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CAPSTONE PROJECT

by

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CAPSTONE PROJECT

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CHAPTER 1. LITERATURE REVIEW

Atoms for Peace: Including Nuclear Power as a Renewable Energy Source

Reducing the effects of anthropogenic climate change, which brings strengthening tropical storms, rising sea levels and changing rainfall patterns, is a major challenge in the 21st century (Mann, 2021). There are numerous low carbon alternatives to fossil fuels, often grouped under the umbrella term renewable, and frequently include technologies such as hydropower, geothermal, wind and solar (Pehl et al., 2016). However, nuclear power is explicitly left out of the renewable energy arsenal by many, despite having the lowest total carbon footprint of any energy source, as there are justifiable safety concerns and conflation with nuclear weapons production (Acton & Hibbs, 2014; Ritchie, 2020). Yet, splitting uranium atoms is so energy dense and the fuel so easily recyclable, that it can provide ample quantities of electricity for billions of years, sustainably powering civilization with low carbon energy (Touran, 2020). Nuclear power should be considered a renewable source of energy due to its low carbon intensity, consistent power generation, relative safety and low material intensity.

Comparing the Carbon Intensity of Energy Sources

Modern societies use huge quantities of energy, and this is only predicted to grow with an increasingly digitized world (Saidi & Omniri, 2020). To put the scale of energy use into context, the U.S. currently uses 4,146 terawatt hours (tWh) per year with the production composed of 33% coal, 33% natural gas, 20% nuclear, 6% hydropower, 4.7% wind, 1.6% biomass, 1.0% petroleum, 0.6% solar and 0.4% geothermal (Electrified, 2019). However, there are environmental impacts from all the energy technologies powering homes and businesses.

Examining the deleterious impacts of electricity sources by units of energy is essential in determining the long-term viability of the technology. Ritchie (2020) found that brown coal had the highest human deaths from accidents and air pollution per terawatt hour at 32.72 tWh while solar had the fewest with only 0.02 tWh. Nuclear and wind were also minuscule compared to fossil fuels with deaths per terawatt hour at 0.07 tWh and 0.04 tWh respectively (Ritchie, 2020). The energy source with the highest tons of CO_2-equivalent produced from each energy source per 1 gigawatt hour (gWh) was coal with a stark 820 tons CO_2, and for comparison, oil produced 720 tons, natural gas 420 tons, biomass 78-230 tons, hydropower 34 tons, nuclear 3 tons, wind 4 tons, and solar 5 tons in turn (Ritchie, 2020). Appraising these sources of energy show how technologies differ in their risk to human life and carbon intensity (Fig. 1).

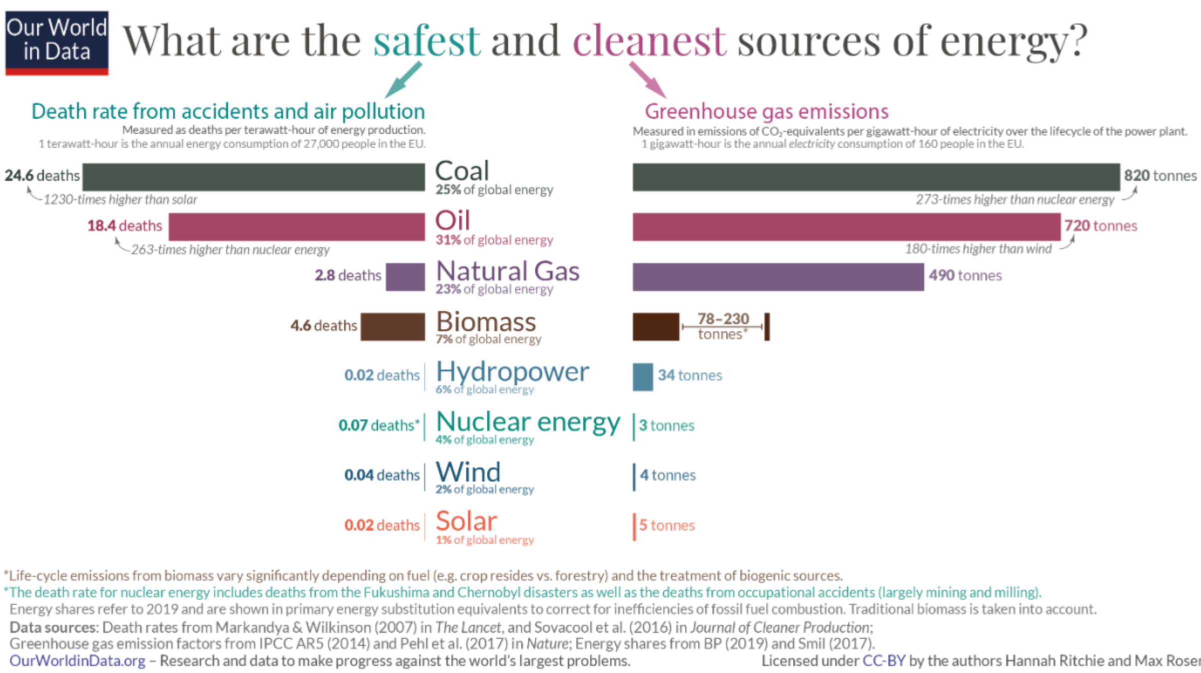

Figure 1. Ritchie 2020 Comparing deaths per tWh and Greenhouse gas emissions in CO_2-equivalent tons per gWh from various energy sources

A recent forecasted life cycle analysis found that the energy generated from fossil fuels with carbon capture in a modelled 2050 energy system would have 78-109 grams per CO_2 equivalent per kilowatt hour ($CO2eqkWh^{-1}$), while nuclear, wind and solar would range from

3.5-11.5 gCO_2eqkWh^{-1} (Pehl et al., 2016). Even with yet unproven carbon capture technology centered in the model, generating energy from wind, solar and nuclear was far less carbon intensive than fossil fuels. Low carbon sources support a sustainable future for energy production, yet technical limitations challenge the widescale adoption of some technologies.

Firming energy production: Dealing with the inherent intermittency of wind and solar through complimentary nuclear power

Although wind and solar radiation are natural processes on Earth, the mechanisms used to convert that energy into a usable source of electricity, as well as the batteries needed to store that energy for later use, are produced from finite resources and require large areas of land to produce adequate quantities of electricity. Battery storage is the key to allowing energy produced from wind and solar farms to be used by consumers, especially in locations with low solar radiation and inconsistent winds (Manber and Stenquist, 2018; Paik et al., 2021). The problem of varying levels of wind and solar output is known as intermittency and is the key issue facing the large-scale adoption of wind and solar to mitigate emissions from the energy sector.

A recently proposed wind and solar development project by the company Xlinks purports to produce roughly 10.5 gW or 8% of the UK energy demand by 2029 from a new wind and solar farm in Morocco. The project will connect the 1500 km solar and wind farm in the Saharan desert to the U.K. consumer via an underwater High Voltage Direct Current Transmission line where it will be stored in lithium-ion batteries in Devon (Bellini, 2021; Hook, 2021). The CEO of Xlinks lauds the project as a means to reach net zero targets for the UK by reducing the intermittency of wind and solar through combining the two sources and placing them in an area that experiences abundant sun compared to the cloud-covered British Isles. However, this ambitious plan exemplifies the challenges that underlie an energy economy reliant on wind and solar energy. The site is 3,800 km away from the UK to explicitly solve the unavoidable intermittency problems brought about by cloud cover and variable winds. The CEO is quoted saying “This is renewable energy that acts like a baseload... we have none of the intermittency” (Hook, 2021). The CEO all but says that wind and solar are not viable at scale in the UK due to the challenging weather conditions.

The issues of land use constraints and intermittency in wind and solar deployment are not limited to the U.K. In South Korea, novel subsidies have been proposed to account for the low-capacity factor inherent in intermittent sources (Paik, Chung & Kim, 2021). An analysis of Japanese land suitability found only 0.9% of available land for onshore solar pv and wind deployment (Onda et al., 2020). Furthermore, the authors noted that if all the available land was developed into wind and solar farms, this would generate 130.2 tWh/yr, a mere 15% of current Japanese energy demand (Onda et al., 2020). Yet, there is already a proven way to achieve large quantities of consistent power regardless of the weather, with low land constraints and free from significant amounts of fossil fuels: nuclear fission.

A low carbon way to provide power 24 hours a day is through nuclear power. There are numerous varieties of nuclear power plants, and they all have one thing in common: consistency (Technical assessment, 2020). There are presently 94 U.S. nuclear reactors actively producing 20% of U.S. electricity (U.S. energy, 2020). Yet, this technology has been excluded from the push for green energy. Former governor, Andrew Cuomo, shutdown Indian Point Nuclear Station, a power plant that was generating more power than the entire state’s wind and solar combined: approximately 1000MW of low carbon electricity which has since been replaced with fossil fuels (Mcgheehan, 2021). The shuttering of nuclear plants is also trending around the world with Germany vowing to dispose of all of them by 2022, and Diablo Canyon in California set to shut down next year (Mcgheehan, 2021). This trend results from of a lack of education about nuclear power feeding into people's fear of this technology.

Nuclear Risk: Weighing the historical meltdowns with future climate trends

There have been two major nuclear plant disasters that led to a discharge of radiation during the 60 years of civilian nuclear power, both from operator error, which has led to a justified skepticism about the safety of this technology (Acton & Hibbs, 2014). The first, Chernobyl, was caused by human error and resulted in increased rates of documented thyroid cases in the area surrounding the power plant, which are almost certainly caused by the increase in ionizing radiation from the nuclear plant (World Health Organization, 2006). However, no substantial increase in the occurrence of leukemia was shown in the area (World Health Organization, 2006). These data are difficult to interpret due to the large number of confounding variables associated with long-term epidemiolocal study (World Health Organization, 2006).

