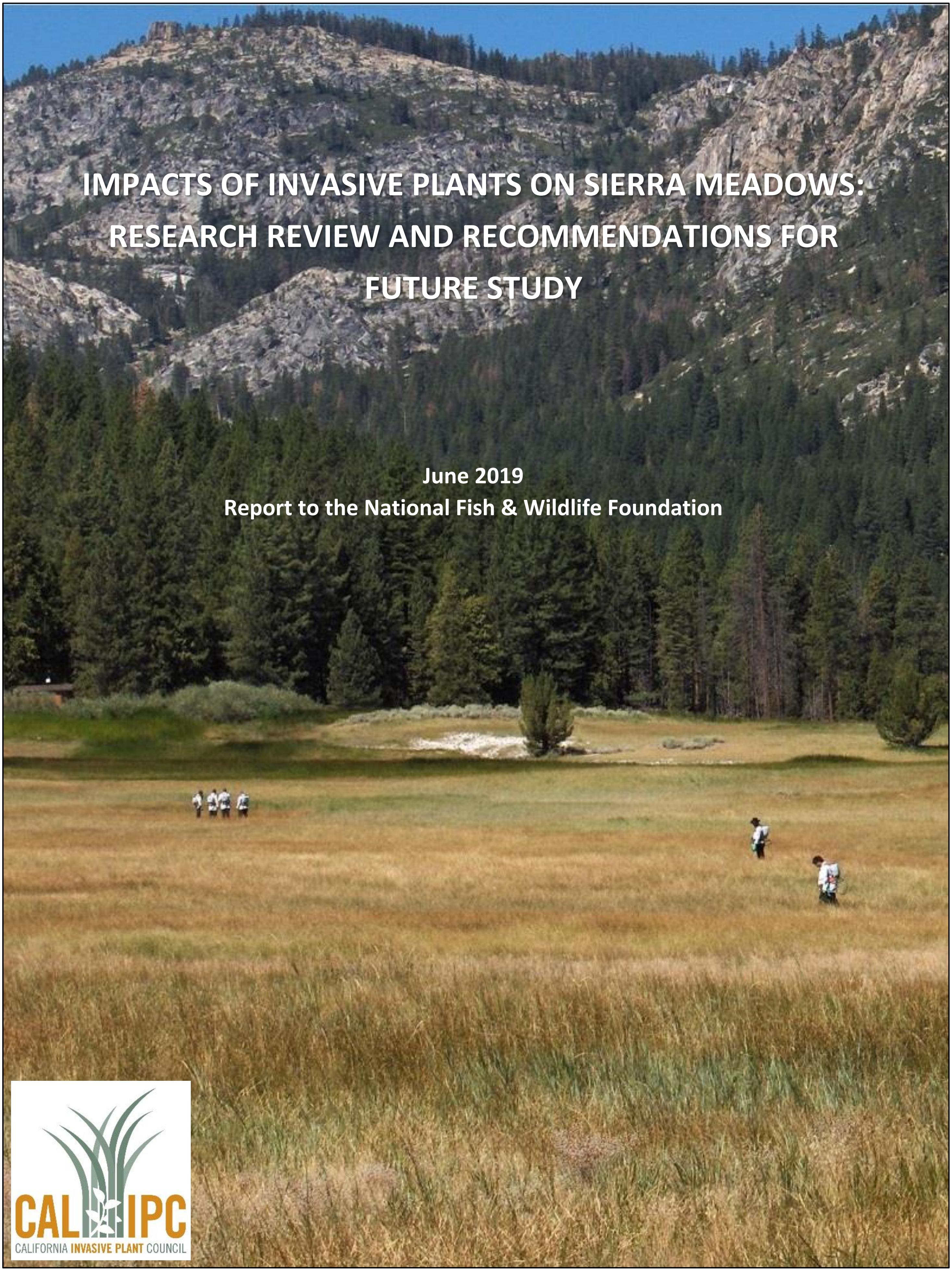

# IMPACTS OF INVASIVE PLANTS ON SIERRA MEADOWS: RESEARCH REVIEW AND RECOMMENDATIONS FOR FUTURE STUDY

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Report to the National Fish & Wildlife Foundation

CAL-IPC

CALIFORNIA INVASIVE PLANT COUNCIL

## 1. OVERVIEW

In this report, we summarize existing research on the impacts of invasive plants on Sierra Nevada meadows and propose future study to further address critical questions regarding their potential impacts and functional role. We focus on the impacts of invasive plants on water, carbon and wildlife because these are natural resource values that are a top concern with climate change and meadow degradation. We define invasive plants as those non-native plant species that can have biotic or abiotic impacts that are deemed to be harmful to biodiversity or natural services.

Sierra Nevada meadows are comprised primarily of herbaceous plant species and have surface water or shallow groundwater at a depth of <1m (Weixelman *et al.* 2011). High water table typically limits the establishment of upland trees and shrubs that occur in surrounding areas. Wet meadows have some surface water and are comprised mostly of rhizomatous grasses, sedges and rushes and interspersed with a few rhizomatous broad-leaved (forb) or bulb-forming plants. Moist meadows are more heterogeneous, consisting of proportionally more forbs and, occasionally, moisture-tolerant shrubs. Dry meadows contain some shrubs, more forbs, and fewer rhizomatous sedges and rushes.

Wildlands across the country are increasingly impacted by various human-related disturbances. Over 20 years ago these were already listed as: (1) recreational use and management, (2) livestock grazing and management, (3) fire management, (4) introduction of alien species, (5) water diversion/hydrological impairment, (6) impacts of climate change (at that time considered atmospheric pollutants), and (7) management of adjacent lands (Cole and Landres 1996). The same stressors still exist for mountain meadows. Excessive livestock grazing and hydrological impairment have been reduced in many meadows, but other stressors, including invasive species and climate change, remain and have increased in their relative potential impact.

Intact meadows are a valued resource because they support high biodiversity and sensitive species, have aesthetic value, and function as mountain reservoirs by absorbing water from melting winter snowpack and releasing it slowly through the water table and as surface flow. Historic disturbance from overgrazing, logging, beaver hunter, and mining have degraded Sierra meadows by impacting hydrology. Climate warming trends pose new threats by changing habitat conditions for resident species and by making meadows conditions more favorable to invasive species.

