions of crab spiders, including *M. celer*, at the regional scale of CRMO are unclear.

Here, we present the first assessment of genome-wide patterns of population structure of *M. celer* at CRMO. We predict that the geologically recent lava flows separating the kipukas sampled at CRMO might hinder the movement of *M. celer*. between kipukas over various distances. Therefore, we expect this separation to create population structure of *M. celer*. at CRMO. To evaluate this hypothesis, we used Restriction-site-Associated DNA sequencing (RADseq; (Andrews et al., 2016)) to identify and genotype a large number of polymorphic nuclear loci at 13 localities in CRMO. The results of this study are critical for understanding the dispersal patterns that affect ecological processes, such as community assembly, as a habitat is altered and fragmented over time by a lower quality and/or inhospitable matrix.

Methods

Library preparation and sequencing

To measure population structure of *M. celer* at CRMO we collected spiders using beating sheets in thirteen kipukas (denoted "a" – "m" in Figure 2.1). Collection occurred May 2017 and specimens were placed in 95% ethanol in the field and then stored at the University of Idaho, Moscow, ID, USA at -80°C until DNA extraction.

We extracted DNA for genetic sequencing from spider legs (two – six per individual) using an OmniPrep Genomic DNA Extraction Kits (G-Biosciences, St. Louis, MO, USA) (refer to Table 2.1).

DNA quality and quantity were assessed by agarose gel electrophoresis and with a Qubit fluorometer (Thermo Fisher Scientific, Waltham, USA).

We constructed a library for single-digest RADseq library for 84 individuals (2-13 individuals per kipuka), following the protocol of Ali et al. (2016), but without the final target capture step. We used the restriction enzyme PstI, which recognizes a 6 base pair (bp) cut site, and individually barcoded each sample. Then, we pooled all samples into one library and performed size selection to select fragments from 300-700 bp. We amplified the library using 12 PCR cycles and sequenced in one lane of paired-end 150 bp reads using an Illumina Hi-Seq4000.

Sequence processing and genotyping

We removed PCR duplicates using Stacks v.2.2 (Rochette, Rivera-Colón, & Catchen, 2019) with the 'clone_filter' unit. We filtered reads with the 'process_radtags' unit from Stacks using default setting options of -q and -r, respectively, these options filter by read quality using a sliding window and rescue barcodes with up to two errors. Based on the recommendations of (Rochette & Catchen, 2017) for parameter optimization in *de novo* analysis, we tested a range of M and n values from 1 to 9 (fixing M = n) and m = 3. For each parameter combination, we filtered the raw results keeping only loci shared by at least 80% of samples (-r 0.80) using the 'populations' unit from Stacks and plotted the number of loci and number of polymorphic sites. We chose M = n = 3 and m = 3 based on the plateau in number of loci and stabilization of the distribution of polymorphic sites (Rochette & Catchen, 2017). We removed loci genotyped in less than 50% and less than 90% of all samples to produce two datasets for subsequent analyses.

Population Structure

To assess genetic clustering, we applied three methods to the filtered dataset. First, we performed principal components analysis (PCA) using PLINK v1.9 (Purcell et al., 2007). We plotted individuals on PC1 v PC2 and PC2 v PC3 for the two datasets. Second, we tested for fine-scale population structure using fineRADstructure v. 0.3.2 (Malinsky, Trucchi, Lawson, & Falush, 2018). Given that this analysis has been shown to be highly sensitive to missing data, we only used the dataset that retained SNPs genotyped in more than 90% of all individuals. We ordered the RAD loci according to linkage disequilibrium using the sampleLD.R script provided in fineRADstructure in order to reduce the likelihood of overconfident clustering. Using the reordered loci, a co-ancestry matrix was inferred by fineRADstructure and used as input for the Markov Chain Monte Carlo (MCMC) clustering algorithm. The MCMC chain ran for 100,000 iterations with a burn-in of 100,000 and a thinning interval of 1,000. Third, we used TESS3 (Caye, Deist, & Martins, 2016), which is useful in

determining genetic barriers or genetic discontinuities in continuous populations, to incorporate spatial information to inform individual ancestry estimates. The default values of the program were implemented, and each run was replicated 5 times. The most likely value of K corresponded to the minimum of the cross-entropy criterion, across the range K = 1–15. Additionally, we calculated F_{ST} (Wright, 1951) between kipukas with vcftools (Danecek et al., 2011).

Genetic diversity

We calculated the percent polymorphic sites as well as genetic diversity (observed heterozygosity (H_O), expected heterozygosity (H_E), nucleotide diversity (π) and F_{IS}) per population from variant and all positions using Stacks v2.2 (Rochette et al., 2019).

Results

Quality of RAD genotyping

A total of 537,724,472 (268,862,236 PE) reads were obtained following sequencing of 84 individuals. After using the Stacks 'clone_filter' unit to remove low quality reads, ambiguous barcodes, and overrepresented sequences, 405,957,342 reads remained. A catalog containing 7,341,938 pre-filtered loci was created for all individuals.

For each individual, an average number of 112,256.2 ± 64,544.8 unfiltered loci were assembled with an average read depth of 7.4 ± 0.3 per stack. Due to low read count, one individual was discarded. This resulted in 83 retained individuals, an average of 6.38 individuals per locality, with the number of reads per individual ranging from 127,600 to 3,773,676 (average per individual = 1,258,772.9). Filtering at 50% and 90% missing genotypes produced a final dataset containing 11,206 SNPs and 2,115 SNPs, respectively, distributed across the 83 individuals. This resulted in a mean depth per individual of 24.7 and 54.7 respectively and a mean missing per individual of 40.9% and 10.5%.

Population structure

The PCA did not reveal clustering based on the geographic location of the samples (Figure 2.2). One individual from kipuka 'l' (S67) was separated on PC1 (7.40% explained variation) from a large cluster of individuals and an individual from kipuka 'm' was separated from that larger cluster on PC2 (6.97% explained variation). Another individual from kipuka 'h' was separated on PC3 (6.69% explained variation). Using fineRADstructure, we visualized the patterns of haplotype similarity (Figure 2.3). The structure provided by the fineRADstructure analysis mostly corroborated the results of the PCA analysis in that there is little clustering based on geographic location. Individual S67, from kipuka 'l', has very low relatedness to all other individuals, which is also reflected in the PCA.

For TESS3 (Figure 2.4), the cross-validation criterion did not exhibit a clear plateau or a change in curvature without a wide-variance in error. This indicates that there is no support for a best value of K from the TESS3 analysis (Caye et al., 2016; François & Durand, 2017). Considering all K values with a biologically meaningful interpretation is recommended (Meirmans, 2015) due to the large degree of uncertainty in determining the optimal value of K (Evanno, Regnaut, & Goudet, 2005; Pritchard, Stephens, & Donnelly, 2000) and differing values of K may reflect different demographic processes. Up to seven clusters would be biologically plausible. Pairwise F_{ST} values range from -0.108 to 0.018 (Table 2.2).