An additional unforeseen consequence of humans being barred from the Chernobyl Exclusion zone has been the resurgence in forest cover from 41% in 1986 to 59% in 2020 (Matsala et al., 2020). A study on the microbiota of four small mammals trapped in the Exclusion Zone found limited effects of radiation dosage and microbiome composition (Antwis et al., 2021). The dose rates impacting wildlife in the CEZ were found to be comparable to background dose rates across Europe (Beresford et al., 2018). These published data indicate the ecological impacts of radiation to wildlife may not be as severe as previously thought.

The second, and most recent accident occurred on March 11, 2011, when the Fukushima-Dachaii nuclear power plant operated by the Tokyo Electrical Power Company (TEPCO) was hit by two tidal waves following a 9.0 earthquake. This disabled the cooling system for two of the reactors along with the back-up generators, batteries and connection to the power grid (Acton &

Hibbs, 2014). Due to the loss of cooling systems, the fuel overheated and emitted large quantities of radiation into the surrounding atmosphere (Acton & Hibbs, 2014). An estimated 2.37 Pbq or petabecquerels of the radionuclide Cesium 137 was released into the surrounding environment (Onda, 2020). The becquerel is the SI unit for radioactivity and is equivalent to one nuclear decay per second (Onda, 2020). One way to measure the reach of Cesium 137 is to examine the bioaccumulation in different larvae populations of the caddisfly *Stenopsyche marmorata* (Matsuo et al., 2021). The highest concentrations of cesium 137 were found to be within 5 kilometers of the power plant and generally decreased the further away from the contaminate area (Matsuo et al., 2021). In the nearby Kurial Islands, there was an addition of 3% - 15% of C^{137} to the mean background soil dose of 2600 Bq m^2, which the authors concluded to be an inconsequential amount from a radiological point of view (Ramzaev et al., 2018). Understanding the flux of radioactive material and communicating the increased risk of various cancers from acute radiation exposure is essential if the world is going to continue to use nuclear power (Onda, 2020). Weighing the risks of nuclear power compared to the consequences of climate change will be a major source of contention over the coming decades.

Material Intensity of Renewables

The current best available technology for storing energy comes in the form of lithium-ion batteries. Månberger & Stenqvist (2018) modelled future demand of 12 important rare earth metals and found that, of the rare earth's examined, lithium will most likely experience severe global scarcity. The authors constructed a model of metal intensity demand under different scenarios meant to meet the goal of remaining under the 1.5 C mean global temperature rise by 2060. Under the highest lithium use scenario, demand would be 233% more than the current estimated reserves by 2060. Even in models that increased recycling from the current 10% to

80%, the authors found only an extension of reserves under ten years, indicating that new forms of energy storage must be employed to achieve industrial scale energy storage.

Another issue with lithium is its water footprint. To extract lithium, copious amounts of water must be employed, often in water scarce regions like Bolivia, Chile and Argentina which contains 67% of the known economically viable lithium reserves (Schomberg et al., 2021). The extraction process pumps lithium-rich groundwater to surface ponds where it evaporates so the metal can be extracted from the resultant brine. A recent life cycle analysis found that there is a Water Scarcity Footprint (WSF) of 33,155 m^3 from lithium mining for a 2 mWh battery (Schomberg et al., 2021). The environmental footprint of lithium and the extraordinary quantities required to power future energy demand calls the use of the term renewable into question.

In contrast to a possible near-term shortage of rare earth material for wind and solar infrastructure, basic nuclear fission is reliant on Uranium, a widespread element on Earth. A recent analysis found that using currently available breeder reactors, nuclear power can support 2019 human energy consumption (594 Exojoules) for 4.4 billion years through the recycling of fuel from breeder reactors and the energy density inherent in nuclear technology (Touran, 2020). This large number exemplifies the two greatest concepts in nuclear technology. First, it is extremely energy dense as it uses the nuclear force that holds atoms together to generate energy rather than weaker chemical bonds. Second, it is the only energy technology that currently captures 100% of its waste and can recycle it efficiently, a rare trait among energy sources.

The 100% WWS Debate

The general discourse surrounding the energy transition focuses on the implementation of low carbon wind and solar machines to transition away from fossil fuels and can be traced back to a single paper by a controversial researcher named Mark Z. Jacobson. The paper and lead researcher claim to be the basis for the energy section of the Green New Deal. The paper lays out a roadmap for 100% wind, water and solar for energy production for each state in the union. The authors asserted that this could be met with ~30.9% onshore wind, ~19.1% off-shore wind, ~30.7% utility photovoltaics, ~7.2% rooftop pv, ~7.3% concentrated solar power with storage, 1.25% geothermal and the remaining 4% with wave and hydropower (Jacobson et al., 2015). The authors further claimed that 100% wind, water and solar generation could be achieved without the explicit use of battery storage (except in electric vehicles) or nuclear power in a section consisting of three paragraphs citing a grid integration model paper that Jacobson authored, which has also subsequently been disputed in the literature.

Another key flaw in the paper is under the section titled Resource Availability, which examines the resources for wind and solar in the U.S. The authors present areas of the country with variable amounts of solar radiation and consistent wind resources yet fail to even mention the physical rare earth metal resources required to harness the energy of the wind and the sun, of which almost none is mined or manufactured in the U.S (Jacobson et al., 2015). Though many studies in the literature draw the connection between the material resources required for wind and solar machines (Månberger and Stenqvist, 2018). In a rebuttal paper Clack et al. (2017) found four major faults in the conclusions based on improper modelling, poorly documented and implausible assumptions, lack of adequate documentation of electricity system modelling and an inaccurate model for wind and solar output. Remarkably, Jacobson sued the authors of the rebuttal paper for defamation of character, stifling needed academic debate about the merits of a grid reliant on 100% wind, water and sun without considering other scenarios (Hitzik, 2018).

Many high-profile scientists have begun to take a stand for nuclear power. Chief among them is the legendary Dr. James Hansen, one of the first atmospheric scientists to testify in

Congress on the dangers of anthropogenic climate change. He is co-authored with Chinese colleagues on a succinct paper summarizing the benefits of nuclear and advocating for a collective human approach to this global issue. They point to little reduction in carbon intensity of German electricity after two decades of Energiwiende and the relative safety and power of nuclear technology, as well as significant next generation reactors that upgrade safety and efficiency (Cao et al., 2016). Fortunately, the winds have begun to change and the upcoming COP26 in Glasgow, Scotland will be a marker for where the energy transition stands.

Conclusions

Wind, water and solar technologies are an important part of reducing emissions but present real challenges in meeting the challenge of a 100% low carbon energy sector. Through their intermittency, material resource intensity and specific environmental requirements, wind and solar can not get the job done alone (Clack et al., 2017). Yet with the inclusion of nuclear power as a complementary, low carbon renewable, humanity may be able to reach negligible greenhouse gases from energy generation in the coming decades (Pehl, 2017).

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CHAPTER 2. GRANT PROPOSAL

Comparing Invasive Plant Expansion Along a Roadway Across the Elevational Gradient in the Colorado Front Range

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Section 1. Abstract

Invasive species can negatively impact native plant communities and are easily spread through anthropogenic actions. Human built roadways increase nonnative plant introductions through facilitating propagule dispersion. However, little is known about the influence of roadways on invasive plant distribution across the elevational gradient in the Colorado Front Range. To examine this relationship, I will randomly sample points along Colorado Highway 5 leading up to the summit of Mt. Evans. At each plot along this 2,000-meter elevational gradient, I will collect percent cover of native and non-native species along with the environmental variable's aspect, slope and distance from roadway. I will construct multiple logistic regressions with elevation and environmental variables as predictor variables for non-native percent cover. These results will shed light on how elevation and environmental variables influence the expansion of non-native plants in the Colorado Front Range.

Section 2. Objectives, Hypothesis, Anticipated Value, Literature Review, Specific Aims

Objectives

This research aims to determine the non-native plant abundance along a roadway spanning 2,000 meters of elevation gain in the Colorado Front Range. The results will determine if increasing elevation decreases the abundance of non-native plants with high anthropogenic influence. The results of this study will help shed light on the distribution of invasive plant species in Colorado and assist land managers in identifying areas of conservation priority.

Question and Hypothesis

Q1: Does increasing elevation decrease non-native plant relative abundance along roadways in the Colorado Front Range?

H1: Due to increasing habitat specificity at higher elevations, non-native plant abundance will decrease with increasing elevation.

Q2: Does proximity to roadways increase the abundance of non-native plants?

H2: Due to roadways creating novel habitats, non-native plant abundance will increase nearer to the roadway.

Anticipated Value

Invasive plants exert deleterious effects on native plant populations and change the composition of plant communities (Catford et al., 2017; Harms & Hiebert, 2006). Determining the relative abundance of non-native plants at varying elevations is important in prioritizing areas to manage for invasive plants. The results of this proposed study will illuminate which montane habitat types are most at risk to invasive plant species with similar levels of anthropogenic influence. As the Front Range of Colorado becomes more heavily influenced by human activity, understanding which areas are most susceptible to plant community change from invasive species is important to managing for native biodiversity.

Literature Review

Non-native plant introductions are increasing globally through anthropogenic influences such as agriculture, urban horticulture and hiking (Catford et al., 2017; Tyler et al., 2015). Land managers across the globe try to control the spread of invasive species through various actions such as targeted pesticide application, increasing native diversity in the landscape with native plant seeding and even altering microbial function to limit exotic plant spread (Byun et al., 2018; Neve et al., 2015; Shartash & Brown, 2021). Limiting the spread of invasive species is important as novel organisms can exert deleterious effects on native plant populations through numerous mechanisms including plant-soil feedbacks, novel chemicals, increased competitive ability and disruption of native mutualisms (Catford et al., 2017; Harms & Hiebert, 2006). However, human disturbance aids in the expansion of invasive plants to new habitats through spreading invasive propagules and altering land use.

Anthropogenic influence, along with a changing climate, are two of the main drivers in expanding invasive plant range (Beans, Kilkenny & Calloway, 2012). One major human influence in spreading invasive plant species is roadways as vehicles can spread non-native seeds (Catford et al., 2017). Watkins et al., (2003) found that exotic plants were found most frequently within 15 meters of roadways.