The recent publication of several planning documents and technical reports (e.g., Stillwater Sciences 2011, 2012, American Rivers 2012, Vernon *et al.* 2019), along with the establishment of the Sierra Meadows Partnership and Strategic Plan (Drew *et al.* 2016) have together led to an increase in collaboration and interest in meadow restoration and associated hydrogeomorphologic research. Our discussion will not include restoration-specific research relating to methodology and specific functional goals unless implications of results are linked to invasive plants. Instead, we focus here on invasive plant issues that may affect the outcome of restorations, exacerbate degraded conditions in damaged meadows, or damage otherwise pristine meadows.

Managers, restorationists, and researchers alike agree that hydrologic function is a prerequisite for healthy meadow systems and that the ultimate end goal of a meadow restoration is a native-dominated community that has typical meadow functions and species. Restorations are commonly implemented with the expectation that restoring hydrogeomorphology will automatically lead to the return of native meadow species and associated resilience. While an “if you build it they will come” approach has some merit, the plants that will come may be non-native and, potentially, invasive. Figure 1 (adopted from Viers *et al.*, 2013), with potential transition of a degraded meadow to a highly vulnerable meadow (as indicated by the yellow arrow added), shows the inherent risk in a restoration that does maintain the functions that it was intended to provide. So we are left with the important question—will non-native plants provide the same functions as native vegetation or will they degrade meadow function? Given the recent surge in restoration activities and increasing levels of recreational access and associated inadvertent introductions of non-native species, a better understanding of invasive plant impacts is urgently needed in order to strategically inform what management activities to implement, where to focus, and which species should be aggressively addressed in meadows.

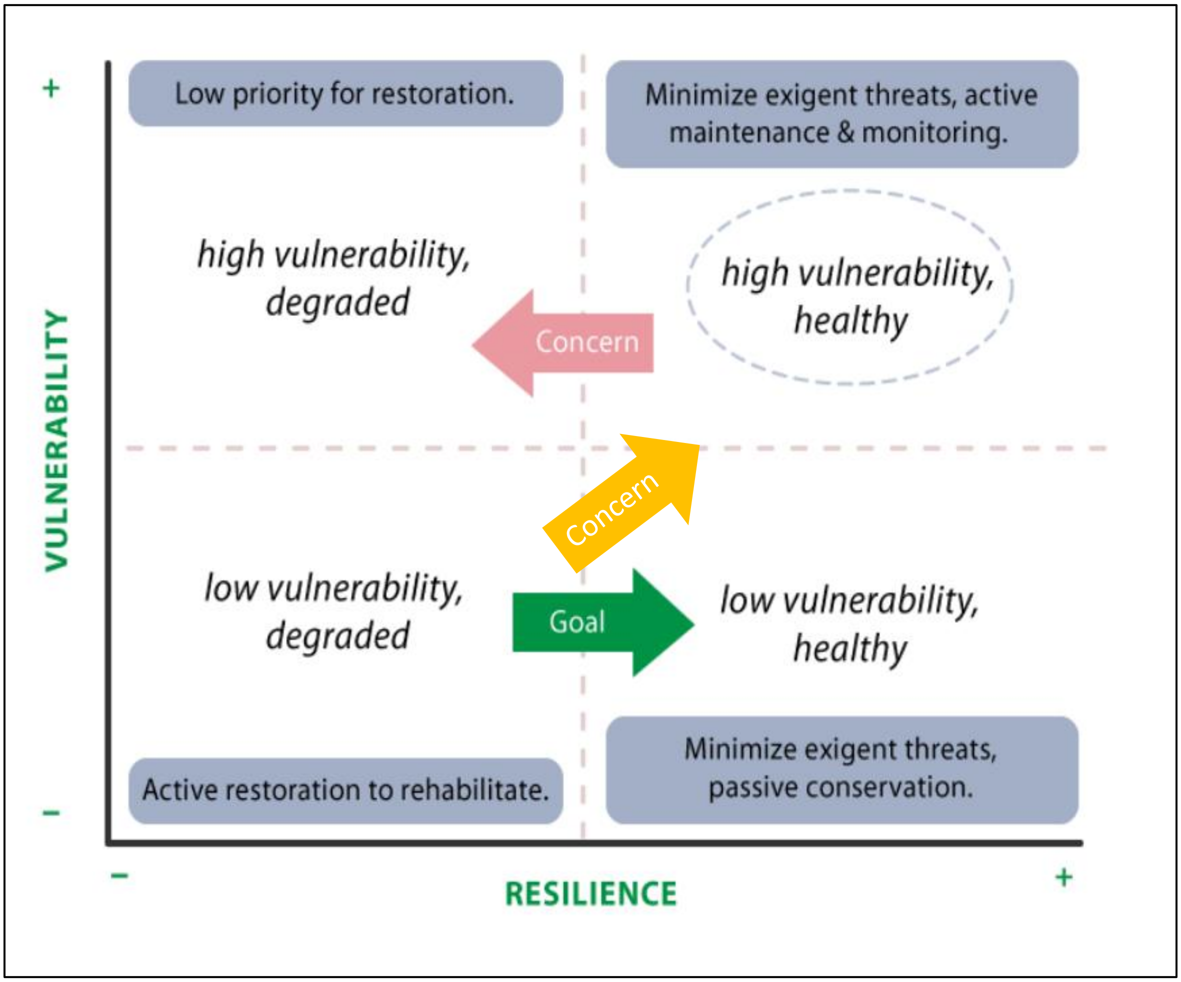


**Figure 1.** Conceptual diagram showing states of resilience and vulnerability for meadows in relation to restoration (Viers *et al.*, 2013). We have added yellow "concern" arrow to illustrate the potential for active restoration activities to inadvertently increase vulnerability to invasive plant damage.

Recent meadow restorations (e.g., Childs Meadow, Oso Meadow) have re-established hydrologic function to highly disturbed meadows. These sites can serve as test sites for the ultimate restoration success of current techniques, not only for long-term maintenance of hydrological function but also for recovery of historic biodiversity. As such, restorations continue to be implemented, it is important that we recognize that restoration-related disturbance can introduce and spread invasive plants that can alter ecosystem processes and degrade biodiversity, potentially reducing the effectiveness of restoration. This accentuates the need for solid information to guide restorationists and managers in addressing potential damage from invasive plants.