Genetic diversity

No evidence of inbreeding in *M. celer* at CRMO was found and all of the genetic diversity metrics were generally similar across all sampled kipukas. As seen in Table 2.3, the percent of polymorphic sites per population ranged from 3.948 (kipuka 'k') to 26.5144 (kipuka 'h') with an average of 13.3426. With all positions, the observed heterozygosity at the population level ranged from 0.1256 (kipuka 'h') to 0.6076 (kipuka 'k') with an average of 0.2759; the expected heterozygosity for each population ranged from 0.1144 (kipuka 'h') to 0.4019 (kipuka 'k') with an average of 0.2225; the nucleotide diversity for each population ranged from 0.1198 (kipuka 'h') to 0.5485 (kipuka 'k') with an average of 0.2624; and the inbreeding coefficient in each population ranged from -0.0886 (kipuka 'k') to -0.0128 (kipuka 'm') with an average of -0.0264. When considering all nucleotide positions, the observed heterozygosity dropped to 0.0238 (kipuka 'd') and to 0.0351 (kipuka 'l'); the expected heterozygosity decreased to 0.0159 (kipuka 'k') and to 0.031 (kipuka 'l'); the nucleotide diversity ranged from 0.0217 (kipuka 'k') to 0.0335 (kipuka 'l'); and the inbreeding coefficient within each population ranged from −0.0055 (kipuka 'j') to 0.0008 (kipuka 'd').

Overall, when looking at variant sites only, kipuka 'h' had the lowest diversity (H_O: 0.1256; H_E: 0.1144; π: 0.1198) and kipuka 'k' had the highest diversity (H_O: 0.6076; H_E: 0.4019; π: 0.5485) (see Figure 2.1 and Table 2.3). However, sampling bias may have skewed these statistics given that these two populations had the minimum and maximum number of individuals (and percent polymorphic sites) per population with kipuka 'k' having 2 individuals and kipuka 'h' having 13 individuals.

Discussion

Contrary to what we expected, we find panmixia in this species of crab spider at CRMO. Three independent tests; PCA, fineRADstructure, and TESS3, all with differing assumptions, indicate little genetic structure in the population based on geographic location. Of the pairwise F_{ST} indices for *M. celer*, which represent each kipuka we sampled, all were <0.02, further suggesting panmixia. Even the most geographically distant populations within the lava flow matrix ("a" and "m"), which are

nearly 35 kms apart, had an F_{ST} value of ~0.003 (See Figure 2.1 and Table 2.2). This suggests that despite the geographic distance between these distant sampling sites separated by lava flows, gene flow is occurring between populations within the lava field or connectivity to outer regions surrounding the lava flows. Therefore, dispersal of these crab spiders is not currently negatively impacted by the fragmented structure of the landscape at CRMO. Additionally, although not tested here, the landscape at CRMO could allow for movement of *M. celer* from the area surrounding the monument into the lava and kipuka matrix as well as movement within the monument between the kipukas and lava flows.

The finding of panmixia in *M. celer* could reflect the occurrence of long dispersal distances in juvenile stages (spiderlings) annually that occur immediately following emergence (Gertsch, 1939; Schmalhofer, 2011). After emergence from their egg sacs, spiderlings engage in passive dispersal in a process known as ballooning and with the use of drag lines, sometimes use multiple ballooning events and/or draglines (Homann, 1934). Each spiderling releases a silk thread until the wind picks up the spider and carries it away (Edwards, 1986). This ability to disperse by ballooning allows spiders to travel by wind to different habitats. Additionally, spiders have the ability to reinitiate ballooning if a habitat is encountered that does not have suitable a "microhabitat" (Riechert & Gillespie, 1986). However, ballooning at CRMO could be costly as the chances of landing in unsuitable habitat is large.

M. celer females lay 145 eggs on average (Muniappan & Chada, 1970), therefore, the overall dispersal cost could be offset as there is a likelihood that some spiderlings would end up in a favorable habitat by dispersing and an increased access to new resources (Dean & Sterling, 1985; Simonneau, Courtial, & Pétillon, 2016). Furthermore, ballooning is also advantageous as it reduces the chance of cannibalism between brood mates (Sheldon et al., 2017; Weyman, 1993) and the dispersal of individuals away from related offspring reduces the negative genetic consequences of inbreeding. Given that these spiders have the ability to use ballooning to disperse long distances and high fecundity to offset any loss due to ballooning into an unfavorable habitat, the observed panmixia could be explained by high rates of gene flow observed across the sampled locations at CRMO.

High rates of gene flow have been observed in other arthropods. For example, a study of five Andean dung beetle species found panmixia (Linck, Celi, & Sheldon, 2020), which may be in part due to the common resource of dung that becomes a point of gene flow between different populations of each species when the dung is visited at the same point in time. At CRMO the kipukas may be acting as a common resource for *M. celer* as they contain abundant vegetation and common habitat for copulation, thereby facilitating gene flow between the kipukas leading to panmixia of the population

and also the possibility of dispersal post-copulation to avoid cannibalism. However, a using a common resource doesn't necessarily lead to panmixia of a species. In a study of two pine-feeding butterflies (Halbritter, Storer, Kawahara, & Daniels, 2019), although both species rely on pine species for larval feeding, one species was found to be panmictic while the other showed strong evidence for population structure. The availability of certain vegetation may restrict movement in the adults of these species, more so in one species showing population structure (*Neophasia terlooii*) than the panmictic species (*Neophasia menapia*) (Halbritter et al., 2019). The restriction of movement of a species is dependent on a combination of dispersal ability and resource use and the characteristic(s) of their habitat matrix.

Invertebrates that move by passive dispersal and live in a fragmented habitat are at a disadvantage as they may end up in a poor habitat. Being surrounded by a mostly inhospitable matrix makes movement between patches risky. Additionally, movement between some fragment patches may be diminished or nonexistent due to distance. This reduced movement could lead to decreases in the effective population size of each fragment and ultimately impact the stability of each population into the future. This could be particularly important in an environment with abiotic stresses that could be exacerbated with climate change (e.g., temperature fluctuations worsening in the future).

Rates of gene flow in *M. celer* may have important implications for community assembly, which can be affected by an organism's dispersal ability and strategy during various life stages. The lava flows at CRMO could act as a model for anthropogenic fragmentation caused by farming, urban sprawl, and other anthropogenic effects. In this case, we do not see population subdivision in *M. celer* based on the natural fragmentation at CRMO. This impact is particularly interesting that these naturally fragmented populations have been separated by a chronologically well-defined geologic landscape consisting of vegetated islands separated by lava flows. If populations are sampled after an eruptive period, we might expect strong population structure and more gene flow in subsequent generations as assembly of the community occurs and movement of these *M. celer* individuals is less restricted. It is unknown whether the kipukas are continuously occupied or re-colonized, or if a mixture of both occurs after an eruptive period. However, perhaps we missed the snapshot in time of the beginning stages of the assembly of this community if kipukas are recolonized post eruption that may show development of strong population structure as a result of the last eruptive period 2 kya and sampled these kipukas at a point in community assembly where panmixia in *M. celer* in CRMO has already taken place. Another scenario, if kipukas are continuously colonized by *M. celer* there could be a pattern of cycles present of panmixia then strong population structure developing post eruption and then decreasing through time back to panmixia, until the next eruptive period restricts movement and

potentially decreases population size. Not all fragmentation, natural or anthropogenic, may cause a reduction in gene flow and increase in population structure, however, as this may be dependent upon a species ability to disperse at different life stages, changes in resource availability, and length of time since fragmentation.