Additionally, four-wheel drive roadways were found to be the best predictor for invasive plant occurrence in 27 protected areas in the Appalachian Mountains (Daniels et al., 2019). Though roads can serve as a source for non-native plant introductions, this relationship has yet be studied in the Colorado Front Range even though invasive species are extremely prevalent.

There are a significant number of non-native species invading Colorado habitats including *Linaria dalmatica, Alyssum simplex* and *Bromus inermis* (Bishop et al., 2019; Jamieson et al., 2012; Larson et al., 2021; Tyler et al., 2015). In fact, of the approximately 3,276 floral taxa found in Colorado 524 or 16% are considered non-native (Ackerfield, 2015). A broad scale species distribution model of 15 non-native grasses and forbs across the American West found that the most influential predictors of the 15 common invasive plants were minimum temperture, climatic water defecit, precipitation seasonality and fire hisotry (McMahon et al., 2020). In the Colorado Plateua, *Bromus tectorum* covered approximately 3.8% of mapped parks across with concenrations as high as 21% (Bishop et al, 2019). In a manipulative experiment in Boulder County, non-native grass species were found to decrease in abundance when histroic nitrogen contents and winter precipitation levels were imposed (Concilo et al., 2016). These studies suggest there is a significant relationship between environmental conditions and invasive species expansion in Colorado. However, no studies have examined how roadways contribute to the spread of non-native species in the Colorado Front Range. Examining the relationship between elevation, roadways and non-native plant abundance will help managers determine best practices for mitigating the spread of invasive species.

Specific Aims

The results of this study look to determine where invasive species are spreading in the Colorado Front Range. In determining which elevations hold the most invasive species, land managers can prioritize where to focus mitigation. The analysis will also shed light on the effect of roadways on montane ecosystems. Understanding the interplay between human disturbance, elevation and non-native plant abundance will add valuable data to the field of invasion ecology, especially in montane areas.

Section 3. Methods

Site selection

To assess the impacts of elevation and proximity to roadways on invasive species distribution, I will randomly select plots along Colorado Highway 5 from the beginning of Highway 5 at 2,300 meters to its apex at 4,350 meters. Using ArcGis I will create a polygon of the road with a 25-meter buffer on each side of the road and randomly place 100 points in this polygon. Plots will be excluded if terrain is impassible.

Plant Sampling Methods

Each randomly selected point will be located with a handheld GIS using longitude and latitude coordinates. Each point will mark the southwest corner of the 1 by 1 m quadrat. For each point, distance from road, elevation, slope and aspect will be measured. Within each quadrat, all plants will be identified to species and denominated native or non-native. Each species found in the quadrat will be visually estimated for percent cover to determine relative abundance. The percent bare ground and litter will also be visually estimated.

Data Analysis

To determine if non-native plant species increase with elevation along roadways, I will perform logistic regressions with precent non-native cover as the response variable and elevation, aspect and slope as the predictor variables. If data do not conform to the assumptions of logistic regressions, I will log transform the data. I will determine the model that best explains the variance in the data through a drop in deviance test. To test whether distance from roadway effects non-native plant abundance, I will perform a logistic regression with non-native plant abundance as the response variable and distance from roadway as the predictor variable after accounting for elevation, aspect and slope. If data do not conform to the assumptions of a logistic regression, I will log transform the data. All analyses will be performed in the R statistical coding language (R Core Team, 2021).

Potential Negative Impacts

Potential negative impacts should be minimal. However, there is a possibility I inadvertently track invasive plant species seeds into previously uninvaded areas. To mitigate this, I will rinse my boots and quadrats before moving between sites. Additionally, I will be working in sensitive alpine areas and will ensure that I avoid disturbing native flora as much as possible by walking in a straight line to the site and using rocky substrate as much as possible.

Project Timeline

Table 1. Project Timeline

Date	**Activity**	**Deliverable**
July 1-July 20, 2022	Collect 30 plots of quadrat data for the three sites	Identify each species in plot, estimate percent cover, bare ground and litter. Collect unknown specimens for lab ID
July 21-24, 2022	Identify unknown plant species using microscopes and dichotomous keys. Seek expert help from DBG if needed	Identify all species found in field and determine native or non-native status
July 24-25, 2022	Perform data analysis	Quantify the abundance of native v non-native plants at each site
July 25-31, 2022	Write final report	Final report

Section 4. Budget

Budget

Table 2. Project Budget

Item	**Justification**	**Quantity**	**Cost per unit**	**Total**
Garmin GPSMAP 64x with altimeter	To identify selected points with GPS coordinates and measure elevation	1	$380.00	$380.00
1 x 1 m Quadrat	Necessary to mark plots	2	$12.00	$24.00
Pencils	To collect data	1	$10.00	$10.00
Brown Paper Bags	To hold unknown ID specimens and collect data	1	$15.00	$15.00
Gas Reimbursement	$0.56 per mile, 46 mi round trip to base of road. Up to 66 mi roundtrip to summit 20 field days= $62.00/day	20 field days	$62.00/day	$1,240
Salary	Compensation for work	1	$2,000	$2,000
Project Total				$3,669

Appendix

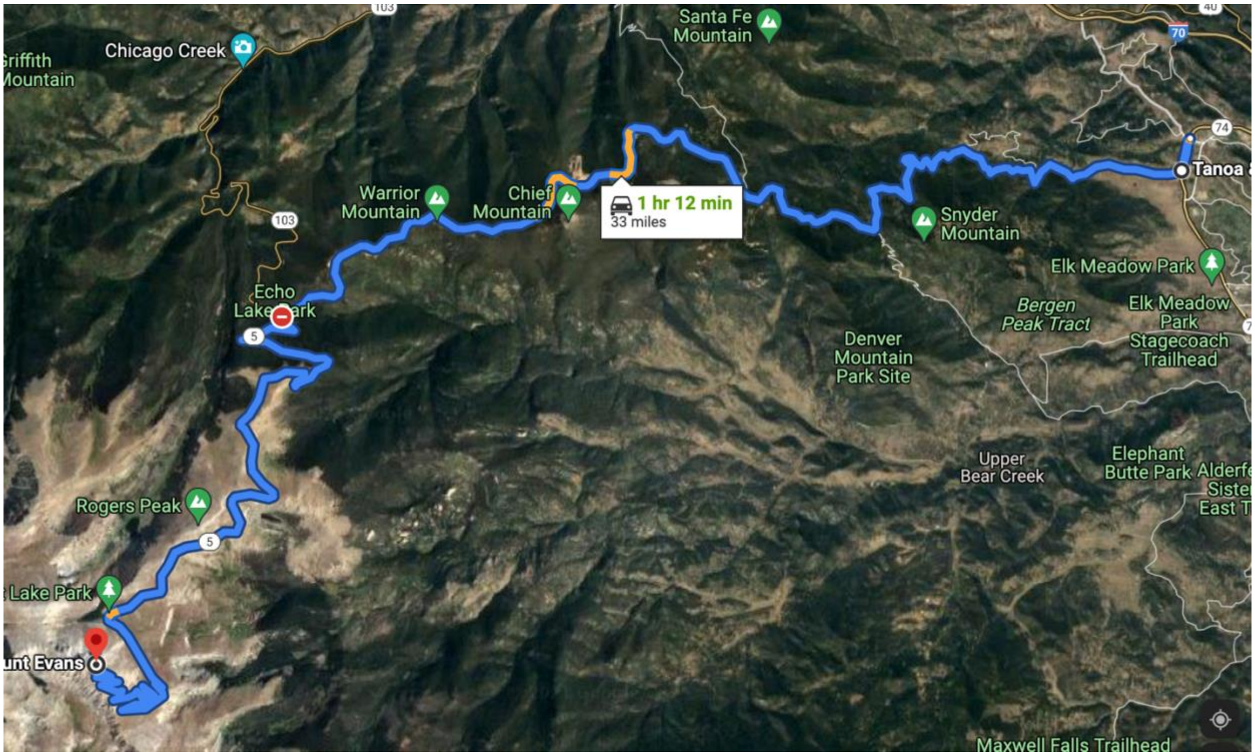

Figure 1. Study site from the beginning of Highway 5 in Evergreen to the summit of Mt. Evans

Qualifications of researcher

Dermot C. Swanson
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402-320-2998

<u>Education</u>

M.S. Environmental Biology, Regis University, Denver, CO May 2022

B.S. Environmental Science, B.A. Biology, Regis University, Denver, CO May 2021

<u>Research Experience</u>

Denver Zoo Elephant Stereotypy Class Research, Regis University Fall 2021

- Coded elephant nighttime behavior examining stereotypy when bull elephants are in and out of musth
- Behavioral data collection, data analysis

Daniel's Park Grassland Management Study, Regis University Fall 2021

- Compared grazing regimes in short grass steppe to determine grazing impact on plant community composition
- Plant Identification, data analysis, field data collection

Primate Ecology Field Work, La Suerte Biological Field Station, Costa Rica, May 2018

- Designed research study on locomotion & tree use in White-faced capuchins (*Cebus capucinus)* and mantled howler monkeys (*Alouatta palliata)*
- Collected 25 hours of instantaneous focal sampling data
- Analyzed data and presented findings to faculty

SEED Institute Fellowship, Regis University, Denver, CO 2019-2020

- Researched competitor University sustainability practices and web design
- Presented findings and recommendations for enhancing sustainability practices to Regis Administration

Publications

Swanson, D. (2020). *Cultivating a Plant-Human Connection in the Age of the Anthropocene*.

https://epublications.regis.edu/theses/997

Presentations

Oral Presentation(Zoom): Regis University Honors Thesis Defense May 2020

Cultivating a Plant-Human Connection in the Age of the Anthropocene

Honors and Awards

Regis University Core Leadership Scholarship 2017-2020

Community Engagement and Leadership

Regis University Student Government 2018-2020

- Worked to implement more sustainable campus practices and policies

Regis Sustainability Club Founder and President 2017-2020

- Created a campus space for those concerned with the loss of biodiversity and societal disregard for human health to organize