## 2. RESEARCH REVIEW

Sierra meadows have received increased research and conservation attention in recent years. As a result, we now have a much better understanding of historical damage from overgrazing and other unsustainable land uses as well as the potential impacts of climate change. Primary conservation concerns driving research include: losses in meadow water-holding capacity, losses in water input as warming reduces snowpack, and associated threats to meadow-dependent sensitive plant and animal species. Additionally, researchers and practitioners have a growing interest in quantifying greenhouse gas emissions and carbon sequestration in meadows—whether intact, degraded, and restored. Therefore, we will specifically address the role that non-native plants may play in maintaining—or damaging—these same meadow functions.

A detailed review of existing research on wet meadows was prepared for this project by Evan Wolf, PhD, and is provided in Appendix 3. Our report summarizes key aspects of that document, expands on others, and includes information on dry meadows, since these are also common in the Sierra Nevada and may be vulnerable to different stressors than wet meadows. Comparatively little research has been conducted on the role of invasive species in the processes of concern—hydrology, carbon storage, and wildlife habitat—despite land manager and federal agency reference to invasive species as amongst their top management priorities and a documented expansion of several species presence in meadows (National Fish, Wildlife and Plants Climate Adaptation Partnership 2012). As highly degraded meadows are restored and as land use in many areas continues to introduce plant propagules, a better understanding of how different invasive species influence hydrology, carbon budgets, and local biodiversity is critical to long-term meadow management.

### 2.1 Geographic Patterns, Climate Change and Increased Human Activity

Regional drying and warming trends in addition to historic disturbance threaten mountain meadows both by making conditions less favorable for species that require wetter conditions and by potentially making them more habitable for invasive species, which bring additional impacts. Research suggests that the southern Sierra may be somewhat buffered from the effects of climate change because of their higher-elevation headwaters (Westering and Bryant 2008). In contrast, the eastern slope of the central Sierra Nevada is predicted to experience the greatest amount of change in runoff across the region (see Viers *et al.* 2013 for a detailed review).

Projections also show that warming and drying trends may impact the meadow hydrology more at mid-elevations than high- or low-elevations because the relative change in seasonal moisture will be greatest there. Run-off patterns may become more "flashy," increasing erosion. Sediment from areas disturbed by forest fires can also wash into meadows. Information on potential changes associated with climate is being collected in an online database (climate.calcommons.org) that has been established by the California Landscape Conservation Cooperative for sharing climate change data.

Although invasive plant species were historically rare in mid-elevation regions of the Sierra Nevada (D'Antonio *et al.* 2004), these meadows are predicted to become more suitable for several invasive plant species currently restricted by temperature tolerances (Cal-IPC 2011). Increased habitat suitability combined with increased opportunity for movement of propagules through recreational access is predicted to increase the rate of invasive species' establishment in the future (Hellmann *et al.* 2008). Activities that inadvertently move seeds and other propagules, disturb ground, and provide openings for plants to become established are a particular risk. Recreational activities, whether by foot, horse, or motorized vehicle, as well as road and trail maintenance can all inadvertently introduce propagules of invasive plants.

Drought-related bark beetle infestations have resulted in major tree mortality in the Sierra Nevada. Operations to remove dead trees provide disturbance by opening the canopy and ground for new vegetation, and the operations use equipment and personnel that can transport weed propagules, so this is a high-risk situation for spreading invasive plants. Meadow restoration work and management activities are also especially prone to introducing invasive plant propagules, whether from contaminated equipment and clothes or as part of revegetation materials (see Dickman and Reyes 2014). Adherence to proper best management practices is an important step that can be taken to reduce the spread of invasive plants (see the BMP guide associated with this report, Cal-IPC 2019b) but these risks cannot be eliminated entirely.

## 2.2 Soil Water Budgets

Concerns about California's water supply have led to a focus on water sequestration and retention in Sierra Nevada meadows. Meadow restoration and hydrologic monitoring are now an emphasis, with several projects currently underway (see www.sierrameadows.org/our-work). Predicted temperature rise is expected to decrease annual snowpack, which will result in less surface water and increased stress on meadow systems (PRBO Conservation Science 2011). As a result, several research projects have been initiated to track meadow hydrology in intact, degraded, and restored meadows. Preliminary data suggest that desired increases in soil water table are being achieved with restoration (see Hammersmark *et al.*, 2008, Ohara *et al* 2013), though increases in other indicators of meadow function are not always as clear (Pope *et al.* 2015). Changes in invasive plant cover associated with recontouring are not typically tracked to our knowledge, so their effect is largely unknown.

Although the body of research on changes in soil moisture with restoration and drying and warming trends is growing, the influences of non-native species that invade meadow systems have only rarely been investigated. Transpiration of water by plants is a major outflow of water from wetlands, and a shift to a faster-growing and/or a greater leaf-area plant community that is typical of invasive species could cause hydrologic impacts (e.g., Loheide II and Gorelick 2005, Hammersmark *et al.* 2008; Nash *et al.* 2018). Invasive plant effects on hydrology are likely to be based on their growth rates and specific leaf area, both of which are highly correlated with plant transpiration (Pagter *et al.* 2005). Fast, early-growing annual plants (many invasives fit this profile) can extract soil moisture from surface layers, leaving a deficit for later-growing plants, but tend to be limited by growing season in high-altitude environments near treeline (see Jackson and Bliss 1982).

Le Maitre (2004) predicted that biological characteristics of plant species drive the extent of water use in systems where neither light nor water are limiting (such as Sierra meadows). Hence, the particular identity of an invader is key to understanding its impacts. Deep-rooted plants such as yellow starthistle can access water below dry surface layers, allowing for co-occurrence with shallow-rooted annuals when in lower density (Borman, Johnson & Krueger 1992, Gerlach 2004) but reducing moisture lower in the soil profile and likely precluding species with deeper roots. In a lowland California grassland systems, soil moisture levels were lowest in yellow starthistle-invaded sites, followed by perennial grassland sites and annual grassland sites, which maintained significantly higher soil moisture than those with yellow starthistle (Enloe *et al.* 2004). Shallow-rooted plants may, in contrast, not affect soil moisture availability at lower soil profiles but will capture and capitalize surface water, outcompeting other germinating species and precluding their establishment.

