

Nicpon K, Lane J, Cudkowicz B, McLaughlin J. 2026. Native plant association with *Lupinus rivularis* on coarse sediments following dam removal; Elwha River, Washington. *Northwest Science* 99(1): *in press*.

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Native Plant Association with *Lupinus rivularis* on Coarse Sediments Following Dam Removal; Elwha River, Washington

Running footer: Lupines May Support Elwha Revegetation

3 tables, 4 figures

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Abstract

Facilitating native revegetation is important in restoration following dam removal, which exposes large areas of bare sediment vulnerable to invasion by exotic species. Coarse sediments in drained reservoirs provide a hostile growth substrate due to low moisture retention, low nutrient concentrations, low organic matter, and exposure to wind and intense sun. Revegetation on the Mills Reservoir bed, the largest restoration site in the Elwha River dam removal project, included seeding of riverbank lupine (*Lupinus rivularis*) to ameliorate harsh sediment conditions and facilitate succession. We assessed relationships between *L. rivularis* and other plants by measuring cover of native and introduced plants in coarse sediment plots stratified by three levels of *L. rivularis* density. We quantified relationships between lupine density and plant cover using a linear mixed model with sampling areas treated as a random factor. We evaluated relationships with species richness using a Kruskal-Wallis test. Our results revealed positive associations between *L. rivularis* and native species but not introduced species. The mechanism for these results needs further study, particularly determining whether the relationships are correlative or causal. Regardless of the mechanism, seeding with native nitrogen-fixing species could have broad application as dam removal projects increase in coming decades and revegetation of former reservoirs becomes a pervasive challenge.

Key Concepts

- Successful restoration of coarse sediments in dam removal sites requires suppression of introduced species and establishment of a diverse native plant community.
- *Lupinus rivularis* abundance is correlated with establishment of native vascular plant species and does not correlate with introduced species on dewatered coarse sediment.

Keywords

Ecological restoration, lupine, revegetation, soil amelioration, dam removal

Introduction

Dam removals are increasing at regional, national, and global scales, creating a need for post-removal restoration strategies. Revegetation of drained reservoirs is a key restoration priority because reservoirs are often the river reaches most severely impacted by dams and dam removals (Shafroth et al. 2002, Bellmore et al. 2019). Hastening revegetation is needed to stabilize residual reservoir sediment, impede the spread of introduced plants, and expedite reconnection of riverine and terrestrial environments (Hjältén et al. 2016). While the need for knowledge about reservoir revegetation is great, information to guide implementation is lacking (Chenoweth et al. 2023), especially for large dam removals (O'Connor et al. 2015, Bellmore et al. 2019). Most large reservoir sediment deposits lack shade and lie distant from nutrient sources, including litterfall and marine-derived nutrients. Consequently, large reservoir revegetation usually requires improving local growing conditions *in situ*, which is slower and more difficult than revegetating small reservoirs influenced by adjacent processes (Johnson et al. 2023).

Harsh conditions for plant growth hinder revegetation on large, dewatered reservoirs. Reservoir sediments contain low concentrations of many nutrients (Cavaliere and Homann 2012) and moisture drains rapidly in coarse sediments, causing stress in young plants (Chenoweth et al. 2023). The absence of sediment organic matter or structural legacies compound sediment moisture limitation (Kardouni et al. 2023). These conditions simultaneously hinder establishment of native plants and facilitate the spread of introduced plants, which often are adapted to survive in disturbed environments (Funk 2013). Developing strategies to alleviate reservoir sediment

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conditions is one of the most important restoration needs associated with dam removal (Chenoweth et al. 2011).

Revegetation programs often emphasize active planting of native trees and shrubs (Chenoweth et al. 2023). Elwha planting results have been mixed, contingent on location within the reservoir, sediment conditions, and timing relative to reservoir drawdown (Chenoweth et al. 2023, Shafroth et al. 2024). Revegetation has been rapid in substrates with high moisture retention, where dense stands of trees and shrubs established naturally and grew rapidly. Active planting was unnecessary in these areas, including fine sediment deposits and areas near perennial streams. Natural woody plant establishment also occurred on sediment terraces with prolonged exposure to a shallow water table during pauses in reservoir drawdown. In contrast, woody plant revegetation has been low and slow in coarse sediments with low moisture retention. Active planting in coarse sediments increased species diversity but not abundance (Chenoweth et al. 2023). Dispersing seeds of native grasses and forbs by hand or airplane had equivocal effects on plant cover in coarse sediments and reduced non-native plant frequency and species richness (Morgan 2018, Chenoweth et al. 2023).