Skills

Excellent Oral and Written Communicator
Terrific Customer Service
Fluent in written and oral Spanish
GIS and R proficient
Data Analysis

<u>Work Experience</u>

Romero House Live-in Coordinator, Regis University, Denver, CO 2020-present

- Cultivated community based on tenets of simplicity, solidarity and spirituality
- Facilitated weekly community night, spirituality night for students
- Supervised and assisted students in hosting biweekly Hospitality Night in which we opened our home to the community to share food and conversation

Horticulture Technician, Denver Country Club, Denver, CO Summer 2021

- Planted and maintained numerous beds, pots and baskets of cultivated flowers
- Extensive identification and removal

Landscape Technician, Forest Green Lawn and Landscaping, Omaha, NE Summer 2020

- Installed and maintained soft and hard landscaping projects
- Operated truck and trailer daily, skid loader and ditch witch
- Cultivated Plant identification and site selection

Engaged Scholar Activist Manager, Regis University, Denver, CO 2020-2021

- Managed 6 student employees
- Coordinated student volunteer opportunities with community partners

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CHAPTER 3. JOURNAL MANUSCRIPT

Host Species has Non-Uniform Effects on the Vitality of Root Hemiparasite *Castilleja* Species

Abstract

Root hemiparasitism is a common form of plant parasitism that involves facultative attachment to host root systems through a specialized organ called a haustorium. However, due to challenges in long term field observations of hemiparasitism, manipulative experiments are essential in unearthing the relationship between host and parasite. To assess the host most suitable for cultivating vigorous individuals of the widespread, hemiparasite genus *Castilleja*, I analyzed data from a manipulative study that pairs six *Castilleja* species with six host species and a no-host control. Data were collected over two years at regular intervals during the growing season on *Castilleja* survival, size and number of inflorescences. Each *Castilleja* species displayed a different response to hosts species. However, all six *Castilleja* species had lower survival rates when paired with *Achillea millefolium* than without a host. Generally, *Artemisia frigida* produced the most vigorous *Castilleja*, especially in terms of number of inflorescences and size. These results indicate that *A. millefolium* has antagonistic effects towards the hemiparasitic *Castilleja* while *A. frigida* is the most ideal host for producing vibrant *Castilleja* in a horticultural setting. Additionally, these results shed light on host-parasite interactions in the genus *Castilleja* with implications for wild populations.

Introduction

Parasitic flowering plants are widely diverse in growth habit and phylogeny, comprising close to 1% of extant angiosperm taxa (Kraslenko et al., 2021; Teixiera-Costa, 2021). All parasitic angiosperms connect to the host either through the roots or the shoots with a specialized organ called the haustorium, which has evolved independently 12 separate times (Teixiera-Costa, 2021; Westwood et al., 2010). Plant parasitism can be defined by photosynthetic ability, with hemiparasites able to produce carbon independently, while holoparasites must receive all their carbon from the host (Westwood et al., 2010). The most common form of plant parasitism is root hemiparsitism, where the parasite opportunistically attaches to host roots, but can survive independently (Phoneix & Press, 2005). Despite the prevalence of root hemiparasitsm, host preference is not well understood in most parasitic species.

The physiology of host plants consequentially impacts the function of parasites and suggests that there may be preference for certain hosts (Haynes, 2021; Mathies, 2017). One hypothesis posits that nitrogen fixing plants are favored due to a lack of usable nitrogen in the environment, though there are mixed results supporting this theory (Haynes, 2021). In an experimental study with the root hemiparasite *Melampyrum arvense* L. (Orobanchaceae) grown with 27 host species, the mean mass of *M. arvense* grown with legumes was 11.7 times that of other forbs (Mathies, 2017). However, *Pedicularis cephalantha* Franch. ex Maxim (Orobanchaceae), a root hemiparasite, grew better with a grass host than a nitrogen fixing legume (Yong-Quan et al., 2010). These results suggest that host preference may be species specific and influenced by multiple factors.

The genus *Castilleja*, or paintbrushes, has been frequently used as a study system for investigating root hemiparsitism in both natural and controlled settings (Clancy et al., 2013; Haynes, 2021). This widespread genus is a parasitic generalist, able to attach to a wide diversity of plant species with over 100 host species described (Montes-Hernandez et al., 2015; Press, 1998). However, determining host species in natural settings can be a challenge due to the fragility of the haustorium and limitations on long-term monitoring (Montes-Hernandez et al., 2015). For example, in the range limited *Castilleja christii* N.H. Holmgren (Orobanchaceae), only two host species were found, *Artemisia tridentata ssp. vaseyana* Nutt. (Asteraceae) and *Pedicularis contorta* Benth. (Orobanchaceae), and no long-term data is available on the survival rates of parasites with the different hosts in this population (Clancy et al., 2013). Likewise, an investigation into hosts of *Castilleja tenuiflora* Benth. (Orobanchaceae) in Central Mexico noted five possible species spanning three diverse families: *Baccharis conferta* Kunth. (Asteraceae), *Bidens triplinervia* Kunth. (Asteraceae), *Abies religiosa* (Kunth) Schltdl. & Cham. (Pinaceae), *Trisetum spicatum* (L.) K. Richt. (Poaceae) , and *Lupinus montanus* Kunth. (Fabaceae), but haustorial connection could not be determined in the field (Montes-Hernandez et al., 2015). Thus, horticultural studies on the relationship between *Castilleja* and host species are essential in drawing causal relationships between root hemiparasite vitality with unique host species.

To quantify how survival and growth of *Castilleja* plants is affected by differing host physiology, I analyzed data from an experiment conducted at the Denver Botanic Garden pairing six host species with six *Castilleja* species. I analyzed the results of this experimental study to answer the question: How does host species impact the vigor of six hemiparasitic *Castilleja* species? Given the wide range, hardiness and previous success in growing *Castilleja*, all six *Castilleja* species will grow most robustly in trials with the host plant *Artemisia frigida* Willd. (Asteraceae) (Love & McMaddon, 2017). I predict the trial with *A. frigida* will have the highest number of surviving *Castilleja*, the greatest number of inflorescences and the largest growth size. Finally, due to their hemiparsitic nature, *Castilleja* will grow best in trials with host plants compared to the negative control without a host. Analyzing these data will indicate the most ideal host species to pair with *Castilleja* in horticultural collections and provide insight into the parasitic nature of this species in wild populations.

Methods

Study Design and Study Species

The study was conducted at the Denver Botanic Gardens Chatfield Farms in southern Jefferson County over two successive years, 2020-2021, with a third year ongoing. Six *Castilleja* (Orobanchaceae), species were used in the experiment: *Castilleja integra* A. Gray, *Castilleja linariifolia* Benth., *Castilleja angustifolia* (Nutt.) G. Don, *Castilleja sessiliflora* Pursh., *Castilleja chromosa* A. Nelson, and *Castilleja scabrida* Eastw. These species were chosen based on a wide native distribution, previous work in the literature showing their vitality in horticultural trials, and commercial seed availability. Host species were selected based on range overlap with study *Castilleja* species and literature indicating adequate hosts for *Castilleja*. Six host species were chosen: *Artemisia frigida* Willd. (Asteraceae), *Eriogonum jamesii* Benth (Polygonaceae), *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (Poaceae), *Achillea millefolium* L. (Asteraceae), *Penstemon pinifolius* Greene (Plantaginaceae), *and Penstemon strictus* Benth. (Plantaginaceae). Each seed was cold stratified for six weeks to break dormancy before being germinated in a greenhouse. *Castilleja* seedlings were paired with a host plant after 4-6 weeks of growth. Each plant was root washed before planting following best horticultural practice. Four individuals, two *Castilleja* and two hosts were planted into 3.5'' pots in the greenhouse for an additional 12-16 weeks before being hardened and planted in outdoor experimental plots. *Castilleja*-host pairs were planted in 26 rows with 12 plants per row spaced 12'' apart. The plots were 20' by 40' with irrigation lines every 18''. Plants were watered as needed for 4-6 weeks until establishment. Each treatment was replicated 6 times in year one and 9 times in year two, except for the *B. gracilis* trial in year two which was replicated 6 times. Additionally, due to seed contamination with *C. sessiliflora*, the year two *B. gracilis -C. linarifolia* trial was included in the *C. sessiliflora* trial, giving it an *n* of 84, and there was not *B. gracilis* data for *C. linarifolia.*

Data Collection

Data were recorded in early spring, mid-summer and early fall, except in year one which only had two measurements, early spring and fall. The *Castilleja* individual was denoted visible if there was noticeable aboveground growth, which acted as a proxy for survival. Aboveground plant size was measured in three dimensions, height and two widths. Height was measured from the ground to apical growing point. The first width was measured across the plant at its widest point with the second measurement taken perpendicular to the first. These three measurements were multiplied together to get aboveground plant size in cm^3. Each stem with colored bracts was counted as an inflorescence and were not counted if in bud or without coloration. All data were recorded by Michael Guidi and Jameson Coopman.

Statistical Analysis

To determine the probability of survivorship for each trial, I fit six logistic regressions, one for each *Castilleja* species, with proportion of surviving original plants as the response variable and host species as the predictor variable. After checking for overdispersion in the data, I back transformed the odds ratio to probability and calculated 95% confidence intervals. I then fit a generalized linear hypothesis test with Tukey HSD adjustments to account for multiple comparisons to determine which host species trials were significantly different. All statistical analysis was performed in R Statistical Programming (R Core Team, 2020).

To determine which host resulted in the largest *Castilleja* individuals, I first log10 transformed the size data for all species to better fit the assumptions of normality. Then I performed six one-way ANOVAs, one for each *Castilleja* species, with log10 transformed size as the response variable and trial as the predictor variable. I performed post-hoc Tukey HSD analysis to determine which trials significantly differed from other trials after accounting for multiple comparisons.