Research on water budgets in other grassland systems may be helpful in providing a better understanding of the potential effects of invasive species. In Sierra Nevada meadow sites where stream channel incision has caused water levels to drop, those species that are dependent on shallow water die off creating establishment opportunities for deep-rooted shrubs like the native *Artemisia rothrockii*, lodgepole pines (*Pinus contorta*), and shallow-rooted annuals (Berlow *et al.* 2002, Darrouzet-Nardi *et al.* 2006). Presumably, deep-rooted invasive species or, alternatively very shallow-rooted species that capitalize only on surface water, such as *Bromus tectorum,* may also be favored. The question remains whether these species, by becoming established, will either inherently modify hydrology or other resources enough to preclude a return to moist meadow conditions and associated recolonization of native herbaceous vegetation (see Berlow *et al.* 2003). As channeling drops the water table, wetland properties of meadows can be lost (Purdy *et al.* 2011) resulting in a shift from wetland to upland vegetation and potential for type conversion. Current regional trends toward warmer temperatures, decreased precipitation, and increasing fire frequency are likely to favor invasions by plant forms that further exacerbate soil drying.

Water use by native and non-native plants has been compared in other vegetation communities. In a meta-analysis of over 40 studies comparing plant water use, Cavaleri and Sack (2010) found that research generally showed higher water use (stomatal conductance) for non-natives at a leaf scale, equivocal water use rates at a plant scale, and consistently higher sap flow rates per area in highly invaded versus uninvaded areas, though data were limited. Results from an ongoing large-scale study in South Africa designed to quantify the water use of non-native trees compared to shorter-stature native vegetation (Gorgens and Van Wilgen 2004) indicate a modestly higher water use by non-natives compared with natives in high rainfall areas. Water use by giant reed (*Arundo donax*) is estimated to be two to eight times higher than that of native riparian vegetation that it has displaced, depending on available water resources (Cal-IPC 2011, Watts and Moore 2011, Cal-IPC, in prep, Zimmerman unpubl. data). Estimates of water use of *Tamarix* are highly debated and appear dependent on the particular habitat, season and native vegetation that the species is replacing (Moore and Owens 2001, Stromberg *et al.* 2009, Cleverly 2013). Clearly, water use rates should continue to be evaluated across systems and species.

### 2.3 Greenhouse Gas Emissions/Sequestration

We found no research describing the differences in carbon storage between native plants and invasive plants in Sierra Nevada meadows, yet vegetation change is a key aspect of a meadow's carbon budget. We can gain some insight by recognizing that plant traits significantly affect greenhouse gas sequestration and emission (Ward *et al.* 2009). Debate persists whether strategies and rates of carbon capture are fundamentally the same for plant species regardless of whether they are native, non-native, or invasive when controlling for environment (see Funk and Vitousek 2007, Leishman *et al.* 2010).

An oft-cited trait of invasive plants is their high productivity per area, which should in general shift a plant community towards greater net carbon storage. Invasive plants tend to grow faster, allocate a higher portion of resources to leaves and stems (rather than to roots) and contain more biomass than native neighbors (Van Kleunen *et al.* 2010). These traits suggest that invasive plant species have high photosynthetic rate and gross primary production. Whether or not this translates into higher ecosystem carbon storage depends on whether the invasive plant material is similarly decomposable to native biomass. Higher productivity may be counterbalanced by faster decomposition rates (typically of many thin-leafed species with high nitrogen), or, alternatively, compounded by slower decomposition rates of, e.g., silica-rich species. Areas of meadows in the Rocky Mountains that have been invaded by leafy spurge (*Euphorbia esula*) and Canada thistle (*Cirsium arvense*) have lower litter decomposition rates than other sites (Pritekel *et al.* 2006) and therefore are predicted to have negative Net Ecosystem Exchange (meaning the sites are absorbing carbon).

Despite fast growth rates and large stature, invasive plants that invest heavily in aboveground growth may not contribute much to soil carbon storage. Belowground growth of roots and rhizomes is the primary means of plant carbon storage in organic-rich meadow soils (Chimner *et al.* 2002, Rasse, *et al.* 2005, De Deyn *et al.* 2008), and the dominant native plants that typify Sierra meadows are densely rooted clonal monocots (Manning and Padgett 1995, Potter 2005, Fites-Kaufman *et al.* 2007). Clonal reproduction and high below- to above-ground biomass ratios are common traits in wetland plants (Moor *et al.* 2017). Invasive plant species that successfully dominate wetlands to the detriment of local vegetation diversity are often clonal monocots as well (e.g. *Phragmites australis, Phalaris arundinacea* and *Holcus lanatus* (Maurer *et al*. 2002, Annan *et al.* 2008), but it is unclear as yet whether they store a similarly large proportion of their carbon underground. Regardless, above-ground biomass will be lost with large-scale disturbances such as wildfire whereas belowground biomass will not.

Thus, it is difficult to assess whether an invasive plant's local expansion results in a net increase or decrease in C sequestration relative to native plants when below-ground carbon and risks from carbon loss through wildfire (or grazing) are considered. Lastly, bacteria and fungi are increasingly being acknowledged as significant contributors to soil carbon storage, and contributors to soil carbon that are highly sensitive to climate change (Allison *et al.* 2010). Therefore, invasive plants that affect soil microbial communities may influence greenhouse gas sequestration patterns.

Preliminary data on meadow restorations involving re-contouring are promising with respect to long-term carbon sequestration, in that belowground sequestration and water retention rates appear to increase while aboveground sequestration does not (Wilcox, unpublished data on Feather River, but see Pope et al., 2015); however the effects of possible incursions by specific non-native plant species on carbon budgets have not yet been evaluated and in at least one case restoration activity inadvertently led to the introduction of non-native species and undesired biotypes of unknown effect (Demetry 2016). Several other restoration research programs are collecting data on carbon storage. The California Department of Fish and Wildlife is measuring $CO_2$, $N_2O$, $CH_4$ flux and net C storage at Osa Meadows in addition to groundwater and surface water. Hutchinson *et al.*, are implementing and monitoring a meadow restoration along the Yuba River as part of a Proposition 1 Cap-and-Trade project. Yarnell *et al.*, have preliminary results from restoration monitoring at Childs Meadow that suggest increases in net carbon sequestration at fenced and dammed enhancement sites relative to grazed and natural beaver dam sites. Carbon budgets and vegetation change are being monitored as part of restoration activities at Bean Meadow by UC Merced.