Table 2.1 Data per specimen including the population, sample name, number of legs removed for DNA extraction, and total yield of DNA collected (µg).

Population ID	Specimen	Sample Name (see Figs. **2.**3 and **2.**4)	# Legs used for DNA extraction	Amount of DNA extracted (µg)
a	CRMO_2017_2_10	S68	2	1689.6
a	CRMO_2017_2_17	S69	2	303.6
a	CRMO_2017_2_24	S70	2	304.48
a	CRMO_2017_2_28	S71	2	251.68
a	CRMO_2017_2_29	S72	2	294.8
a	CRMO_2017_2_30	S73	2	362.56
b	CRMO_2017_3_06	S34	2	2622.4
b	CRMO_2017_3_08	S35	2	265.76
b	CRMO_2017_3_15	S36	2	994.4
b	CRMO_2017_3_16	S37	2	412.72
b	CRMO_2017_3_18	S38	2	400.4
b	CRMO_2017_3_21	S39	2	400.4
c	CRMO_2017_8_06	S56	2	466.4
c	CRMO_2017_8_07	S57	2	655.6
c	CRMO_2017_8_09	S58	2	677.6
c	CRMO_2017_8_15	S59	2	664.4
c	CRMO_2017_8_16	S60	2	457.6
c	CRMO_2017_8_20	S61	2	448.8
c	CRMO_2017_8_11	S74	2	388.08
c	CRMO_2017_8_13	S75	2	528
d	CRMO_2017_13_18	S04	4	326.48
d	CRMO_2017_13_19	S05	4	1918.4
e	CRMO_2017_14_09	S40	4	1337.6
e	CRMO_2017_14_11	S41	4	519.2
e	CRMO_2017_14_16	S42	4	492.8
e	CRMO_2017_14_17	S43	4	858
e	CRMO_2017_14_18	S44	6	624.8
e	CRMO_2017_14_22	S45	4	388.96
f	CRMO_2017_15_20	S01	5	2481.6
f	CRMO_2017_15_22	S02	5	2094.4
f	CRMO_2017_15_23	S03	3	924
f	CRMO_2017_15_09	S76	4	1117.6
f	CRMO_2017_15_13	S77	4	915.2
f	CRMO_2017_15_16	S78	4	717.2
g	CRMO_2017_18_05	S46	4	519.2
g	CRMO_2017_18_09	S47	4	484
g	CRMO_2017_18_14	S48	4	1029.6
g	CRMO_2017_18_15	S49	4	717.2
g	CRMO_2017_18_19	S50	4	1619.2
g	CRMO_2017_18_21	S51	4	1020.8
h	CRMO_2017_24_12	S09	4	546.1
h	CRMO_2017_24_21	S10	3	1478.4
h	CRMO_2017_24_22	S11	4	968
h	CRMO_2017_24_31	S12	4	915.2
h	CRMO_2017_24_16	S28	4	1337.6
h	CRMO_2017_24_18	S29	4	941.6
h	CRMO_2017_24_20	S30	3	554.4
h	CRMO_2017_24_23	S31	4	743.6
h	CRMO_2017_24_24	S32	6	849.2
h	CRMO_2017_24_30	S33	4	1223.2
h	CRMO_2017_24_14	S52	5	470.8
h	CRMO_2017_24_15	S53	4	514.8
h	CRMO_2017_24_17	S54	4	770

i	CRMO_2017_620_16	S23	4	696.6
i	CRMO_2017_620_21	S24	3	655.6
i	CRMO_2017_620_23	S25	3	341.44
i	CRMO_2017_620_26	S55	4	594
j	CRMO_2017_621_18	S13	4	851.4
j	CRMO_2017_621_20	S14	4	941.6
j	CRMO_2017_621_27	S15	4	1460.8
j	CRMO_2017_621_34	S16	5	1214.4
j	CRMO_2017_621_17	S62	4	853.6
j	CRMO_2017_621_25	S63	4	849.2
j	CRMO_2017_621_28	S64	4	717.2
j	CRMO_2017_621_23	S81	4	598.4
j	CRMO_2017_621_24	S82	3	941.6
j	CRMO_2017_621_30	S83	4	853.6
k	CRMO_2017_622_13	S26	6	712.8
k	CRMO_2017_622_18	S27	4	1117.6
l	CRMO_2017_KP1_14	S06	4	1170.4
l	CRMO_2017_KP1_17	S07	3	853.6
l	CRMO_2017_KP1_30	S08	4	602.8
l	CRMO_2017_KP1_15	S65	4	440
l	CRMO_2017_KP1_19	S66	4	417.12
l	CRMO_2017_KP1_20	S67	4	1557.6
l	CRMO_2017_KP1_13	S79	5	1636.8
l	CRMO_2017_KP1_21		4	1434.4
l	CRMO_2017_KP1_23	S80	4	646.8
m	CRMO_2017_KP2_12	S17	4	1830.4
m	CRMO_2017_KP2_14	S18	4	968
m	CRMO_2017_KP2_15	S19	4	721.6
m	CRMO_2017_KP2_19	S20	5	624.8
m	CRMO_2017_KP2_20	S21	4	756.8

Table 2.2 Pairwise *F*st values, above diagonal is Weir and Cockerham weighted *F*st estimate and below diagonal is Weir and Cockerham mean *F*st estimate (Weir & Cockerham, 1984).