To quantify the difference in inflorescence number between host species, I fit six Poisson regression, one for each *Castilleja* species, with number of inflorescences as the response variable and host species as the predictor variable. I then back transformed the data to determine the multiplicative change in number of inflorescences compared to the trial without a host and calculated 95% confidence intervals. Any significant differences between host species were explored with a generalized linear hypothesis test with Tukey HSD adjustments to account for multiple comparisons.

Results

Each species of *Castilleja* showed a unique response to host plants with regard to survival, size and inflorescence number (Figure 1, Figure 2, Figure 3).

Castilleja integra: All trials had some *C. integra* individuals survive (Figure 1). The host with the highest proportion survived was *P. pinifolius* 0.92 (95% CI: 0.82, 0.97), followed by *B. gracilis* 0.85 (95% CI: 0.73, 0.94) and Absent = 0.85 (95% CI: 0.74, 0.93). *E. jamesii* 0.83 (95% CI: 0.71, 0.92), and *A. frigida* = 0.75 (95% CI: 0.62, 0.86) had similarly high levels of survivorship while *A. millefolium* 0.25 (95% CI: 0.14, 0.38) and *P. strictus* 0.22 (95% CI: 0.08, 0.44) had the lowest survival rates. There were 10 trials that differed significantly: *A. millefolium* - Absent ($p < 0.001$), *P. pinifolius* - Absent ($p < 0.001$), *A. frigida* - *A. millefolium* ($p < 0.001$), *B.*

gracilis - *A. millefolium* (p <0.001), *E. jamesii* - *A. millefolium* (p <0.001), *P. pinifolius* - *A. millefolium* (p <0.001), *P. strictus* - *A. frigida* (p = 0.006), *P. strictus* - *B. gracilis* (p = <0.001), *P. strictus* - *E. jamesii* (p = <0.001) and *P. strictus* - *P. pinifolius* (p <0.001). Though *P. strictus* and *A. millefolium* did not have size data, none of the trials differed significantly from one another (Figure 2). Three trials showed an increase in the percent size compared to the Absent trial: *E. jamesii* 88% (95% CI: -40%, 486%), *P. pinifolius* 4% (95% CI: 77%, 222%) and *B. gracilis* 55% (95% CI: -52%, 402%), while *A. frigida* decreased -37% (95% CI:-80%, 97%). All trials except *P. strictus* had some individuals produce inflorescences (Figure 3), but none of the trials differed significantly in the number of inflorescences. Only two trials showed an increase in the number of inflorescences compared to the trial without a host, *B. gracilis* 9% (95% CI: -42%, 310%) and *E. jamesii* 4% (95% CI: -73%, 288%), while three trials showed a decrease in inflorescence number, *A. millefolium* -88% (95% CI: -99%, 11%), *A. frigida* -8% (95% CI: -70%, 213%), *P. pinifolius* -20% (95% CI: -74%, 238%).

Castilleja scabrida: All trials yielded surviving *C. scabrida* individuals except *P. strictus* (Figure 1). The trial with the highest proportion survived was *E. jamesii* 0.77 (95% CI: 0.64, 0.87) followed by *P. pinifolius* 0.65 (95% CI: 0.51, 0.77) and *B. gracilis* 0.62 (95% CI: 0.47, 0.76). The *A. frigida* trial had a survival rate of 0.54 (95% CI:0.40, 0.68), Absent = 0.35 (95% CI: 0.23, 0.49) and *A. millefolium* had the lowest 0.08 (95% CI: 0.03, 0.18). There were 6 trials that were significantly different: *A. millefolium* - Absent (p = 0.036), Absent - *E. jamesii* (p = 0.001), *A. millefolium* - *A. frigida* (p <0.001), *A. millefolium* - *B. gracilis* (p <0.001), *A. millefolium* - *E. jamesii* (p <0.001), *A. millefolium* - *P. pinifolius* (p <0.001). The size data had no trials differ significantly and *A. millefolium* and *P. strictus* had no size data (Figure 2). Compared to the Absent trial, four trials showed an increase in size: *A. frigida* 172% (95% CI: 22%, 507%), *P. pinifolius* 113% (95% CI: -5%, 374%), *B. gracilis* 57% (95% CI: -32%, 259%) and *E. jamesii* 100% (95% CI: -11%, 346%). All trials produced inflorescences except *P. strictus* and *A. millefolium* (Figure 3). Compared to the Absent trial, all four trials with inflorescences showed an increase: *A. frigida* 325% (95% CI: 179%, 64,534%), *B. gracilis* 174% (95% CI: -95%, 5,416%), *E. jamesii* 50% (95% CI: -96%, 4,726%) and *P. pinifolius* 250% (95% CI: 85%, 7,282%). Three trials differed significantly in the number of inferences produced: *B. gracilis - A. frigida* (p = 0.047), *P. pinifolius - A. frigida* (p = 0.011) and *E. jamesii - A. frigida* (p = 0.034).

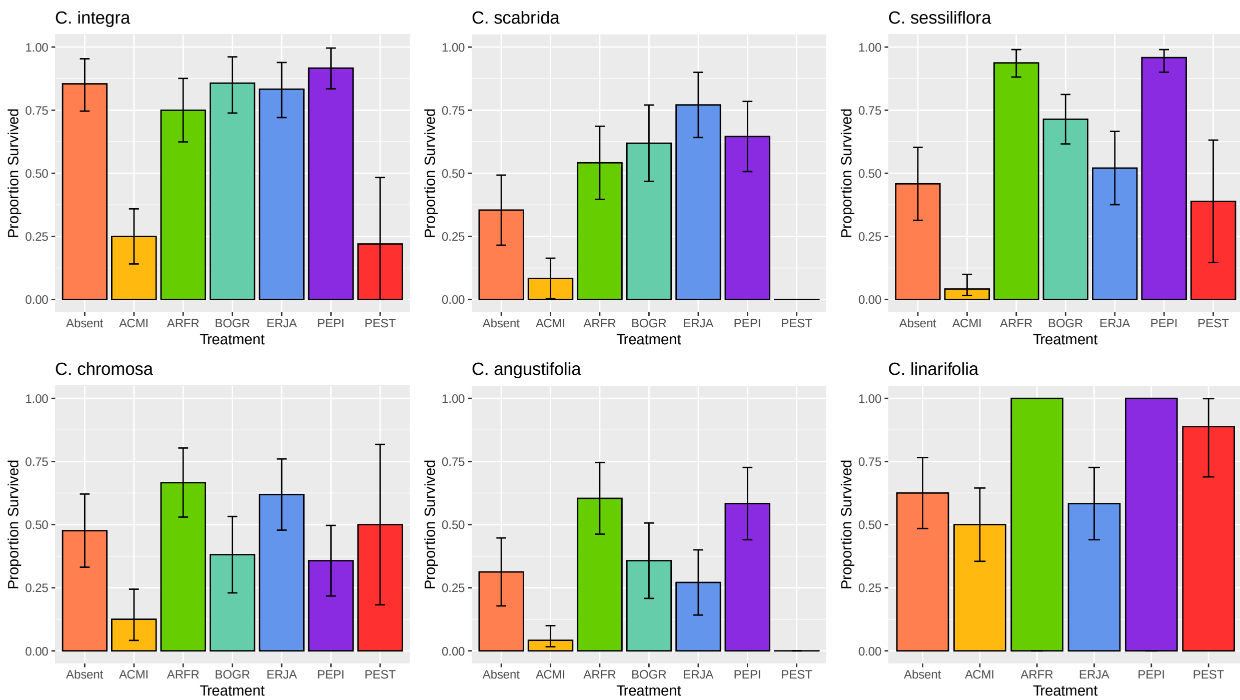

Figure 1. Proportion of surviving individuals for each *Castilleja* species in each trial. Bars show standard error, no bars denote 100% survival. No host control (Absent) = orange, AMCI (*A. millefolium)* = yellow, ARFR (*A. frigida)* = green, BOGR (*B. gracilis*) = turquoise, ERJA(*E. jamesii)* = blue, PEPI (*P. pinifolius)* = purple, PEST *(P. strictus)* = red.

Castilleja sessiliflora: All trials had surviving *C. sessiliflora* individuals (Figure 1). The trial with the highest proportion survived was *P. pinifolius* 0.96 (95% CI: 0.88, 0.99) followed by *A. frigida* 0.95 (95% CI: 0.85, 0.98) and *B. gracilis* 0.71 (95% CI: 0.61, 0.80), *E. jamesii* 0.52 (95% CI: 0.38, 0.66), Absent 0.46 (95% CI: 0.32, 0.60), *P. strictus* = 0.39 (95% CI: 0.19, 0.62) and *A. millefolium* = 0.04 (95% CI: 0.01, 0.12). There were 13 significantly different trials: *A. millefolium* - Absent (p = 0.002), *A. frigida* - Absent (p <0.001), Absent - *P. pinifolius* (p <0.001), *A. millefolium - A. frigida* (p <0.001), *A. millefolium - B. gracilis* (p <0.001), *A. millefolium - E. jamesii* (p <0.001), *A. millefolium - P. pinifolius* (p <0.001), *A. millefolium - P. strictus* (p = 0.029), *E. jamesii - A. frigida* (p = 0.001), *P. strictus - A. frigida* (p <0.001), *P. pinifolius - B. gracilis* (p = 0.049), *P.* pinifolius - *B. gracilis* (p = 0.002), *P. strictus - P. pinifolius* (p <0.001). The size data was quantifiable for all trials except *A. millefolium*, and the trials had no significant differences (Figure 2). Compared to the Absent trial, all trials showed increases in size: *A. frigida* 586% (95% CI: 149%, 1787%), *B. gracilis* 114% (95% CI: -13%, 425%), *E. jamesii* 144% (95% CI: -11%, 570%), *P. pinifolius* 227% (95% CI: 19%, 800%), and *P. strictus* 89% (95% CI: -52%, 646%). The Absent trial had no inflorescences and thus the data was not relativized to the control (Figure 3). *A. frigida* had a count of 23 inflorescences with 5 individuals, *B. gracilis* 25 with 12 individuals and *P. pinifolius 4* with 3 individuals.