Above-and below-ground abiotic effects extend beyond carbon budgets. Methane flux is important to monitor in order to determine net impacts of meadow changes on greenhouse gases. For example, Wickland *et al.* (1999) found that wet meadows produced nearly 70% more methane than dry meadows, and that differences were significant enough to change a site from being a carbon sink to being a source. Production of acetate, a root exudate, drives methanogenesis in native arctic wetland species (Strom *et al.* 2003). In addition, the aerenchyma tissue in wetland plants that provides aeration to roots also serves as a conduit for rapid transport of methane from its origin in the soil to the atmosphere (Shannon *et al.* 1996).

It is possible that, because higher biomass production typically leads to more methane production under wet conditions (see Bhuller *et al.* 2014), wet areas dominated by invasive plants may have higher methane emissions than areas dominated by less productive native plants, thereby counteracting what would otherwise be carbon gains. Similarly, if an invasive plant dries out soil relative to other vegetation, then nitrous oxide emissions may actually increase (via stress related metabolic activity from ammonia-oxidizing bacterial communities), reducing the rate of soil sequestration of carbon and potentially counteracting the direct effects of drying on methane production (see Mummey *et al.* 2000, Avrahami and Bohannan 2009).

Lastly, some species alter nutrient budgets in addition to carbon. At a low elevation wetland in northeast California, invasive perennial pepperweed (*Lepidium latifolium*) altered surface soil properties by concentrating calcium and magnesium in its aboveground biomass (Blank & Young 2002). Although these changes do not directly affect carbon budgets, the authors do point to potential ecosystem impacts of invasive species from a nutrient cycling perspective.

### 2.4 Plant Community, Biodiversity and Wildlife Impacts

We found few studies that linked invasive plant species with sensitive species or biodiversity impacts specifically in Sierra Nevada meadows. Outside of the Sierra Nevada there are numerous examples of invasive plants displacing native plants, altering invertebrate and fungal communities (e.g., Belnap and Phillips 2001, Pritekel *et al.* 2006), affecting wildlife habitat (e.g., Dukes & Mooney 2004), and degrading ecosystem services (see Funk *et al.* 2014). Observed trends are not uniform and may be highly dependent on several factors, such as initial site conditions, historical constraints, plant physiological tolerances, and plant physical structure and chemical composition (see Vila *et al.* 2011 for a review). Furthermore, the mechanisms underlying species invasions are key to fully understanding their impacts on wildlife and other species and are frequently masked by apparent competition (Levine *et al.* 2003).

### 2.4.1. Impacts on vegetation community

Angert *et al.* (2009) and Huxman *et al.* (2013) proposed that decreased native plant abundance and diversity in a desert annual forb system in the presence of non-native species was because a "missing phenotype" had been introduced. Non-native species were able to maintain consistently high relative growth rates with high water use efficiency, breaking a common physiological trade-off observed in native desert annuals that has been linked with maintaining local community diversity (Figure 2). It is not known to date whether and which non-native plant species follow the "missing phenotype" hypothesis and whether this hypothesis holds for mountain meadows where water is typically not limiting.

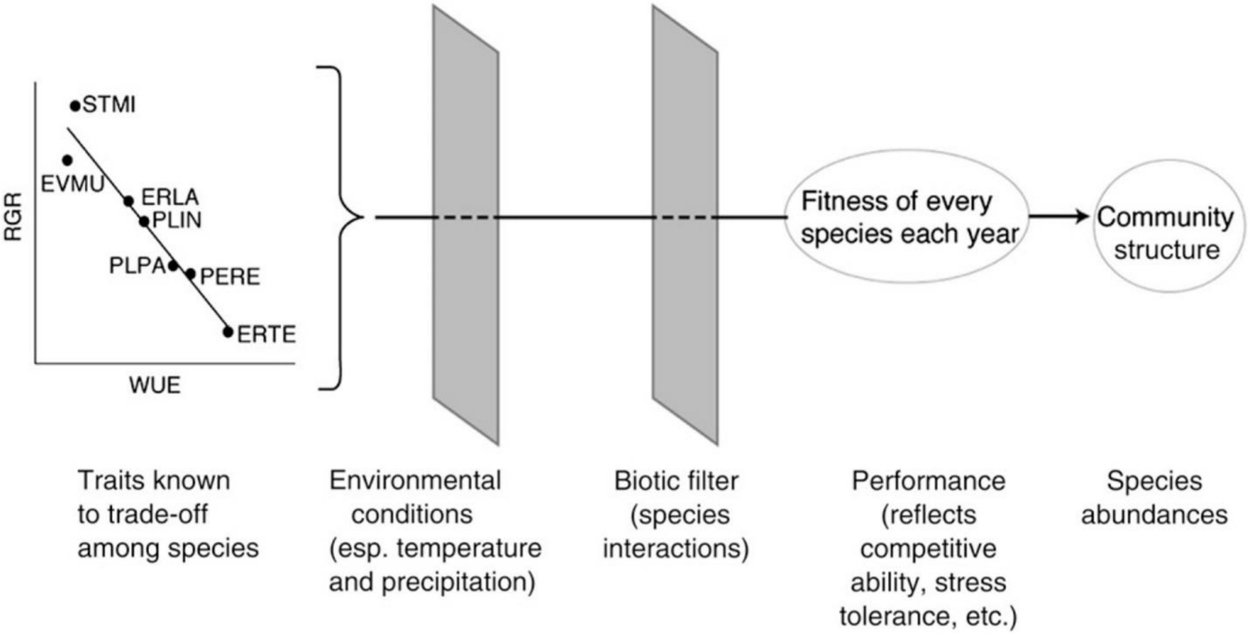


**Figure 2.** Conceptual diagram showing how resource use and growth rate (here water use efficiency, WUE, and relative growth rate, RGR) trade-offs can maintain species diversity and community structure (from Huxman *et al.*, 2013). Four-letter codes represent native desert annuals that follow a classic tradeoff between WUE and RGR that facilitates species diversity over time and space. Non-native species tested did not fall along this plane but had both high WUE and RGR (data not shown).