	a	b	c	d	e	f	g	h	i	j	k	l	m
a	-	0.010901	-0.0016182	-0.0024845	0.017059	0.028782	0.0067101	-0.01635	-0.013372	0.0028037	-0.022422	-0.0024009	0.019504
b	0.001976	-	-0.0039227	-0.038199	-0.004336	-0.0047574	-0.0082659	0.00099454	-0.018282	-0.0059172	-0.072086	-0.018708	-0.0099502
c	-0.0030597	0.00089337	-	-0.03005	0.0066027	-0.0098087	-0.0042609	-0.0067154	-0.0090427	-0.002595	-0.044429	-0.0055936	-0.012417
d	-0.030193	-0.054415	-0.067911	-	-0.057858	0.031964	0.0025208	-0.026807	0.0034431	-0.036199	0	-0.068869	-0.056869
e	0.0062548	-0.0022416	0.002866	-0.071178	-	-0.011662	-0.0014984	0.005198	-0.016272	0.0076395	-0.016435	0.015806	0.0047035
f	0.0076116	0.00035046	-0.0098882	0.01825	-0.0047927	-	-0.0035471	0.0042487	0.010334	-0.0050923	0.0052541	-0.017902	-0.0063636
g	0.0019588	-0.0036809	-0.0034524	-0.024391	4.23E-05	-0.0018043	-	-0.0073897	0.0062318	0.012692	-0.0089912	-0.012578	0.013917
h	-0.01966	-0.0017846	-0.0047064	-0.076986	0.0030598	-0.013206	-0.0082133	-	-0.019777	0.0024563	-0.083346	0.011879	0.0080894
i	-0.0090462	-0.015562	-0.011029	-0.014106	-0.017705	0.0083618	-0.0037285	-0.022423	-	-0.022649	0.0078713	-0.011987	0.00098692
j	-0.0034148	-0.0018504	-0.0003195	-0.072265	0.0083207	-0.0069134	-0.0015165	-8.83E-05	-0.01879	-	-0.060172	0.019102	-0.0007342
k	-0.051277	-0.084047	-0.07099	-0.0055096	-0.048728	-0.013906	-0.044116	-0.10759	-0.0059684	-0.09904	-	-0.047745	-0.051763
l	-0.0069506	-0.010984	-0.0010192	-0.086576	0.003738	-0.016374	-0.0078944	0.0088539	-0.024182	0.0081005	-0.089633	-	-0.0097992
m	0.0028481	-0.0042811	-0.0058537	-0.072572	0.0022654	-0.0026175	0.0047316	0.0011696	-0.0090063	0.0017137	-0.075371	-0.0063976	-

Table 2.3 The statistical values of genetic diversity per population from variant and all positions data (H_O, observed heterozygosity; H_E expected heterozygosity; π, nucleotide diversity; F_{IS}, inbreeding coefficient).

Population	Latitude	Longitude	Number of Individuals	Polymorphic Loci (%)	H_O		H_E		π		F_{IS}	
					Variant Positions	All Positions	Variant Positions	All Positions	Variant Positions	All Positions	Variant Positions	All Positions
a	43.55636	-113.35151	6	12.2145	0.2625	0.0321	0.2207	0.0270	0.2452	0.0300	-0.0345	-0.0042
b	43.5566	-113.34678	6	13.1579	0.2360	0.0311	0.2027	0.0267	0.2248	0.0296	-0.0237	-0.0031
c	43.49886	-113.36283	8	17.2294	0.1849	0.0319	0.1643	0.0283	0.1771	0.0305	-0.0224	-0.0039
d	43.46912	-113.35586	2	4.2628	0.5588	0.0238	0.3927	0.0167	0.5471	0.0233	-0.0177	-0.0008
e	43.4699	-113.35419	6	14.2503	0.2278	0.0325	0.1961	0.0279	0.2169	0.0309	-0.0245	-0.0035
f	43.44107	-113.34049	6	10.3277	0.2393	0.0247	0.2096	0.0217	0.2329	0.0241	-0.0131	-0.0014
g	43.43863	-113.34184	6	12.0655	0.2432	0.0293	0.2110	0.0255	0.2324	0.0280	-0.0234	-0.0028
h	43.28466	-113.29964	13	26.5144	0.1256	0.0333	0.1144	0.0303	0.1198	0.0318	-0.0142	-0.0038
i	43.33333	-113.32037	4	8.2920	0.3264	0.0271	0.2737	0.0227	0.3190	0.0265	-0.0175	-0.0015
j	43.3317	-113.32077	10	18.0238	0.1637	0.0295	0.1437	0.0259	0.1524	0.0275	-0.0303	-0.0055
k	43.33321	-113.32108	2	3.9480	0.6076	0.0240	0.4019	0.0159	0.5485	0.0217	-0.0886	-0.0035
l	43.43129	-113.30869	9	18.8183	0.1865	0.0351	0.1649	0.0310	0.1778	0.0335	-0.0206	-0.0039
m	43.3388	-113.3086	6	14.3496	0.2242	0.0322	0.1970	0.0283	0.2177	0.0312	-0.0128	-0.0018

Figure 2.1 Map of Craters of the Moon National Monument and Preserve, Idaho, USA. Map inlays showing 13 kipuka locations where *Mecaphesa celer* spider collections occurred, each population denoted with a letter.

Figure 2.2 Principal Components Analysis (PCA) between populations (refer to Figure 2.1) for data with loci genotyped in 50% of all individuals (A & B) and genotyped in 90% of all individuals. A) and C) Principal components analysis with the first two axes plotted; B) and D) PCA of axis 2 and 3.