Castilleja chromosa: All trials had some *C. chromosa* individuals survive (Figure 1). The host with the highest proportion survived was *A. frigida* 0.67 (95% CI: 0.52, 0.80), followed by *E. jamesii* = 0.62 (95% CI: 0.47, 0.76), and *P. strictus* 0.5 (95% CI: 0.24, 0.76). The Absent trial had a survival proportion of 0.48 (95% CI: 0.33, 0.63), *B. gracilis* 0.38 (95% CI: 0.24, 0.53) and A. millefolium = 0.14 (95% CI: 0.06, 0.27) had the lowest survival rates. Only 3 trials differed significantly: *A. millefolium* - Absent (p = 0.026), *A. millefolium - A. frigida* (p <0.001) and *A. millefolium - E. jamesii* (p <0.001). No trials differed significantly in size and *A. millefolium*, *P. strictus* and *P. pinifolius* did not have any size data (Figure 2). Compared to the control without a host, all three trials with data had an increase in size: *A. frigida* 9% (95% CI: -1%, 20%), *B. gracilis* 0.6% (95% CI: -9%, 11%), *E. jamesii* 7% (95% CI: -3%, 18%). The Absent trial had no inflorescences and thus the data was not relativized to the control (Figure 3). The *A. frigida* trial had a total count of 10 inflorescences on six individuals and *E. jamesii* had a count of 1 inflorescence on one individual.

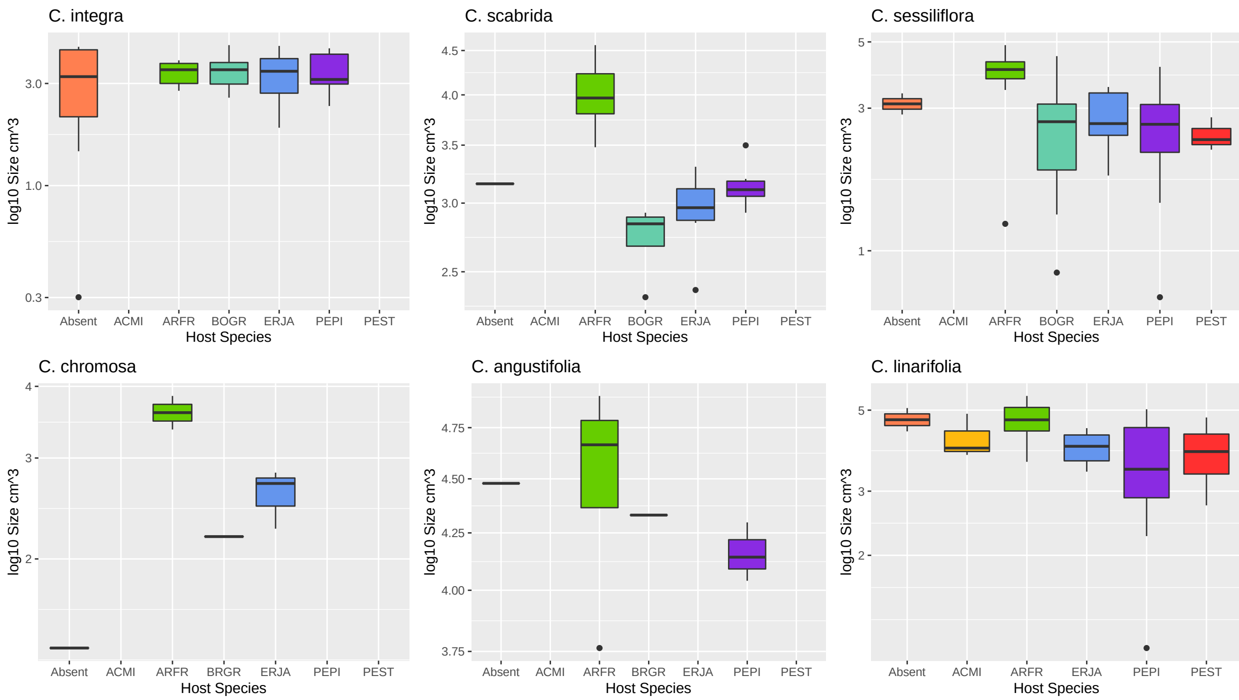

Figure 2. Log10 transformed size of *Castilleja* individuals in each trial. Error bars show 95% confidence intervals. No host control (Absent) = orange, AMCI (*A. millefolium)* = yellow, ARFR (*A. frigida)* = green, BOGR (*B. gracilis*) = turquoise, ERJA(*E. jamesii)*= blue, PEPI (*P. pinifolius)* = purple, PEST *(P. strictus)* = red.

Castilleja angustifolia: All trials had *C. angustifolia* individuals survive except *P. strictus* (Figure 1). The trial with the highest proportion survived was *A. frigida* 0.60 (95% CI: 0.46, 0.73), followed by *P. pinifolius* 0.58 (95% CI: 0.44, 0.72) and *B. gracilis* 0.36 (95% CI: 0.22, 0.51). The next highest was Absent 0.31 (95% CI: 0.19, 0.45) and *E. jamesii* 0.27 (95% CI: 0.16, 0.41) with the lowest being *A. millefolium* 0.04 (95% CI: 0.01, 0.12). There were 6 trials that were significantly different: *A. millefolium* - Absent (p = 0.030), *A. millefolium* - *A. frigida* (p <0.001), *A. millefolium* - *B. gracilis* (p = 0.016), *A. millefolium* - *P. pinifolius* (p <0.001), and *P. pinifolius* - *E. jamesii* (p = 0.030). The size data had no trials differ significantly and *A. millefolium*, *E. jamesii* and *P. strictus* did not have size data (Figure 2). Compared to the trial without a host all trials with size data increased in size: *A. frigida* 91% (95% CI:-4%, 280%), *B. gracilis* 2% (95% CI: -50%, 108%) and *P. pinifolius* 47% (95% CI:-27%, 192%). The number of inflorescences did not differ significantly between trials and *A. millefolium*, *E. jamesii* and *P. strictus* did not have inflorescences data (Figure 3). Compared to the trial without a host, two trials showed increased number of inflorescences, *A. frigida* 592% (95% CI: 47%, 31%) and *P. pinifolius* 246% (95% CI: -0.33 %, 1,684%), while *B. gracilis* showed a decrease -4% (95% CI: -89%, 717%).

Castilleja linarifolia: All trials had *C. linarifolia* individuals survive, though none were statistically significantly different (Figure 1). Both *A. frigida* and *P. pinifolius* had 100% survival. The other trials had high survival numbers, *P. strictus* 0.89 (95% CI: 0.69, 0.98), Absent 0.63 (95% CI: 0.48, 0.75), *E. jamesii* 0.58 (95% CI: 0.44, 0.72) and *A. millefolium* 0.50 (95% CI: 0.36, 0.64). The size data had no significantly different trials, but all had data (Figure 2). Compared to the Absent trial, all trials increased in size: *A. frigida* 1,390% (95% CI: 267%, 5,944%), *E. jamesii* 98% (95% CI: -52%, 705%), *P. pinifolius* 465% (95% CI: 39%, 2,293%), *P. strictus* 347% (95% CI: -33%, 2,875%) and *A. millefolium* 16% (95% CI: -72%, 372%). All trials produced measurable inflorescences, with three decreasing in the number of inflorescences compared to the Absent trial, *E. jamesii* -72% (95% CI: -99%%, 308%), *P. strictus* -53% (95% CI: -99%, 1,091%) and *A. millefolium* -21% (95% CI: -88%, 423%). Two trials increased in the number of inflorescences produced, *A. frigida* 721% (95% CI: 217%, 3,096%) and *P. pinifolius* 41% (95% CI: -73%, 726%). 8 of the trials differed significantly: *A. frigida* – Absent (p <0.001), *E. jamesii* - Absent (p <0.001), *A. frigida* - *A. millefolium* (p <0.001), *E. jamesii* - *A. millefolium* (p = 0.031), *E. jamesii* - *A. frigida* (p <0.001), *P. pinifolius* - *A. frigida* (p <0.001), *P. strictus* - *A. frigida* (p <0.001) and *P. pinifolius* - *E. jamesii* (p <0.001).