This hypothesis—inspired by Tilman's (1982) and others' models of niche-based community assembly—is especially interesting when applied to mountain meadows, which have high diversity but also are dominated by perennial, clonally reproducing plants and where community structure may also largely be driven by disturbance factors and historic legacies. If the idea holds for mountain meadows, then successful invaders in these systems would again be species that "don't play by the rules" of community assembly (and RGR:WUE or similar functional tradeoffs) and could fundamentally alter the available niche space and local diversity.

Field observations of invasive species' impacts, though scarce for mountain meadows, suggest that some, but not all non-native species reduce native diversity. Pritekel *et al.* (2006) found that meadows in the Rockies invaded by leafy spurge (*Euphorbia esula*) and Canada thistle (*Cirsium arvense*) had lower plant species richness, lower arthropod density, and lower decomposition rates of certain litter fractions than un-invaded meadows, potentially because of lower-palatability and decomposition rates of non-natives. Belnap and Phillips (2001) found that grassland sites dominated by either *Stipa* or *Hilaria* grasses each responded differently when invaded by *Bromus tectorum*. Both showed an increase in thatch cover and an increase in soil and plant-infecting fungal diversity with invasion. Other factors measured (e.g., microbial and soil invertebrate diversity and numbers) varied significantly, but uniquely from the two starting conditions. In both types of grassland, invaded sites were distinctly different, but the implications of those differences were unclear.

### 2.4.2 Impacts on wildlife and rare species

Vertebrates may be affected by invasive plants via changes in habitat structure, forage material, or the food resources that plants support. Examples include avoidance by grazers of areas dominated by prickly or unpalatable species such as Canada thistle or barbed goatgrass (Bayer 2000, Peters *et al.* 1996), and various knapweeds knapweed (Panter 1991, Whitson 1999). The consequences of avoidance are difficult to measure but potentially include reduced effective habitat size for those species and possibly increased energetic cost.

Invasive plant species have been shown to affect various species of concern in meadows, though impacts are not consistent and evidence is restricted to those species that are well studied. Plants with different levels of soluble phenolics, litter C:N ratios, and litter N:P ratios affect the survival of young amphibians differentially (Cohen *et al.* 2012). Reed canary grass (*Phalaris arundinacea),* an invasive species of concern in Sierra Nevada meadows, suppresses the diversity of native wetland herb species in other systems (Barnes 1999) and appears to be facilitated by elevated levels of soil nitrogen (Perry *et al.*, 2004) which can be found in grazed, burned, or urban-adjacent systems. Reed canary grass cover was negatively correlated with native amphibians in actively and passively managed agricultural wetlands in low elevation valley wetlands in Oregon (Rowe & Garcia 2014), whereas another study in New York State found amphibian growth rates did not differ across native and non-native-dominated wetland habitats. Reed canary grass also displaced the endangered aquatic annual plant *Howellia aquatilis* in marsh habitat in Montana (Lesica 1997). Houlahan and Findley (2004) suggest that species dominance threatens rare species and local species diversity, regardless of provenance.

Many bird species are more directly affected by vegetation structure and other habitat characteristics than by plant species composition. For example, black rail occupancy of palustrine emergent wetlands in the Sierra was positively associated with rushes, vegetation cover and wetland size, and negatively associated with non-native annual grasses (Richmond *et al.* 2010). In wetlands around Boston, MA, the abundance of wetland bird species responded in varied and unpredictable ways to purple loosestrife (*Lythrum salicaria*) cover (Tavernia & Reed 2012). Perennial pepperweed (*Lepidium latifolium*) has also been shown to outcompete grasses that provide better food for waterfowl (Howald 2000).

Both native (*Phragmites australis* ssp. *americanus*) and non-native subspecies (*P. australis* ssp. *australis*) of common reed are found in North America; it is unclear which form or forms are present in California*.* Throughout other regions of North America, *P. australis* ssp. *australis* can become a wetland community dominant and has had had community-level effects on other taxonomic groups. Destefano (2013) documents an associated increase in crustaceans, freshwater amphibians (American toads and green frogs), and small mammals (muskrats, shrews, voles), but a decrease in bird diversity. Gratton and

Denno (2005, 2006) reported a large-scale replacement of the herbivore community with detritivores and benthic microalgae consumers in salt marshes where *Spartina alterniflora* was replaced with *Phragmites*. This summary of research points to strong system-specific effects and the difficulty in drawing conclusions relevant to Sierra meadows from other wetland and meadow systems.

## 3. Proposed Future Research

Researchers and land managers are faced with navigating a professional divide between research and conservation implementation. Research results are often not incorporated into management, and management concerns are often not incorporated into research. Here, we propose translational research on invasive plants in Sierra meadows that is informed by the needs of land managers while also addressing fundamental ecological questions for researchers.

Invasive plant management is generally a high priority for land managers because, when effective, it is one of the easiest and most direct methods by which they can maintain and improve habitat quality. Management priorities are typically driven by a need to accomplish as much conservation benefit as possible from limited funding available. This tends to constrain managers' time to learn about research and how to apply it. The Sierra Meadows Partnership provides an excellent platform for researchers and managers to bridge this chasm and to efficiently collaborate for the purpose of effectively strengthening management of meadows for long-term resilience.

Two primary needs have been expressed to us by land managers in the Sierra: (1) Which non-native species can and can't be tolerated in Sierra meadow systems and why, and (2) Which tools and techniques are most effective at removing high-priority invasive plants (and restoring meadows). In this research planning document, we focus on the first question. The second question underlines the ongoing need to share tools and techniques, develop more effective methodologies, and increase researcher interest in methodological questions, and should not be overlooked moving forward. Research on efficacy is crucial to being able to solve land management problems, yet the monitoring required to draw conclusions is not a traditionally accepted part of management. Researcher–manager partnerships are critical to connecting implementation with monitoring in an experimental manner, where possible.

In order to simplify and focus analyses, we propose that studies focus on invasive plants that occur in moist meadows (rather than wet or dry meadow extremes), at mid-elevation (5000' – 7000'). Wet meadows, where surface water persists throughout the growing season, tend to restrict colonization by more generalist species, and dry meadows are less vulnerable to ground water changes and tend not to be targets for hydrogeomorphological restoration (though they are endpoints for degraded moist meadows; see low vulnerability healthy and low vulnerability degraded quadrants in Fig. 1). Mid-elevation meadows in the Sierra represent the leading edge of expansion of non-native plants, in that they were previously infrequently colonized by non-native species and now, due to site-specific and climatic conditions, are colonizable. High elevation meadows are both less accessible and less habitable to many mountain meadow invaders.