Robust plant growth consistently follows seeding of *Lupinus rivularis*, a pioneer species adapted to coarse substrates (Daw 2019, Chenoweth 2023). As a nitrogen-fixing species that grows as an annual, biennial, or short-lived perennial, *L. rivularis* has the potential to increase sediment nutrient content (Callaway 1995). Rapid growth and spread of lupines also can increase sediment organic matter, soil development, and moisture retention, although effects on adjacent vegetation have been variable (Morris and Wood 1989, del Moral and Rozzell 2005, Halvorson et al. 2005).

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The goal of this project was to assess relationships between *L. rivularis*, plant cover, and species richness on coarse reservoir sediments a decade after dam removal. We focused on coarse sediments in the former Mills Reservoir (Mills), the largest restoration site associated with Elwha dam removals and the greatest priority for Elwha revegetation. Following mixed effects of lupine growth reported from Mills (Kardouni et al. 2023) and other systems (del Moral and Rozzell 2005, Riege and Sigurgeirsson 2009, Vetter et al. 2018), we considered two kinds of relationships between *L. rivularis* and other plant species. First, *L. rivularis* could be associated with higher or lower cover and richness of other species. Dense growth of *L. rivularis* could impede other species due to shading or spatial preemption. Alternatively, *L. rivularis* could support greater cover and richness of other species by increasing sediment nutrients, organic matter, and water retention. Second, native and introduced species could have similar or different associations with *L. rivularis*. These associations and underlying driving mechanisms could be consistent across native and introduced species because they involve resources necessary for growth in all plants. Alternatively, associations with *L. rivularis* may be stronger with introduced species than with native species because many introduced species are adapted to open conditions with minimal soil resources. To investigate these potential relationships, we measured cover and species richness of native and introduced plants in plots distributed across coarse sediments with low, medium, or high lupine cover and compared our data with each contingency described above.

Methods

Site Description

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Our study took place in April 2024 within the former Mills reservoir on the Elwha River in Olympic National Park, Washington, USA. The Elwha basin has a maritime climate characterized by wet, mild winters and warm, dry summers. The dam was removed incrementally from 2011 to 2014 after 84 years of impoundment, constituting the largest dam removal in history at the time (O'Connor et al. 2015, Chenoweth et al. 2023). Since dam removal, about 70% of the estimated 23 megatons of accumulated sediment has eroded (Ritchie et al. 2018), leaving the remaining sediment in two distinct landforms: valley walls and terraces. The valley walls border the reservoir bed and the surrounding mature forest and are composed of water-retaining fine sediment (Morgan 2018). Below the valley walls and perched above the river are expansive, well-drained coarse sediment terraces (Chenoweth et al. 2023). Three goals drove the Elwha revegetation plan for the reservoir beds following dam removal: minimizing introduced species, stabilizing residual sediment, and establishing native forests (Chenoweth et al. 2011). This effort included extensive introduced plant control prior to dam removal and active revegetation beginning concurrently with dam removal in 2011, lasting seven years. Active revegetation spanning 14 ha of Mills valley walls and 44 ha of the terraces installed 218,116 plants of 60 species and sowed 2,193 kg of a locally sourced seed mixture composed of local grasses and forbs and including *L. rivularis* (Table 1). The remaining 26 ha of valley wall and 19 ha of terraces were left to revegetate naturally. Sediment texture determined revegetation pathways. In fine sediment, passive revegetation was robust and obviated active methods. Conversely, seeding and planting were needed in coarse sediments to hasten vegetation establishment and impede introduced species spread. In actively revegetated coarse sediments, *L. rivularis* rapidly became the most abundant plant (Morgan 2018, Chenoweth et al. 2023,

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Kardouni et al. 2023). Our work focused on terraces of coarse sediment due to their large extent, resistance to forest establishment, and support of *L. rivularis* growth.

Sampling

In 20## (# years after dam removal and revegetation), we established 18 *L. rivularis* cover class sampling zones within the coarse sediment terraces to represent the full range of *L. rivularis* density (Figure 1). Each zone consisted of a discrete vegetation patch of relatively uniform *L. rivularis* cover, selected and classified as low, medium, or high density based on visual estimates. Mean *L. rivularis* percent cover, including both living and previous-year stems, was 3.4%, 13.9%, and 31.8% in low ($n = 73$), medium ($n = 68$), and high ($n = 92$) cover class zones, respectively (233 plots total). During May and June 20##, we applied systematic sampling in each zone with a random starting point. At each point, we estimated percent cover of all vascular plant species within a 1-m² quadrat, identifying taxa to the lowest possible level. To minimize observer bias, we recorded percent cover values agreed upon by three surveyors. We classified species as native or introduced (status; USDA 2023), regardless of naturalization.