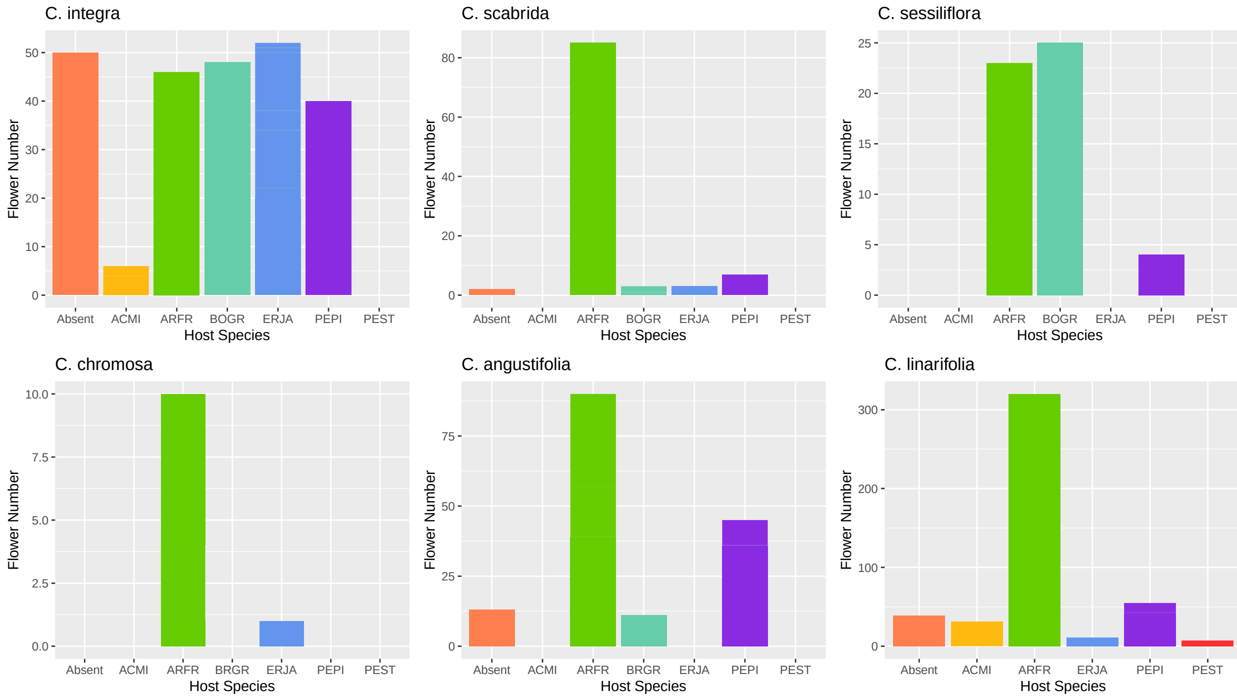

Figure 3. Total count of inflorescence number from each trial. Lack of error bars is due to total count data presented. No host control (Absent) = orange, AMCI (*A. millefolium)* = yellow, ARFR (*A. frigida)* = green, BOGR (*B. gracilis*) = turquoise, ERJA (*E. jamesii)* = blue, PEPI (*P. pinifolius)* = purple, PEST *(P. strictus)* = red.

Discussion

This study set out to determine which of six host species provided the best pairing for producing the most vigorous individuals among six hemiparasitic *Castilleja* species in horticultural settings. Collecting data on the proportion of surviving individuals, aboveground size and inflorescence number provides insight into which host species yields the most vigorous *Castilleja* individuals. I hypothesized that *A. frigida* would be the best host in producing vigorous *Castilleja* and Absent trials would yield the least vigorous *Castilleja* due to the lack of a host. The results show that each *Castilleja* species showed differing rates of survival, size and flowering with each host species. Generally, across *Castilleja* species, *A. frigida* trials produced the most vigorous *Castilleja* while *A. millefolium* trials had the least successful outcomes for each *Castilleja* species.

The highest rates of survival were in *C. linarifolia*, with two trials (*A. frigida* & *P. pinifolius*) achieving 100% survival and the lowest surviving trial (*A. millefolium*) still achieving a modest 50% survival rate (Figure 1). The *Castilleja* species with the lowest survival rates was *C. angustifolia* with the highest trial (*A. frigida*) survival rate at 60%. Interestingly, Love and McMannon (2017) found that of the 34 *Castilleja* species grown, *C. integra* and *C. chromosa* were the highest surviving species in their trials. My results show *C. integra* had high survival rates and consistent flowering, but *C. chromosa* did do not produce many trials with high survivability and had the lowest number of inflorescences out of all species. The differing results may be due to the larger sample size over multiple years in the Love & McMannon experiment compared to the limited sample size and fewer years in my data. Despite the differences among *Castilleja* species, there was a general trend in which host species produced the most vigorous and least vigorous individuals.

Consistent with my first hypothesis, *A. frigida* trials produced the most vigorous *Castilleja* across species. Though *E. jamesii*, *P. pinifolius* and *B. gracilis* often had similar or higher rates of survival than *A. frigida* (Figure 1), *A. frigida* had numerous trials with statistically significant higher flower production than other host species (Figure 3). The combination of consistent survival rates, large sizes and massive quantities of inflorescences suggest that *A. frigida* is the best host species to pair with *Castilleja* species in horticultural settings to produce the healthiest plants. Love and McMannon (2017) found similar results where *A. frigida* produced the most market ready *C. integra* individuals. Similarly, *P. pinifolius* and *E. jamesii* were also included in the top host species (Love & McMannon, 2017). In contrast, numerous studies in Chinese grasslands found that *A. frigida* negatively influenced the growth of neighboring species suggesting an antagonistic allelopathic effect (Li et al., 2011; Wang et al., 2022; Ziao-Jang et al., 2011). However, these studies were looking at allelopathy of *A. frigida* through the release of volatile organic compounds (VOCs) and secondary metabolites, not resisting direct root parasitism. My results indicate that *A. frigida* is susceptible to root parasitism and the parasite grows robustly. Future research could focus on the mechanisms that allowed *Castilleja* to be so successful paired with *A. frigida* when numerous other species were shown to be negatively influenced by this dominant grassland species.

Inconsistent with my second hypothesis, *A. millefolium* trials had lower survival rates than Absent trials in all *Castilleja* species (Figure 1). No *Castilleja* species, except for *C. linarifolia*, had a survival rate above 25% when grown with *A. millefolium*. This could be due to the unique chemical compounds found in *A. millefolium*, which has been used for centuries to treat a myriad of ailments including malaria, hepatitis and jaundice and has proven antibacterial properties (Akram, 2013; Candan et al., 2003). Even more striking, *A. millefolium* has been shown to be resistant to a root parasitic nematode (Balsdera et al., 2021). The unique pathogen resistant properties in the root system could explain why *Castilleja* individuals, which tap into hosts root systems to steal nutrients, were unable to grow successfully with *A. millefolium*. Further research could investigate the specific mechanisms behind *A. millefolium's* defense against plant hemiparasites.

One of the key limitations to this study is the varying sample size for much of the data collected. The survival trials all had relatively robust sample sizes of 48 or 42 for *B. gracilis,* though *P. strictus* only had an *n* of 12 due to being grown only in the second year. However, the size data and inflorescence number had much smaller sample sizes due to only being recordable in mid-summer. These small sample sizes may have skewed the data. Additionally, the year 1 and 2 data were compiled into one dataset, which may not account for the additive effects of the perennial *Castilleja* species. A third year of study is currently being conducted at the Denver Botanic Garden which will provide much more robust data for analysis. Despite these limitations, the results from this manipulative experiment suggest substantial differences between host species' ability to produce vigorous *Castilleja*.

The finding that *A. frigida* is the most consistent host species for producing healthy, robust *Castilleja* across the six species studied has important implications for horticulturalists attempting to successfully grow iconic *Castilleja* species in collections or for commercial purposes. Transplanting previously germinated *Castilleja* seedlings with *A. frigida* seedlings provides the best chance for producing sturdy *Castilleja* capable of flowering prolifically and providing stunning color in the garden. In contrast, some host species, like *A. millefolium,* may have antagonistic effects on *Castilleja* growth and should be avoided near hemiparasites. Furthermore, these data shed light on host compatibility in wild populations of *Castilleja* and hemiparasitic plants generally by showing the differentiating responses of parasites to unique host species. Additional research into the mechanisms driving responses between host and parasite will allow horticulturalists to grow robust *Castilleja* specimens and discover more details about host-parasite interactions.

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CHAPTER 4.

Remediating Ski Industry Impacts on Montane & Alpine Plant Communities

Introduction

Colorado is famous for being at the epicenter of the ski world due to its accessible, majestic mountains and copious amounts of light, buttery snow. In Colorado, the ski industry generates $4.8 billion in annual economic output, supports 46,000 year-round equivalent jobs and provides $1.9 billion in labor income, making it a centerpiece in the state economy (RRC Associates, 2020). However, ski resorts require large scale alterations to the physical characteristics of montane areas by creating and maintaining groomed runs, often through mechanically shifting soil to create a soft grade (Barni et al., 2007; Burt et al., 2009). Mechanically grading runs severely disrupts soil composition and negatively impacts native vegetation (Hudek et al., 2020; Pinitaldi et al., 2007). Furthermore, resorts manipulate snow dynamics by artificially producing snow to create longer seasons and compacting the snow to build easy runs (Rixen et al., 2008). The altered conditions disrupt natural snow formation and delay melting, which severely disrupts the phenology of alpine plants (Wipf et al., 2005; Rixen et al., 2008). To reduce the environmental impacts of ski resorts on montane and alpine plant communities, the industry must work to remediate current mechanically graded runs using best restoration techniques and commit to new run creation without using mechanical grading above 12,500 feet (Burt & Clary, 2016). Implementing alpine plant conservation into resort management can build upon the burgeoning sustainability movement growing across the ski industry working to cultivate care for montane biota through education and environmental certification.

Ski Impacts on Montane Plant Communities

The creation of ski runs perturbs montane plant communities. To create ski runs free of obstacles and with gentle slopes, resorts use heavy machinery to grade the run and remove boulders and tree stumps leaving groomed areas that can be used throughout the season (Pinitaldi et al., 2007). This method for building ski runs, known as mechanical grading, severely damages the underlying soil composition and seed bank of native plants (Barni et al., 2007; Burt et al., 2009; Hudek et al., 2020). In the Sierra Nevada of California, ski runs contained 34% less soil organic carbon than reference areas (Sanchez-Maroñon et al. 2007). Graded ski runs in the European Alps had significantly lower vegetation cover and productivity compared to reference areas (Roux-Fouillet et al., 2011). The altered soil composition and disturbed plant community leads to much higher levels of erosion in mechanically graded runs, destabilizing the newly created areas and impacting watershed sediment loads (Pinitaldi et al., 2007). Thus, resorts have begun to establish methods to improve vegetation communities and build healthier soils.

Some best practices have been established to reduce the impact of mechanically graded ski runs and improve ecosystem function, with varying levels of success. One simple method to improve ecosystem outcomes involves storing and reapplying the topsoil removed during the creation of the run, to preserve the seed bank held in the soil (Hudek et al., 2020). In addition to preserving the natural seed bank, hydroseeding of a native plant mix applied to the site can aid in soil retention and revegetation rates (Hudek et al., 2020). However, seed mixtures should avoid generic, commercial mixes and strive to include seed collected from local populations to achieve best rates of recovery (Argenti et al., 2009). Graded runs that applied basic remediation practices showed an increase in species diversity and evenness and included more native species at levels similar to reference areas, though soil characteristics had reduced organic carbon and higher pH (Hudek et al., 2020). Simple, low-cost remediation methods implemented on mechanically graded runs can improve the ecological health of the mountain plant community.