Below we outline a research plan to better understand how non-native species that invade mountain meadows can uniquely affect local ecosystem properties and biodiversity. Based on the degree to which they differ from commonly occurring native meadow species and from each other, land managers will be better able to prioritize them for control or, conversely, evaluate them more closely for their equivalency with native species that they may be potentially displacing. Non-native species that diverge strongly from their native counterparts either by high carbon assimilation, high soil water use, and low support of wildlife food resources should be prioritized for control.

There are many alternative approaches to answering questions about ecosystem-level effects beyond the study described here, but our approach controls for many environmental variables that may otherwise make species-level comparisons of plant functional traits difficult. Observational studies of the traits studied, wildlife use, and changes in distribution and cover of invasive plant species are still needed. We strongly encourage that these research and monitoring activities be further developed to complement manipulative experiments.

The research plan outlined below uses a multi-tiered, scalable common garden experiment to compare eight non-native species (Table 1) that occur in mid-elevation meadows with each other and with eight commonly occurring native meadow species (Table 2). Functional traits to be compared include total seasonal carbon assimilation, soil moisture draw-down, and support of wildlife food resources and diversity (via arthropods).

The experiment will ideally be replicated across three subsurface moisture regimes that simulate a range of moist meadow conditions. It should be located at one or more mid-elevation research stations (e.g., Sierra Nevada Aquatic Research Lab, Sierra Foothills Research Station or the Owens River Research Station—field stations would need to be supportive of introducing invasive plant species into their fields). Species will be compared based on the following factors: above-ground biomass production and soil organic carbon accumulation (surrogates for greenhouse gas assimilation), impact on soil moisture, direct contribution to food web structure, and approximations of RGR and WUE values (surrogates for diversity and presumed facilitation of diversity; Huxman *et al.* 2013). The experiment is not designed to be an interspecific competition experiment, but rather to evaluate each species independent of its neighbors in a common environment.

By manipulating both moisture availability and species identity, this single experiment will be able to address the following questions:

- How do key invasive plants of mountain meadows affect soil and above-ground carbon accumulation in comparison to the native species that they may be displacing?
- How does soil carbon accumulation vary with subsurface moisture depth?
- How do key invasive plants of mountain meadows differ in their soil moisture depletion rates when compared to common co-occurring native species? Are they interchangeable?
- Which species have high water use efficiencies combined with high relative growth rates?
- Which species support the greatest biomass, diversity and number of arthropods? How do arthropod guilds vary across species? (This will serve as a surrogate for species value in supporting biodiversity in a meadow.)

Species may be considered detrimental to meadow carbon storage if they have low below-ground biomass, detrimental to water storage if they consume high amounts of water, detrimental to community complexity if they do not exhibit functional trait trade-offs (such as RGR:WUE), detrimental to wildlife if they support few – or a depauperate assemblage of – arthropods. Scoring such factors provides an initial basis for prioritizing particular non-native plant species for removal, both for restorationists early in their restoration activities and for managers as part of their long-term management of meadows.

Furthermore, success criteria for restorations can be revised to consider the benefit as well as the range of potential impacts that different species can have (also called out as a restoration-specific research need by land managers). For instance, non-native cover of Kentucky bluegrass or timothy in a meadow may be substantially less deleterious than cover of velvetgrass because the former species function more similarly to their native counterparts than the latter. We recommend that the non-native species selected be species that currently occur in mid-elevation meadows and that they are compared to common native species spanning similar functional groups (rhizomatous grasses, perennial forbs, shrubs). Table 1 (below) includes candidate non-native species currently considered to be problematic in Sierra Nevada meadows. Table 2 provides suggested common native meadow species that have similar life forms as the targeted non-natives. See Appendix 1 and 2 for a larger list of both these species. Prior to implementing the study, researchers should review candidate species with regional land managers in specific region of interest and select the most relevant local non-natives and natives.

**Table 1.** Suggested non-native species that have been identified by land managers or prioritization tools to be deleterious. See Appendix 1 for a larger list of problematic invasive plants in Sierra meadows.

| **Scientific name** | **Common name** | **Functional group** | **Cal-IPC Rating** |
|---|---|---|---|
| *Acroptilon repens* | Russian knapweed | Perennial forb | MOD |
| *Agrostis stolonifera* | Creeping bentgrass | Rhizomatous grass | LIMITED |
| *Bromus tectorum* | Cheatgrass | Annual grass | HIGH |
| *Centaurea stoebe* | Spotted knapweed | Perennial forb | HIGH |
| *Cirsium vulgare* | Bull thistle | Perennial forb | MOD |
| *Holcus lanatus* | Common velvetgrass | Rhizomatous grass | MOD |
| *Leucanthemum vulgare* | Oxe-eye daisy | Perennial Forb | MOD |
| *Rubus armeniacus* | Cut-leaf (or Himalayan) blackberry | Perennial shrub | MOD |

**Table 2.** Suggested native species that are common and/or dominant in mid-elevation prairies. These species can also be replaced with commonly planted restoration species. See Appendix 2 for a larger list of common meadow species.

| **Scientific name** | **Common name** | **Functional group** |
|---|---|---|
| *Achillea millefolium* | Common yarrow | Perennial forb |
| *Agrostis pallens* | Seashore bentgrass | Rhizomatous grass |
| *Artemisia rothrockii* | Timberline sagebrush | Shrub |
| *Calamogrostis canadensis* | Bluejoint reedgrass | Rhizomatous grass |
| *Carex nebrascensis* | Nebraska sedge | Rhizomatous grass-(like) |
| *Cirsium scoparium* | Elk thistle | Perennial forb |
| *Oreostemma alpigenum* | Tundra aster | Perennial forb |
| *Senecio triungularis* | Arrow-leafed ragwort | Perennial forb |

In cases where the invader represents a novel functional group that is otherwise rare in the system (as with annual grasses and forbs), we recommend that species are compared to those dominants that they are most likely to displace. Note that bulb/corm-sprouters are not represented in the non-native category and therefore excluded from this study for simplicity.