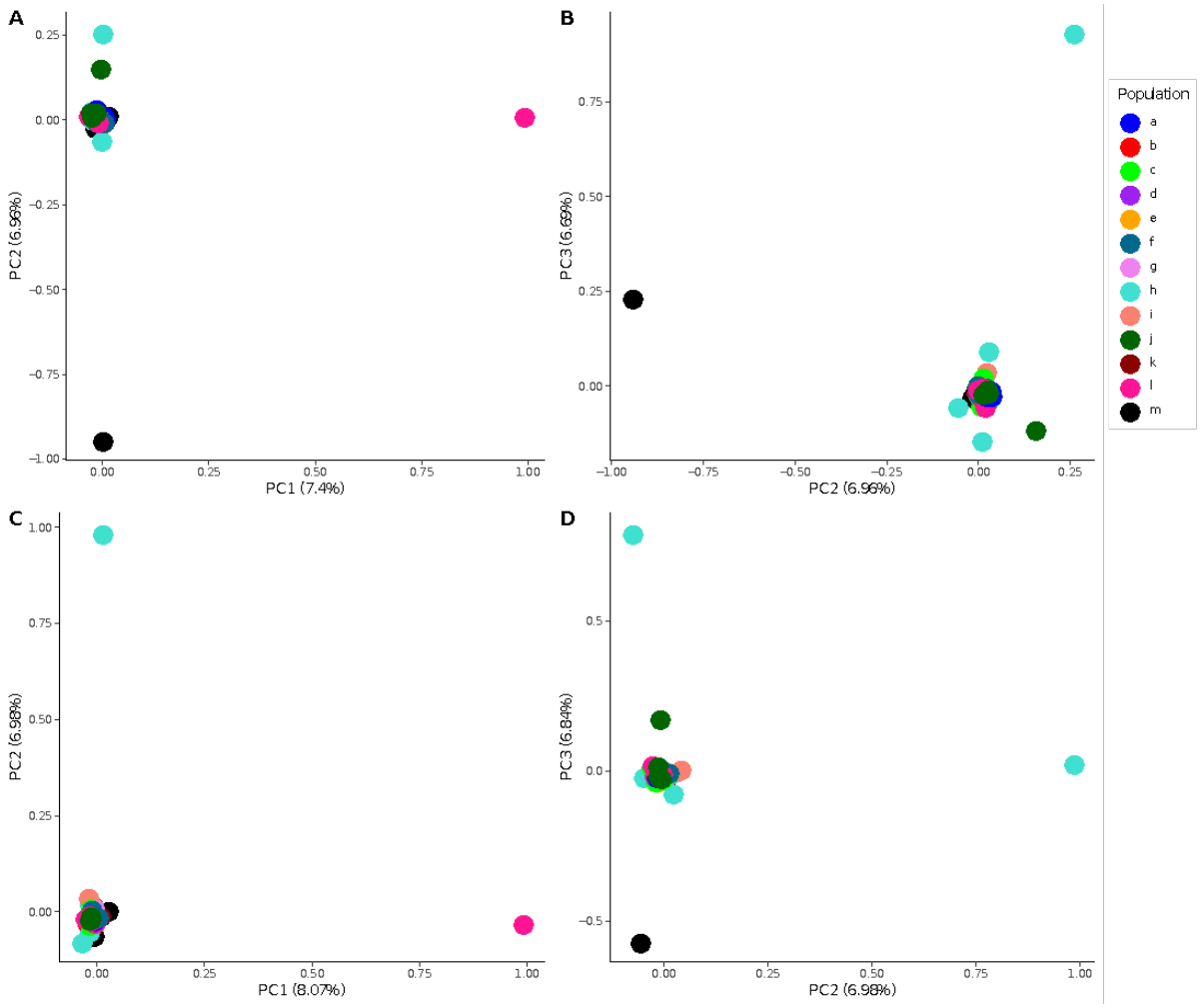


Figure 2.3 The co-ancestry matrix from the FineRADstructure analysis based on the dataset of 2,115 SNPs show the patterns of haplotype similarity. Colors indicate degree of relatedness between individuals, with yellow being low relatedness and black indicating high relatedness. Sampling sites do not show visible structuring.

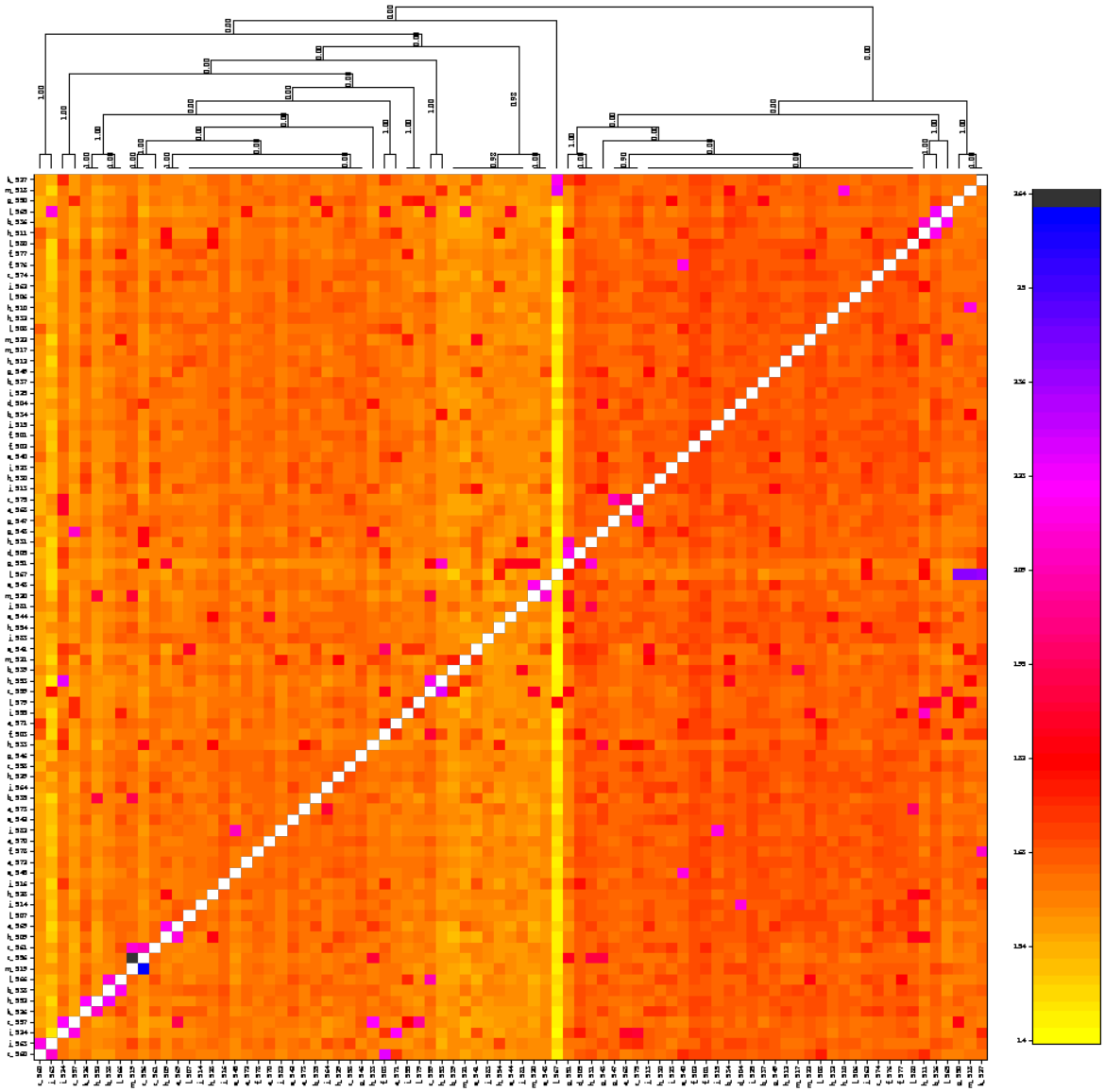
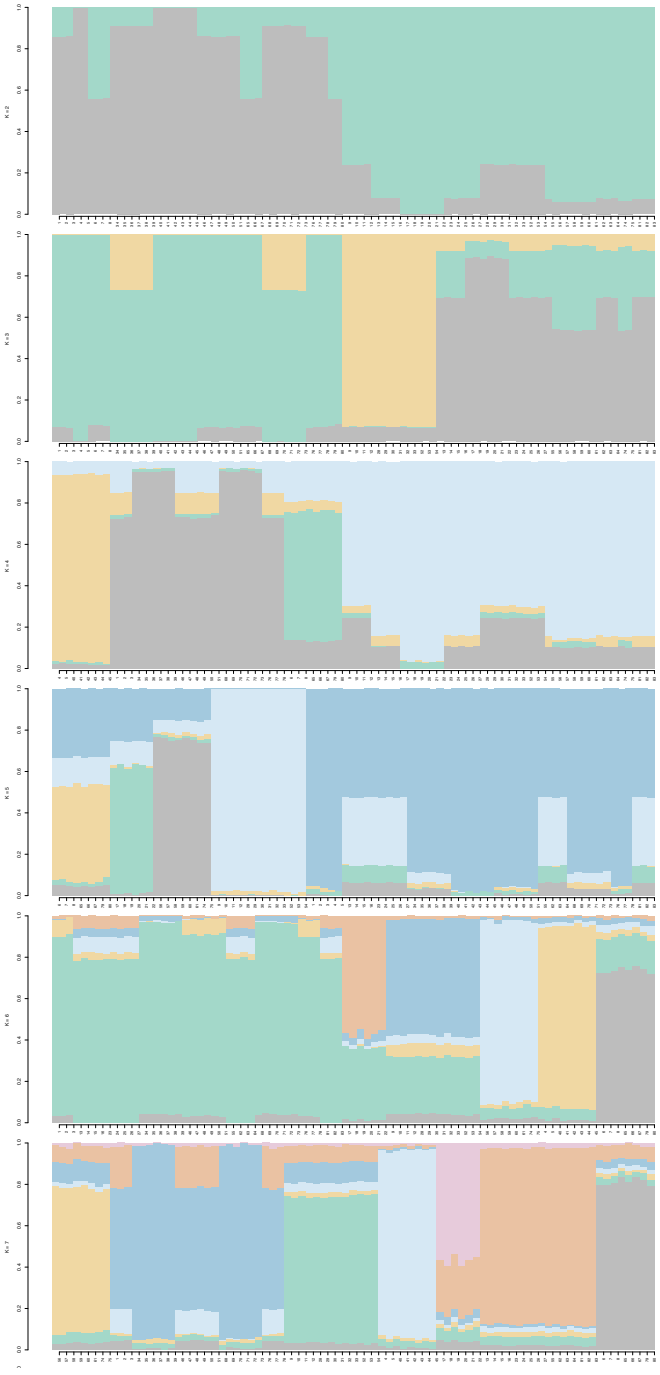