Statistical Analyses

We compared native and introduced plant cover across lupine cover classes by fitting a log-transformed linear mixed model:

$$\ln(y_{ij} + 1) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \alpha_i z_i + \varepsilon_{ij} \quad (1)$$

where y_{ij} represents percent cover (excluding *L. rivularis*) in quadrat j within zone i ; β are fixed factor coefficients; x_1 is status; x_2 is lupine cover class; z_i represent sampling zones, a random

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factor; α_i are random factor coefficients, equivalent to zone-specific intercepts; and ε_{ij} is unexplained variation. We applied a logarithmic transformation to normalize residuals. Because species richness values could not be transformed to normality, we performed a Kruskal-Wallis non-parametric analysis of variance to evaluate fixed factor effects and a post-hoc Dunn's Test to compare cover classes pairwise.

Results

We identified 40 vascular plant species within 233 plots: 26 native and 14 introduced. There were 28 forb species, three grass species, five shrub species, and four tree species (Table 1). Plant cover across all plots was $59.6 \pm 0.2\%$ (mean \pm standard error [SE]). Native and introduced plants constituted 80.1% and 19.9% of plant cover, respectively. Species actively seeded by the revegetation program (Chenoweth et al. 2011) accounted for 57.6% of plant cover, including the two most abundant species, *Achillea millefolium* (25.9% cover) and *L. rivularis* (22.8% cover). The cover mixed model accounted for 43% of inter-plot variation. Except for cover class, all fixed factor terms had large and significant influences on introduced species (Table 2). Sampling zone-specific effects (the random factor) were small relative to both the overall intercept (β_0) and residuals (Table 2). Native plant cover exceeded introduced cover across all lupine cover classes and increased in parallel with lupine cover class, whereas introduced plant cover showed no significant change with changes in lupine cover. Interaction between status (native, introduced) and lupine cover class had a dominant effect on plant cover patterns; cover increased markedly among lupine cover classes for native plants but not for introduced plants (Figure 2). Native plant cover in high lupine cover plots was 2.4 times that of low lupine cover plots.

Patterns in species richness data paralleled plant cover. Species richness averaged 4.9 species per m² (3.2 native and 1.7 introduced). Interactions between status and lupine cover class strongly influenced species richness; native species richness increased among lupine cover classes but introduced species richness did not (Figure 3). Results of Kruskal-Wallis and Dunn's tests determined all effects (status, lupine cover class, and their interaction) were significant for native species but none were significant for introduced species (Table 3). Species composition was similar across lupine cover classes with additional species, including woody plants, found in higher lupine cover classes (Figure 4).

Discussion

Our results show that *L. rivularis* was positively associated with native plant cover and species richness. In areas of high *L. rivularis* abundance, native plant cover and native species richness were markedly greater than in areas of low lupine abundance. We found no relationship between *L. rivularis* and introduced species.

The goals of restoring native ecosystems and minimizing introduced species spread are shared across most dam removals, including the Elwha River Ecosystem Restoration Project (Chenoweth et al. 2023). Rapid growth of native pioneering species, such as *L. rivularis*, may hasten restoration progress by ameliorating growing conditions and limiting the establishment of introduced species. Once established, *L. rivularis* provides shade, organic matter, and nitrogen to the surrounding substrate, improving survival of other species by hastening the transition from desiccation-prone coarse sediment to developed soil (Callaway 1995, Cavaliere and Homann 2012). Our results are consistent with this facilitation mechanism enabling a wider range of native plants to compete more effectively than disturbance-adapted introduced species.

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Alternatively, *L. rivularis* and other species could respond independently to the same abiotic conditions. Clarifying the mechanism underlying association between *L. rivularis* and other species requires further study.