Another major disturbance to alpine plants comes from the artificial snow conditions necessary for skiing. To create easily skied areas, snow grooming machines pack down the snow nightly, resulting in much denser snow and significantly delaying spring snow melt (Figure 1).

Figure 1. Delayed spring snowmelt on a ski run (Freppaz et al., 2013).

The altered snow dynamics delays plant phenology by up to five weeks, severely disrupting natural plant-pollinator cycles (Rixen et al., 2008). Additionally, the creation of artificial snow alters the chemistry of the soil by using additives such as an assortment of salts and a sterile bacteria *Pseudomonas syringae* to the water to induce ice crystallization (Rixen et al., 2008; Roux-Fouillet et al., 2011). Due to water for artificial snow being sourced from local reservoirs, nutrient content and ionic quantities vary dramatically from natural snow (Freppaz et al., 2013). For example, the mean conductivity measured in artificial snow from 10 Swiss ski resorts was 61 μS compared to 15 μS in natural snow conditions (Rixen et al., 2003). The artificial increase in nutrients selects against plants tolerant of low nutrient levels, which are often native plants adapted to harsh, low nutrient soils (Rixen et al., 2003). Unfortunately, the use of artificial snow is only projected to increase due to a changing climate, intensifying the effect on alpine plants and creating a massive expense on ski resorts bottom line.

Climate change severely disrupts the winter sports economy through reduced winter snowpack and shorter cold seasons, increasing reliance on costly and energy intensive artificial snow to make money. This issue currently affects resorts as winter snowpack in northern latitudes decreased 10% since 1966 (Moen & Fredman, 2007). Thus, the percentage of U.S. resorts creating artificial snow increased from 59% in 1984 to 90% in 2001 (Rixen et al., 2003). This trend is predicted to continue as climate models of December snow water equivalent at ski resorts in the Western U.S. forecasts a decrease of 26% (Lackner et al., 2021). Yet, the changing climate, which perturbs both alpine plants and ski resorts, might provide a glimmer of hope for montane plant stewardship. Due to the damages that climate change exerts on the ski industry bottom line, there is a concerted push in many resorts to work towards sustainable practices that reduce greenhouse gas production, increase waste diversion and improve local transportation (Vail Ski Resorts, n.d.). Expanding these programs to include meaningful protection for plant communities could improve outcomes for both local ecosystems and resorts.

Stakeholders

Skiing is a growing industry that includes a wide variety of diverse stakeholders invested in enjoying the sport, spending time in the mountains and generating income from the increased popularity. Unfortunately, creating ski runs, especially through mechanical grading, severely harms montane and alpine plant communities, a sensitive and unique collection of species advocated for by passionate botanists. Striking a balance between the needs and wants of each stakeholder requires collaboration and communication. It is important to find compromise between maintaining the economic viability of this industry while creating positive outcomes for montane and alpine plant communities.

Ski owners and operators

Skiing is big business, generating $4.8 billion in annual economic output in Colorado alone (RRC Associates, 2020). The owners of alpine ski resorts want to continue to increase revenue and create a sustainable business model that remains profitable and injects revenue into the local economy. To accomplish this, owners need large numbers of enthusiastic skiers and lots of snow. Resort management values maintaining a profitable bottom line to ensure that the business remains viable. Thus, finding ways to aid the montane environment is useful when it can benefit the resort through improved soil health and thus ski conditions, while remaining cost-effective. Gaining recognition and certification from sustainability auditors generates good public relations and improves resort visibility and visitation. Additionally, resorts can market hiking in their healthy plant communities as a way to generate summer income. Ultimately, resort owners and operators will work to comply with regulation and best practice in creating healthy plant communities in their resorts if they can benefit from the positive effects.

Botanists and Allies

Alpine and montane plants are extremely sensitive to change, and the ski industry creates an outsized impact on these plant communities. Botanic organizations such as the Denver Botanic Garden and Betty Ford Alpine Garden, work diligently to conserve these unique species through comprehensive in situ and ex situ conservation programs. Improving outcomes for montane plant communities motivates this group of advocates and scientists who respect the diversity and beauty of the minute flora that inhabit mountainous areas. Botanists study plant communities and work diligently to protect them, especially alpine species that exist above treeline. Galvanized by their fascination and admiration for montane plant communities, botanists and environmental activists are motivated to undertake the immense challenge of working with the ski resorts to improve outcomes for alpine and montane plant communities in and around ski areas.

Skiing Enthusiasts

Many people enjoy the thrill of flying down a snowy slope. Globally there are an estimated 400 million visitors annually to over 2,000 ski resorts in 100 countries (Pinitaldi et al., 2013). This rapidly expanding sport has gone from a niche, luxury outdoor activity to a mainstream icon with a massive global audience. The vast majority of skiers likely give little regard to the impact of the sport on plant communities and are looking for cheap lift tickets to enjoy a day filled with groomed runs, great views and adrenaline induced fun. However, incorporating more of the natural parts of skiing into the general culture is a growing trend in the American West as evidence by the increase in backcountry skiing and resorts built without chairlifts (Higgins, 2021). This aligns with a renewed global awakening of the ecological impacts inflicted from human activity, which has begun to shift attitudes towards rewarding ski areas that value sustainability and stewardship of the land.

Climate Activists

There is already a concerted effort in the ski industry to push for a more sustainable energy production system due to the outsized impact climate change has on skiing. Examples of these groups include Protect Our Winters (POW), with a mission to “help passionate outdoors people protect the places they live and love from climate change” (Protect Our Winters, n.d.). Similarly, the Sustainable Tourism and Outdoors Kit for Evaluation (STOKE) rates resorts on numerous sustainability criteria and only certifies resorts that pass 70% of the sustainability metrics (STOKE, n.d.). POW advocates for climate action in local and national policies and is buoyed by a cast of ski and snowboard legends. STOKE ensures that resorts adhere to their sustainability goals by auditing resort functioning to create sustainable practices. In a similar fashion to botanists, these organizations are motivated by a concern and respect for the natural world and work to protect it for future generations. These organizations operate in the business of sustainability and work to achieve favorable environmental outcomes for nature and customer.

US Forest Service

Almost all Colorado ski resorts are located on United States Forest Service (USFS) land and nationally 143 of the 422 ski areas lie on USFS land (Christiansen, 2020). Thus, any large alterations to these areas, like run construction or ski lift implementation, triggers the National Environmental Policy Act (NEPA) process. A major part of this process involves monitoring for threatened and endangered species and considering alternatives to the proposed action (U.S. Forest Service, 2021). In accordance with environmental regulations and following its mandate to manage areas for multiple uses, including recreation and natural resource protection, the USFS is duty bound to conserve the natural resources of the United States of America (Burt & Clary, 2016; U.S. Forest Service, 2013). Following the multifaceted goal of recreation and resource protection involves striking a balance between expanding resort infrastructure to enhance recreation and limiting impacts to the ecological integrity of the land.

Resolution

To alleviate the negative impacts from skiing on alpine plants, while still ensuring a reliable ski economy, resort owners, land managers and conservationists must work together to achieve a sustainable outcome for all parties. First, the ski industry must show that it recognizes the impacts on montane plant communities and work towards implementing remediation practices on existing graded slopes (Hudek et al., 2020). Enlisting the support of alpine plant experts and USFS to create seed mixes from native stock can improve restoration outcomes and engage important stakeholders in the solution (Argenti et al., 2009). Including multiple stakeholders working in tandem to remediate damage to soil and vegetation will reduce erosion, thereby increasing ski run stability and improving plant communities.

A more challenging commitment from the ski industry includes a ban on graded run construction in alpine areas (above 12,500 ft), where the habitat is most sensitive to disturbance (Pinitaldi et al., 2013). As almost all Colorado resorts rent the land from the U.S. Forest Service (USFS), the USFS must implement policies restricting mechanical grading on their land to better follow the mission of the USFS, to sustain the health, diversity, and productivity of the nation's forests and grasslands to meet the needs of present and future generations (U.S. Forest Service, n.d.). However, while explicitly outlawing mechanical grading in the alpine would improve the health of the mountain ecosystem (Burt & Clary, 2016), restricting graded run construction could negatively impact a ski resort's business, especially if only resorts on USFS land are restricted.

Therefore, resorts that adhere to restrictions on mechanically grading the alpine should earn a reduced rate of rent to lease USFS land as the area follows management more in-line with the expressed mission of the USFS. Decreased rent would potentially make up for any reduction in revenue lost to competitor resorts that continue expanding graded runs in the alpine and may actually boost the resort's bottom line, as Colorado resorts paid $30.1 million in rent during the 2018-2019 season (Blevins, 2021). A compromise between USFS and resort management would benefit alpine plant communities while maintaining the economic viability of resorts.

In addition to financial compensation from the USFS, resorts that take the leap to ban mechanical grading in alpine areas will be rewarded with increased publicity from outside sustainability auditors, like STOKE certification. Highlighting collaboration between USFS and Denver Botanic Gardens to restore and protect vegetation communities will draw in skiers looking for a more conscientious form of recreating, a business model already expanding in popularity (Higgins, 2021). Reaping economic benefits from ecological stewardship incentivizes operators to follow through on commitments and protect plant communities. Ski areas can model publicity practices on Vail Resort's Epic promise by expanding educational outreach to highlight efforts protecting mountain ecosystems with guided summer hikes, thus generating income from ecological stewardship (Vail Ski Resort, n.d.). Thinking creatively about ways to engage stakeholders to achieve favorable outcome for ski resorts, outdoor enthusiasts, land managers and montane plant communities, will create a healthier mountain community for all forms of life that call these magnificent places home.

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