Figure 2.4 Individual ancestry at K = 2 through K = 7 as determined from TESS3 analysis. Each bar plot represents a unique individual and the y-axis represents the proportional membership of each individual to a given cluster.



Chapter 3: Building an Engaged STEM Community Through a Science Outreach Series

Introduction

Science literacy, engagement, trust, and communication have never been more important in our society due to the increased politicization of science, mistrust in science, and the spread of disinformation (Hmielowski, Feldman, Myers, Leiserowitz, & Maibach, 2014; Varner, 2014). All parties involved in outreach programs (i.e., the practitioners of science and the community) have much to gain by shared experiences, dialogue, and collaboration to foster mutual trust and achieve a shared understanding of relevant science (Varner, 2014). Researchers also are members of the communities in which they live and can be valuable STEM (Science Technology Engineering Mathematics) role models by engaging with and being active members of the community in a variety of ways. An important responsibility of science and scientific work is to be of service to the public and this engagement can be accomplished in a variety of ways, such as through volunteerism and program leadership. However, as exposure and access to current scientific research varies so does the general science knowledge of the attendees at outreach events. Trust in science has been challenged over the last few decades in the United States, and in particular, trust has decreased for those that identify as conservatives or Republicans (Gauchat, 2012; Hmielowski et al., 2014).

A new notion of science literacy, as a lifelong participation in science, as opposed to a primary focus on children, expands previous views to include activities in society by citizens of all ages (Liu, 2009). Scientific literacy is a necessary facet of a functional society, however, opportunities for engagement with science and science communication have often been inaccessible to a wide audience (Kopke, Black, & Dozier, 2019). Therefore, there is a desperate need to provide opportunities for authentic connections and collaboration among community members to learn, discuss, and engage with STEM content. Creating or finding such opportunities can be difficult when there are actual and perceived barriers that can lead to inaccessibility (Johnson, Ecklund, & Lincoln, 2014; Kopke et al., 2019; Xie, Fang, & Shauman, 2015). Barriers may include overall inaccessibility due to a gap between the "University" community and the greater community, (e.g., "town and gown," Lazzeroni & Piccaluga, 2015) and perception of elitism expressed as the Ivory Tower (Baron, 2010). Public communication about science, if favoring elite audiences, can also widen the divides (Nisbet & Scheufele, 2009). To address information gaps at the local level funding could be allocated to "science information hubs" by, for example, partnering with universities (Nisbet & Scheufele, 2009).

Time constraints also exist for researchers with diverse responsibilities and research commitments, and awards for outreach activities and therefore involvement varies by research area, gender, institution, rank, and year (Ecklund, James, & Lincoln, 2012; Johnson et al., 2014). Although focused on biologists and physicists at research universities in the United States, differences were identified in regards to overall views and importance of science outreach and who engages in science outreach activities (Ecklund et al., 2012). The need to foster scientific literacy and engagement, demonstrate role models in the STEM fields, and provide exposure of current scientific research in accessible ways are especially important, particularly in regions of the country where STEM education for children ranks low against the national average. For example, in the 2021 Kids Count Data Book which outlines state trends, Idaho is below the national average for math proficiency in eighth graders (The Annie E. Casey Foundation, 2021). Idaho also has the lowest per-student education funding of all fifty states and the District of Columbia (National Education Association, 2021). Additionally, the added pressure for researchers to specify the broader impacts of their work has increased since the National Science Foundation (NSF) incorporated "broader impacts" as a mandatory requirement and integral component for research proposals as with many other funding agencies and grant applications (Clark et al., 2016; Ecklund et al., 2012). Practitioners of science are increasingly pushed to engage more and in creative ways with members of the community.

The University of Idaho is a public land grant university located in northern Idaho and has over 10,000 students (undergraduate and postgraduate) on its Moscow campus. Approximately six miles away, across the state border with over 20,000 students is Washington State University in Pullman, Washington. Combined, nearly 55,000 people call the towns of Moscow, ID, and Pullman, WA, home. The region encompassing the towns of Moscow and Pullman, along with the surrounding smaller communities, is known as the Palouse. The Universities are a large presence in these communities yet at times the facets of town and University do not interchange.

Academics can often be isolated from their local community and yet are expected to fulfill requirements like conducting broader impact activities by sharing their science and being engaged in STEM efforts for grant applications, funding requests, and to obtain job promotions. Researchers are often required to complete similar requirements to prepare themselves for future positions with a competitive grant pool and job market. In addition, government and nonprofit agencies benefit from sharing their work with the public. Outreach activities can increase exposure, and help in finding volunteers, securing funding, and with identifying and fostering future collaborations. Scientists have a responsibility to effectively communicate research and general scientific concepts in a variety of settings as they are themselves members of communities (Clark et al., 2016). A shift away from the

one-way transmission model of science communication is occurring, and instead the focus should include opportunities that offer a variety of stakeholders a chance to participate in dialogue and allow for the exchange of views about science (Nisbet & Scheufele, 2009). Finding such opportunities can be hard and engagement by researchers differs by research domain and by rank (Jensen, Rouquier, Kreimer, & Croissant, 2008). In the present article, a program is highlighted that filled a need in the Palouse community by increasing opportunities for communication and collaboration through science education and outreach.