Despite encouraging results, there remains much to learn about lupines and their analogues in diverse restoration programs. First, the association between *L. rivularis* and native plants needs mechanistic clarification. Second, our data from early spring may overestimate the extent of early emerging species and exclude later emerging species such as *Vulpia myuros* and *Bromus* spp., which were abundant in previous summer surveys (Chenoweth et al. 2023, Kardouni et al. 2023, Trier 2024). Third, further study is needed of lupine effects on soil development and relationships with other species over longer time scales. Time since lupine seeding may account for differences in results reported by Kardouni et al. (2023) vs. Figure 3. The apparently inverse relationship between species richness and lupine density reported by Kardouni et al. (2023) four years after seeding flipped to the positive relationship we observed ten years after seeding. Similarly, time since lupine establishment may account for mixed effects of lupine competition vs. facilitation in other systems, particularly pumice plains on Mount St. Helens (Morris and Wood 1989, del Moral and Rozzel 2005) and eroded volcanic soils in Iceland (Riege and Sigurgeirsson 2009, Vetter et al. 2018). In these systems, lupines may inhibit other species initially and facilitate their growth subsequently (Kardouni et al. 2023) via mulching in older stands (del Moral and Rozzel 2005). Uncertainty in lupine effects should be resolved prior to application of lupine-based strategies in specific ecosystems. Finally, with many lupines and other nitrogen-fixing native analogues worldwide, there is much to learn about potential efficacy and limitations of each species in system-specific revegetation programs. For example, revegetation following dam removals on the Klamath River includes seeding *Lupinus albifrons*, a

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strategy informed by Elwha experience and with similar goals (Yurok Tribe 2024). Klamath results may advance understanding of restoration benefits of lupine seeding.

If confirmed, lupine facilitation of restoration offers broad application in other regions. As the rate of dam removal accelerates, especially in North America (O'Connor et al. 2015) and Europe (Belletti et al. 2020), revegetation of reservoir sediments will become increasingly important. Revegetation programs are needed to ameliorate conditions in reservoir sediments to facilitate native plant growth and to mitigate river imperilment, biodiversity loss, and climate impacts (Lynch et al. 2023). Seeding with lupine or other rapidly growing native nitrogen-fixing species may be an effective strategy.

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Conflict of Interest

We declare that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Data Availability

Data are available at <https://doi.org/10.6084/m9.figshare.29453096.v1>.

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Author Contributions

JL, KN, BC, and JM jointly researched, designed, implemented, and wrote this article.