Researchers often seek out attainable and low-risk opportunities to engage with the public, volunteer with youth STEM programs, discuss their research, and gain valuable presentation and speaking skills. In May of 2014, the Palouse-Clearwater Environmental Institute (PCEI) initially had a one-time event coordinated by an employee to fill this need. This first event allowed four graduate student speakers the opportunity to disseminate their research and practice crucial public speaking skills at a local business to colleagues and members of the public with whom they might not normally have interacted. The program morphed into a monthly event series that the author coordinated starting in November of 2015 to fulfill a need for more such opportunities in the region and to strengthen and expand the many facets of an already vibrant and active community. Here I detail the structure and content of the four consecutive years of this program series.

Science After Hours

PCEI is based in Moscow, Idaho, USA and has been connecting people, place, and community since 1986. The mission of PCEI is to increase citizen involvement in decisions that affect the region's environment. PCEI's goals include encouraging sustainable living, providing experiential learning, and offering opportunities for serving in the community, while actively protecting and restoring our natural resources. PCEI is 501c3 nonprofit organization with funding primarily from federal, state, and local grants, contracts, and contributions from foundations, donors, and members. A variety of programs and volunteer and educational opportunities are offered for different age levels. One series, Science After Hours, was created as a primarily adult-focused informal educational program that used the tagline "Learn about all the things you never knew you wanted to know!".

Science After Hours sought to build an engaged and active STEM community in Moscow and the local area by connecting the community, local businesses, and researchers through a science outreach education program targeting adults, including students (high school, undergraduate, and graduate) and members from the greater community.

The speakers for each event were selected and invited to present from individuals who volunteered to present or by referrals from community members or colleagues. The series coordinator would organize these individual volunteers/referrals and coordinate speakers for an evening based around a central theme and availability of the researchers. Alternatively, an entire research group (e.g., lab) might volunteer to present, such that all speakers for that event were members of the same research group. The hosting mechanism was also coordinated by the series coordinator and local businesses were approached to host or would express interest in hosting a Science After Hours event. These events were beneficial to the local businesses as they brought in new individuals who may become patrons, oftentimes the attendees purchased goods (i.e., food, drink, items), and allowed the local business an avenue to support the local nonprofit organization and science and research in the local community.

The Science After Hours series occurred monthly with different speakers, and the business venues that hosted the event rotated. The events were free to attend, and the number of attendees varied from event to event depending on the host capacity of the business and theme of the evening (e.g., generally 20 – 50 attendees). The attendees of these events overlapped in many ways. On the average night attendees were members of the public such as high school students, teachers, and friends and family of the presenters. Additional attendees included members of the research community such as undergraduate students, graduate students, postdoctoral researchers, and faculty.

Each event had a theme; an example of such an event was an evening that focused on conservation efforts with the title and theme “Inside Out: Conservation, Wings, & Slimy Things.” Alternatively, when a “takeover” event occurred, where all presenters were from a single research group, the principal investigator of the research group was included in the title, for example the “Sullivan Lab Takeover: The Pacific Northwest & Beyond” event. Generally, three to four researchers gave presentations on their work for about 15-20 minutes each with question-and-answer time following every presentation. An intermission time occurred during the event to facilitate additional dialogue between researchers and attendees as well as time for attendees to support the local host business(es).

The goals of Science After Hours were multifaceted and above all strived to interconnect the members of the community (i.e., researchers and attendees) and local businesses to build a strong STEM community network. The specific goals were to (1) strengthen the community through dialogue and collaboration, (2) foster STEM role models that engage in community programs, (3) provide an avenue for researchers to gain public speaking and presentation skills, (4) increase scientific literacy and STEM engagement in the community, and (5) provide additional advertising and support to local business hosts. The logistics of the program (i.e., scheduling venues, recruiting

researchers, advertisement of events) were primarily coordinated by the author while a PCEI intern who was also a PhD student at the University of Idaho.

In addition to providing attendees with the opportunity to learn more about current science done by the researchers, the evenings allowed for reciprocal interactions, not only a one-way dissemination of knowledge. Attendees were invited to ask questions and offer insights, and discussions occurred during the time between presentations and continued after the program ended for the evening.

This program benefitted the overall community in many ways, including collaborations between PCEI, science practitioners, community organizations, and local businesses. Some past presenters then volunteered with local nonprofits or for future PCEI events. Some collaborated with PCEI on outreach events for K-12 students focused on their research. The presenters had an opportunity to gain experience communicating their science to a broader audience and address questions from the public about their work. Community organizations that shared their work during a Science After Hours event benefited from increased exposure, access to volunteers, and potential funding or collaboration opportunities. The local business hosts benefitted by having additional people in their doors, potentially spending money, by hosting future STEM events organized by attendees and/or presenters, and by showing support for science research and communication on the Palouse.

As the presenters could also be parents, family members, teachers, coaches, volunteers, neighbors, etc., they interact with many K-12 children in the region, which provides opportunities to be STEM role models. By providing an opportunity for researchers to share their work and increase exposure to current science for four consecutive years, a STEM community was strengthened. New collaborations and opportunities for an increased awareness of ways to support STEM on the Palouse were made between presenters, local businesses, nonprofit organizations, and community members.

Impact of Science After Hours

The impact of Science After Hours on the Moscow/Pullman area included the opportunities provided for researchers to present their work in an informal setting, allowed community members to hear about current science research conducted by other members of their community, and increased exposure of local businesses. Between November 2015 and May 2019, there were a total of 30 events at 13 different host business venues in Moscow, ID (Table 3.1). These events supported 105 presentations by 96 different presenters including undergraduate students, graduate students, postdoctoral researchers, faculty, and others from diverse disciplines (Figure 3.1 and Table 3.2).

As this was a monthly informal series where presenters and locations changed, no formal feedback was collected from attendees. Two pieces of information that the series coordinator did collect from

the audience at each event (by raise of hand) were whether the audience were attending a Science After Hours event for the first time, and whether it was their first experience visiting the local business hosting the event. Every month there would be attendees who indicated that it was their first attendance of a Science After Hours event. Beyond that there were anywhere from several to >10 people raising their hands indicating it was their first time in the hosting local business. The intention with the second question was for the local business hosts to see the number of potential new patrons, coming into their business because of the Science After Hours event.

Further collaboration occurred between the local businesses and PCEI. For example, at times as the series coordinator worked with a local brewery and/or winery to coordinate serving refreshments during the event with permission from the host venue. The businesses in this scenario both benefited that evening and when collaborations occurred in future events. Also, some local business venues would further show their support by advertising that portions of their profit during the event, or the purchase of specific items, would be donated to PCEI's education program. The program was described in a blog post through a consortium that reaches scientists across the United States and included quotes from previous presenters, a local business host, and an attendee (Peterson, 2018).

Replication of a similar outreach program

Opportunities for scientists to interact with the public are lacking and a recognized need. Here we have described an example of a science outreach series initiated by an individual through a local non-profit that we believe can be reproduced and scaled for different settings to create and foster an engaged STEM community. A similar program could be led by or provide speakers from universities and colleges, extension offices, nonprofits, graduate student organizations, clubs, conservation districts, tribal offices, teachers, and program managers (see Table 3.3). As each community does not have local access to presenters through universities or organizations that can discuss current research, the increased use of teleconferencing technologies allows for even more opportunities for engagement that bridge time and space.