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Figures

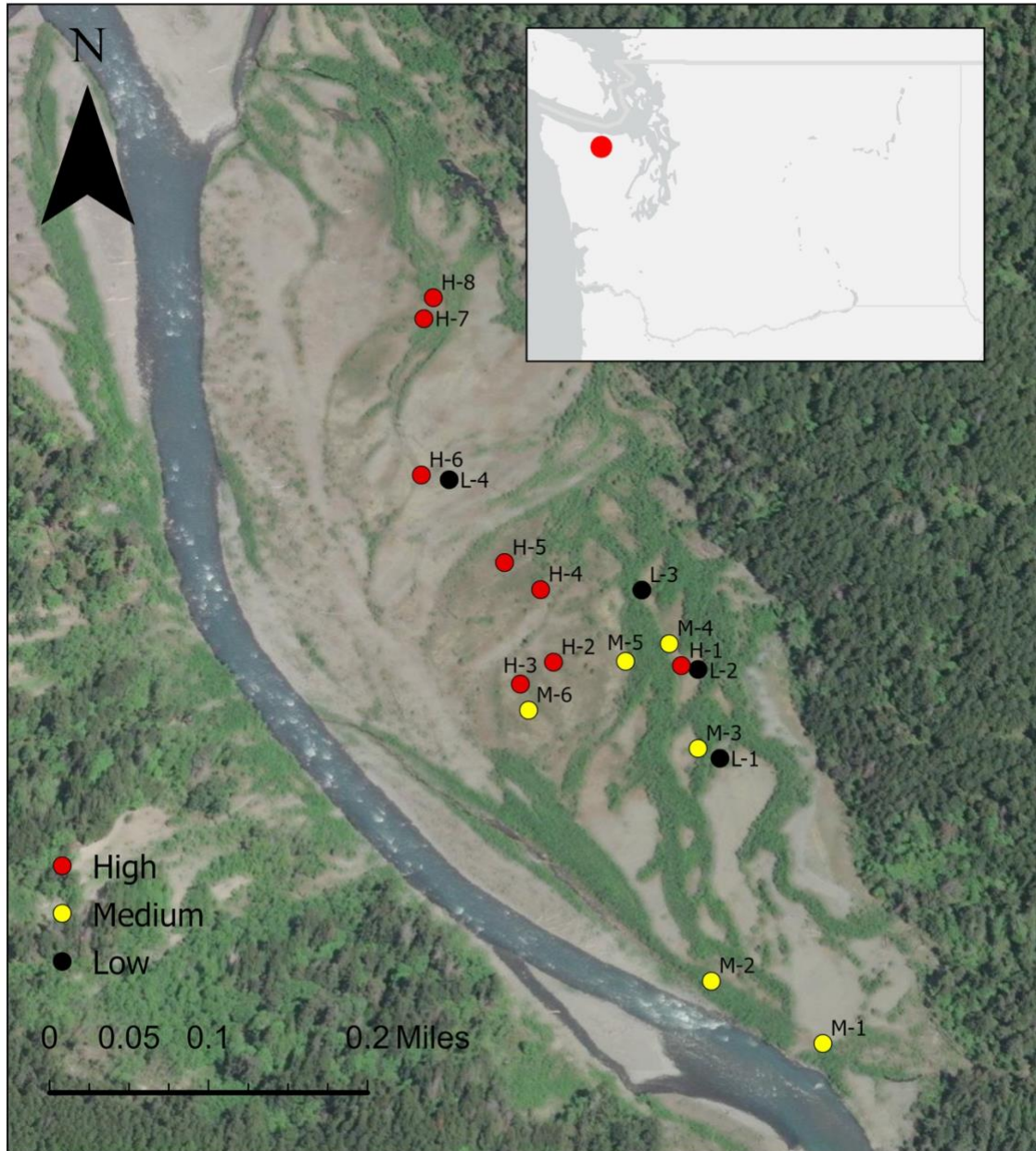


Figure 1. Map of the study site within the former Lake Mills Reservoir. Each point represents one zone from which quadrat data were collected. The study area comprised the coarse sediment terraces east of the river between Windy Arm and the outlet of Rica Canyon.

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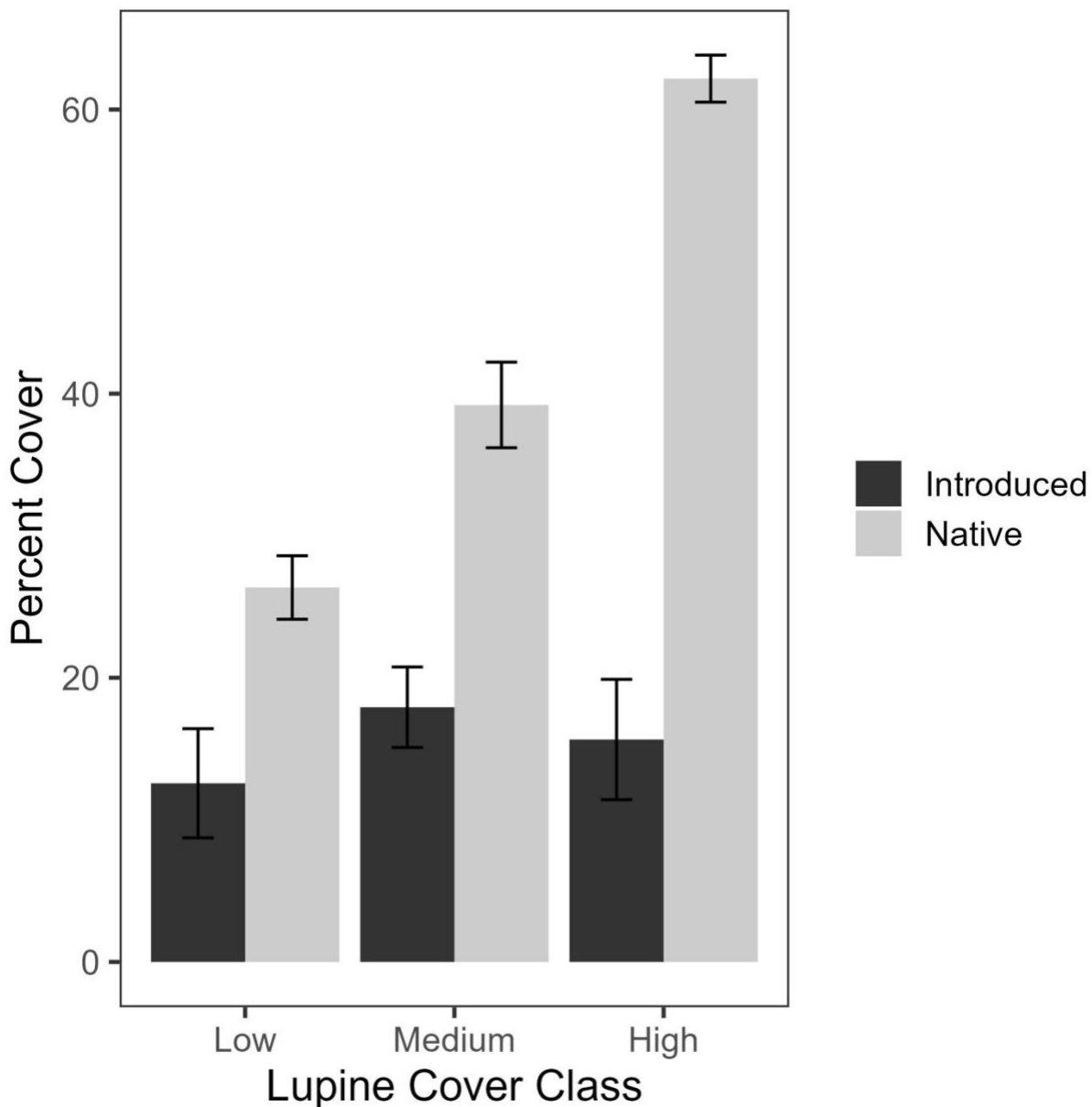