Positions also exist in some capacities at universities to help connect researchers with outreach opportunities (e.g., public outreach officer or education outreach coordinators). This program was different in that it was volunteer led by an individual with connections in the community, with local businesses, and within the university. Additionally, the series was hosted by a nonprofit organization. On average the series coordinator spent between 6 - 10 hours a month on coordination efforts which included logistics with presenters, the local business host, advertising, and the evening itself which included set up and take down of event materials. This time commitment was larger in the beginning when a word-of-mouth network and previous presenters did not exist. Little to no cost was involved

for the program, although a few years into the successful series PCEI applied for and was awarded funding via a community grant to purchase a new projection screen and projector to use for the series in 2017. Local funding options may be available to support such work or materials used, which could include a projector, projection screen, collapsible table for electronics, printing for advertising (if posting physical flyers and not advertising solely online). The computer used for this program was the property of PCEI, so depending on availability, a computer may also be a programmatic expense.

The Science After Hours program series unfortunately went on hiatus due to a combination of factors including the PCEI intern moving for an academic position out of the region, limited existing personnel capacity at PCEI to absorb the responsibilities of the coordinator role for the series, and the COVID-19 pandemic diminishing the possibilities for face-to-face interactions at local business host venues. For the successful continuation of a program like Science After Hours, ensuring a strong connection is necessary among the hosting organization (e.g., PCEI or similar nonprofit), researchers in the area, and local businesses is necessary. Securing a funded position for a coordinator could also help with retention. If a coordinator does need to step down, securing a replacement is essential for program continuance. However, unforeseen circumstances, like a continued global pandemic, will derail opportunities no matter the amount of coordination. It is the author's sincerest hope that the Science After Hours series will return to the Palouse and that similar programs can be implemented around the country to increase science engagement and build strong STEM communities.

Summary

Researchers today need to dedicate much of their time to performing research and must also find ways to contribute to public good (e.g., through broader impacts), whether inherently or to be competitive in the job market, to secure funds, or attain promotions. Science After Hours provided a low-risk opportunity with a relatively small time commitment opportunity for presenters to be able to share their work. For the series coordinator, the initial time investment decreased once a network of researchers who had participated or attended a Science After Hours event referred other individuals to present. Interested individuals then began contacting the coordinator and the events then became booked months in advance. The positive benefits from the Science After Hours program were far reaching and helped to build and strengthen an engaged and supportive STEM community. This program series was mutually beneficial as researchers gained experience speaking with the public to support the broader impacts of their work and local businesses benefited by increased advertising and public awareness of their business within the local community.

Table 3.1 List of local business venues that hosted a Science After Hours event (n=30) and how many individual programs were held at that location between November 2015 and May 2019 (n=13).

Business	Website	Number of Science After Hours events hosted
Camas Prairie Winery (now located in Bovill, ID)	https://www.camasprairiewinery.com	2
White Pine Outfitters Gear Exchange and Fly Shop	https://www.whitepine-outfitters.com	3
Humble Burger	https://www.humbleburger.com	1
Bookpeople of Moscow	https://www.bookpeopleofmoscow.com	4
Lodgepole North American Kitchen	https://www.lodgepolerestaurant.com	2
One World Café	http://www.owc-moscow.com	1
Last Frontier Pizza (now closed)		3
Moscow Food Co-Op	https://www.moscowfood.coop	1
Wild at Art	https://www.moscowwildatart.com	2
Hunga Dunga Brewing Co.	http://www.hungadungabrewing.com	6
Moscow Brewing Company	https://moscowbrewing.com/index.html	3
Mikey's Gyros	https://mikeysgyros.com	2

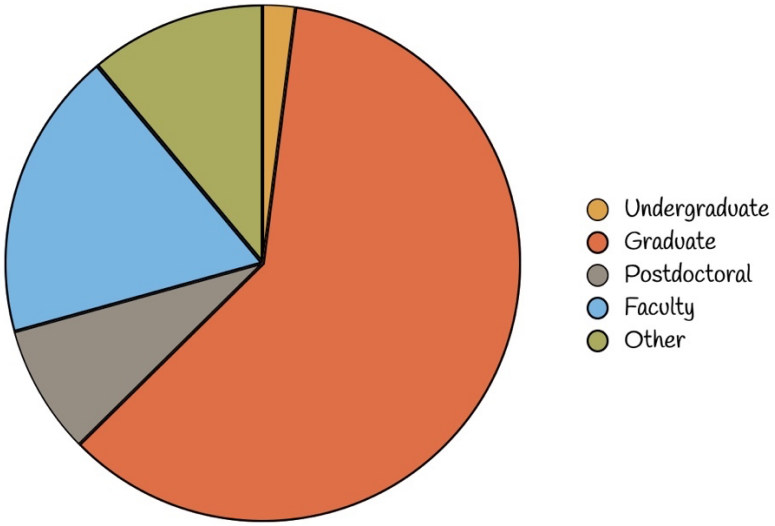
Table 3.2 Number of individual presenters (n=96) from each category (researcher rank or other) and the percent of total presentations given by presenters in each category.

Rank	Number of presenters	Percent of total presentations (%)
Undergraduate	2	2
Graduate student (included M.S. or PhD)	58	61
Postdoctoral researchers	8	8
Faculty	17	18
Other	11	11

Table 3.3 A broad example of organizations and agencies to contact that may be able to either help coordinate a similar one-time program event and/or program series. These organizations could provide a starting network of researchers to contact as possible presenters.

Organization		Website examples
State Soil and Water Conservation Districts or other State Government Offices	There are nearly 3,000 conservation districts, almost one located in every county in the United States.	https://www.nacdnet.org/about-nacd/about-districts/
Tribal Science Council	The TSC is made up of Agency Representatives from each major EPA (Environmental Protection Agency) region.	https://www.epa.gov/healthresearch/tribal-science-council
Extension Offices (local county or university)	Each county within the United States has an Extension office, which is staffed with extension agents who work closely with university-based extension specialists.	http://npic.orst.edu/pest/countyext.htm
Graduate student organizations or associations	The National Association of Graduate Professional Students has five regions in the United States.	http://nagps.org/regions/ Alternatively contacting your local university to inquire if there is a graduate-professional student organization or association.
Nonprofits: education or environmental focused		Search for your local area or region.
United States Department of Agriculture Agricultural Resource Service	The USDA ARS is divided into five geographic areas across the United States.	https://www.ars.usda.gov/people-locations/find-a-location/
North American Native Plant Societies	There is a native plant society located in every state and there are also societies across Canada.	https://nanps.org/native-plant-societies/

Figure 3.1 Proportion of presenters at the Science After Hours programs (n=96 presenters) from each category for the events (n=30) that occurred from November 2015 to May 2019. Presenters included in the “Other” category included, for example, those affiliated with a nonprofit, business, school, or state organization.



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