Figure 2. Mean (± 1 SE) percent cover of native and introduced plants in plots with low ($n = 73$), medium ($n = 68$), and high ($n = 92$) lupine cover.

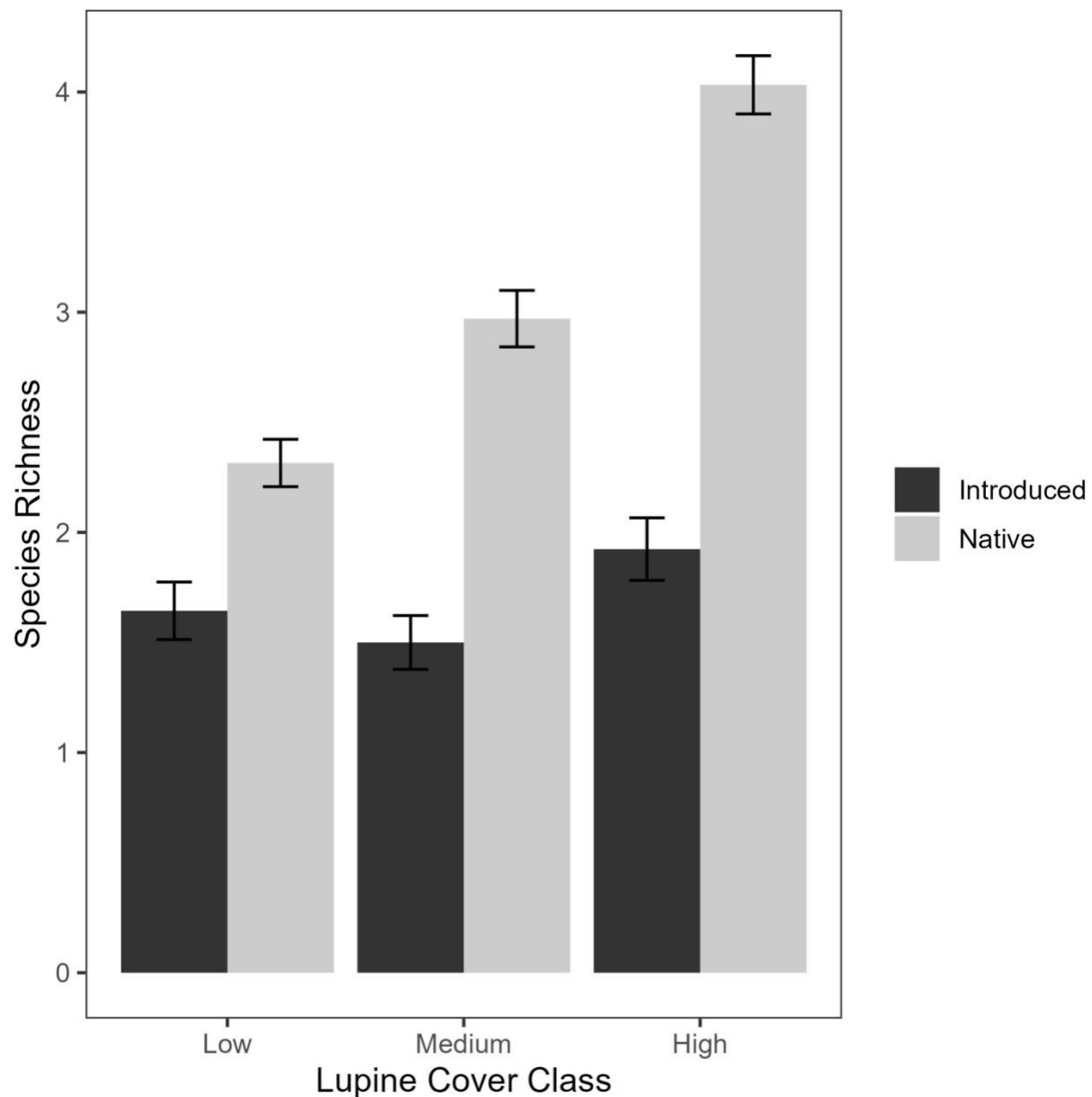


Figure 3. Mean (± 1 SE) species richness of native and introduced plants in plots with low ($n = 73$), medium ($n = 68$), and high ($n = 92$) lupine cover.

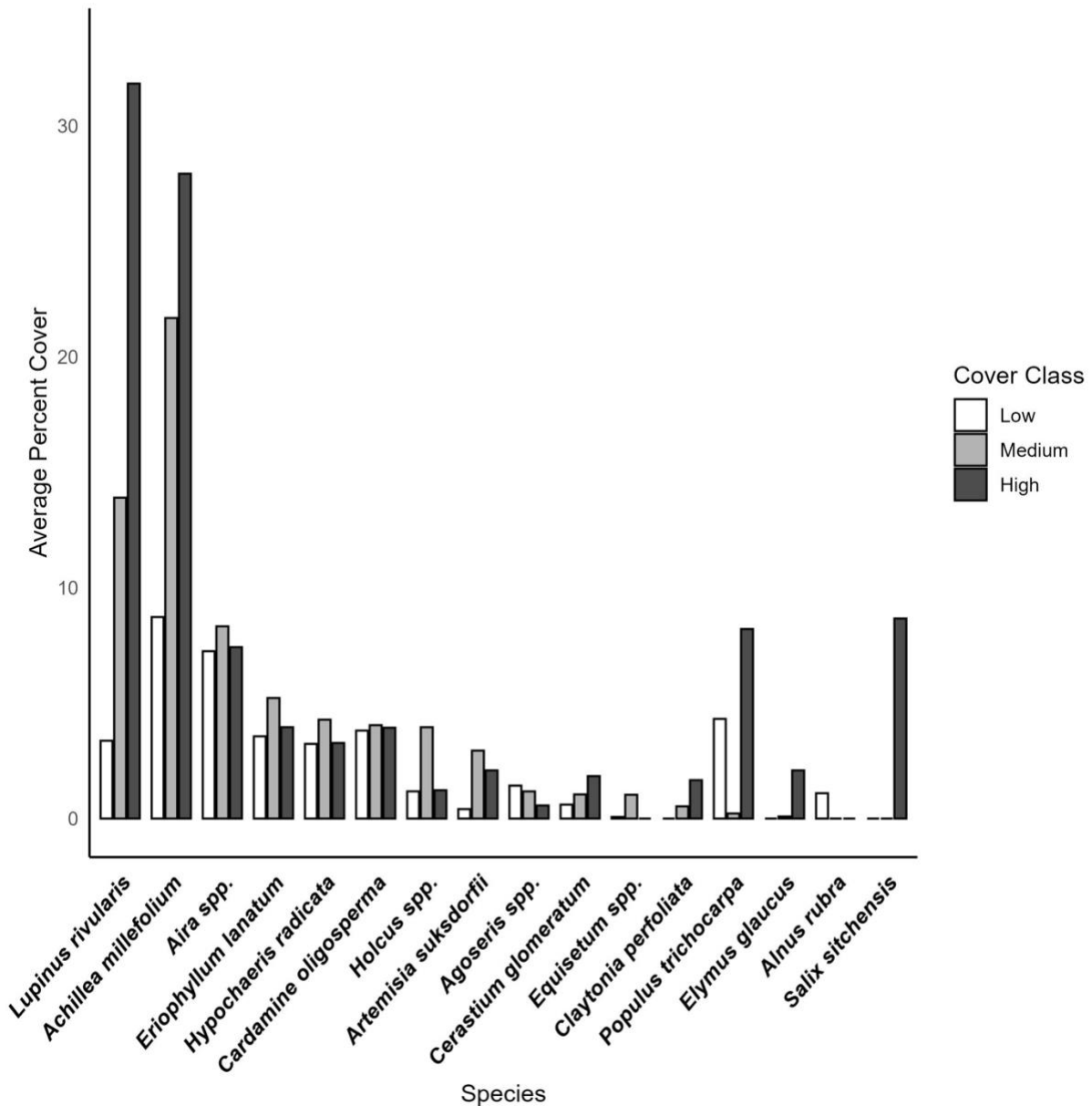


Figure 4. Percent cover by species in plots with low ($n = 73$), medium ($n = 68$), and high ($n = 92$) lupine cover classes. Bar heights represent averages from 233 plots in the former Mills Reservoir.

Tables

Table 1: List of species observed in the Lower Mills Reservoir

Scientific Name	Common Name	Status	Classification
<i>Achillea millefolium</i> *	Common Yarrow	n	Forb
<i>Agoseris</i> spp.	Mountain Dandelion	n	Forb
<i>Aira</i> spp.	Hairgrass	i	Graminoid
<i>Alnus rubra</i>	Red Alder	n	Tree
<i>Anaphalis margaritacea</i>	Pearly Everlasting	n	Forb
<i>Anisocarpus madioides</i>	Woodland Madia	n	Forb
<i>Artemisia suksdorfii</i> *	Coastal Mugwort	n	Forb
<i>Cardamine oligosperma</i>	Little Western Bittercress	n	Forb
<i>Cerastium arvense</i>	Field Chickweed	n	Forb
<i>Cerastium fontanum</i>	Common Mouse Ear Chickweed	i	Forb
<i>Cerastium glomeratum</i>	Sticky Mouse Ear Chickweed	i	Forb
<i>Claytonia perfoliata</i>	Miner's Lettuce	n	Forb
<i>Collinsia parvifolia</i>	Small-Flowered Blue-Eyed Mary	n	Forb
<i>Elymus glaucus</i> *	Blue Wildrye	n	Graminoid
<i>Epilobium</i> spp.	Willowherb	n	Forb/Shrub
<i>Equisetum</i> spp.	Horsetail	n	Forb
<i>Eriophyllum lanatum</i> *	Common Woolly Sunflower	n	Forb
<i>Galium aparine</i>	Catchweed Bedstraw	n	Forb
<i>Geranium robertianum</i>	Herb Robert	i	Forb
<i>Hieracium albiflorum</i>	White Hawkweed	n	Forb
<i>Holcus</i> spp.	Velvetgrass	i	Graminoid
<i>Hypochaeris glabra</i>	Smooth Cat's Ear	i	Forb
<i>Hypochaeris radicata</i>	Cat's Ear	i	Forb
<i>Mahonia aquifolium</i>	Tall Oregon Grape	n	Shrub
<i>Mycelis muralis</i>	Wall Lettuce	i	Forb
<i>Nemophila parviflora</i>	Small-Flowered Nemophila	n	Forb
<i>Pinophyta</i>	Conifer	n	Tree
<i>Polypodium glycyrrhiza</i>	Licorice Fern	n	Forb
<i>Populus trichocarpa</i>	Black Cottonwood	n	Tree
<i>Ribes laxiflorum</i>	Trailing Blackcurrant	n	Shrub
<i>Ribes sanguineum</i>	Red-Flowering Currant	n	Shrub
<i>Rosa gymnocarpa</i>	Baldhip Rose	n	Shrub
<i>Rubus ursinus</i>	Trailing Blackberry	n	Shrub
<i>Rumex acetosella</i>	Sheep's Sorrel	i	Forb
<i>Salix sitchensis</i>	Sitka Willow	n	Shrub/Tree
<i>Senecio vulgaris</i>	Common Groundsel	i	Forb
<i>Stellaria media</i>	Common Chickweed	i	Forb
<i>Taraxacum officinale</i>	Common Dandelion	i	Forb
<i>Trifolium pratense</i>	Red Clover	i	Forb
<i>Veronica arvensis</i>	Corn Speedwell	i	Forb

* seeded species
n = native
i = introduced

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Table 2: Linear mixed model estimates for percent cover as a function of fixed factors: cover class, status, interactions; and sample location zone as a random factor. Base state: status (introduced), cover class (low).

Fixed Factors				
	Cover Class, Status, Cover Class + Status			
	Coefficient	Std. Error	t-value	p-value
Intercept	2.05	0.23	8.95	<0.001
Status (native)	0.74	0.16	4.58	<0.001
Medium Cover Class (introduced)	0.21	0.31	0.67	0.51
High Cover Class (introduced)	0.15	0.29	0.51	0.62
Native+Medium Cover Class	0.70	0.23	3.00	<0.01
Native+High Cover Class	0.94	0.22	4.32	<0.001

+ denotes an interaction term

Random Factor		
	Sampling Zone	
	Variance	Std. Deviation
Zone	0.158	0.397
Residual	0.955	0.977

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Table 3: Results of a Dunn's Test for introduced and native species cover class comparisons

Comparison	Z	p-value
Introduced Species		
h-l	1.28	0.60
h-m	1.76	0.23
l-m	0.48	1.00
Native Species		
h-l	7.72	<0.001
h-m	4.60	<0.001
l-m	-2.82	0.01

h = high lupine cover class

m = medium lupine cover class

l = low lupine cover class

Accepted