The proposed functional and mechanistic comparison of invasive species relative to their native counterparts will provide information to help restorationists and land managers decide when non-native plants in a meadow community are likely to reduce desired function (and contribute to the potential degradation of restoration projects as shown in Fig. 1). Comparisons will also help ecologists refine theories of community assembly, stability, ecosystem function, and resilience. At a broad scale, this could help improve assessments of relative risk for invasion across meadows as they are in Cal-IPC's current Vulnerability Index effort (Cal-IPC 2019a).

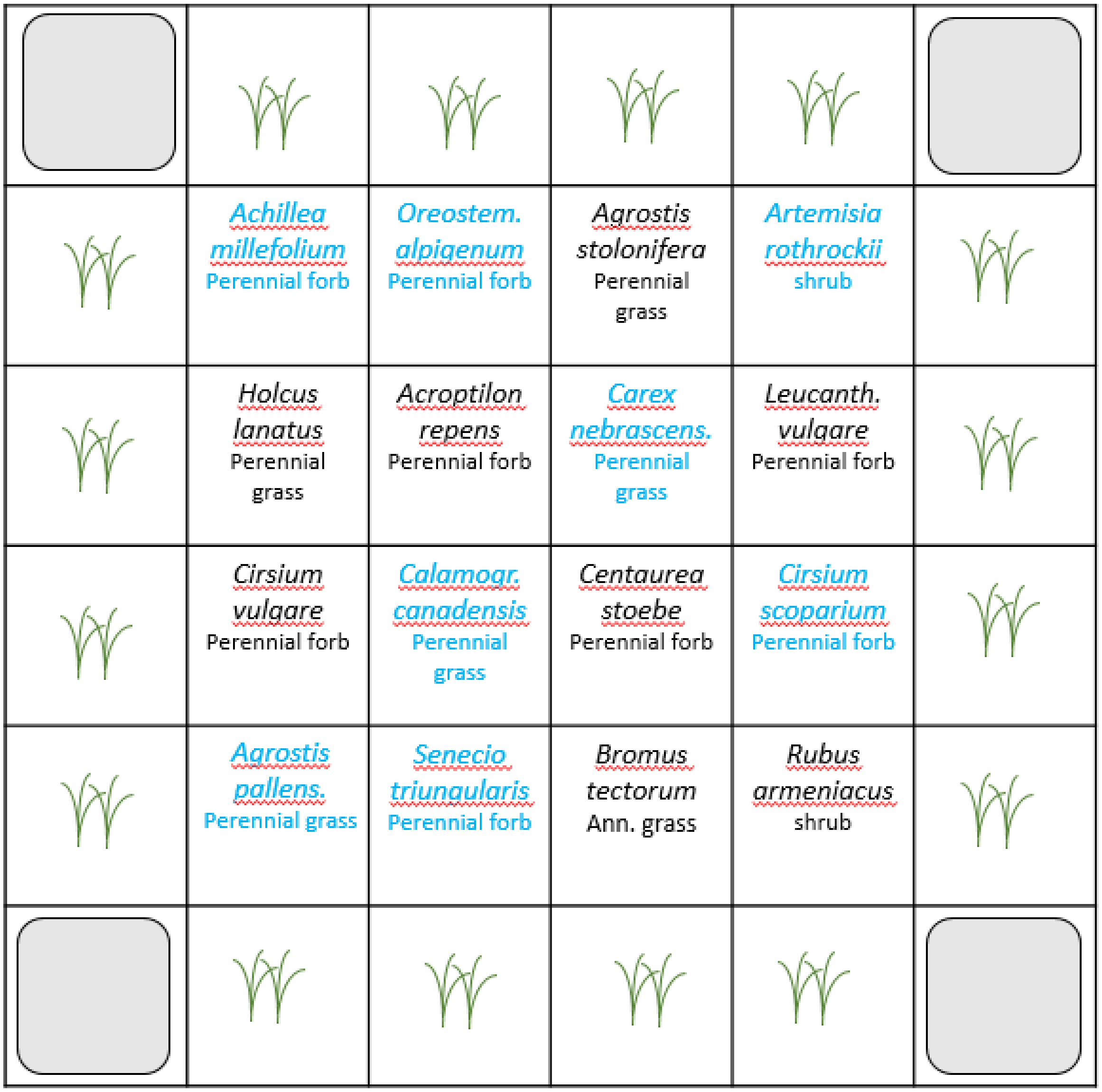
### 3.1 Experimental Design

Each replicate block will consist of a 6m x 6m plot (or 7.25m x 7.25m with between-grid cell spacing) gridded out into 36 1m x 1m cells and is designed to be a single-year study, with cell size being sufficient for each species' natural single-season expansion. All plants will be removed upon treatment completion. Above-ground biomass will be collected upon plant maturity but before seed drop to ensure that weed seeds are not dispersed. If desired, the experiment can be extended to be 2- or multi-year to allow rhizomatous plants to develop more fully. All plant material growing at the study site will be killed upon project completion to ensure that weeds do not spread.

Outer perimeter cells will each be planted with one common dominant native meadow species (e.g., *Carex nebrascensis*) to minimize edge effects. The interior 16 cells will contain 1 x 1m plantings of each of the eight selected native and non-native species (one species per cell, with position randomly selected in each block). Tables 1 and 2 provide a list of eight suggested candidate non-native and native species, respectively, that were chosen to represent multiple functional groups and because (in the case of non-native species) they had been identified as a significant management concern by one or more sources.

Each plant species will be greenhouse-germinated (or propagated) the year prior to the study and transplanted into plots early in the growing season. Percent cover upon transplanting will be standardized to represent approximately 20% cover for perennials.  A minimum of three replicate blocks will be planted for each moisture level (3 replicates x 3 moisture level = 9 blocks; Fig. 4). For logistical purposes, blocks themselves will likely need to be arranged in a grid spatially. Ideally, this experiment would be conducted at multiple mountain field stations. All species except for *Bromus tectorum* (an annual that germinates in spring) should be greenhouse-grown and transplanted out a year prior to when the study begins. *Bromus tectorum* should be seeded directly into its grid cells in early spring prior to transplanting and prior to natural germination timing.

Subsurface moisture can be manipulated by either choosing microsites that vary significantly in ground water table (at or above 1m depth) or, more likely, with the installation of subsurface drip lines at a depth of 0.5m and 0.8m. The shallow subsurface moisture treatment will supplement subsurface water at a constant, monitored rate, at a depth of approximately 0.5m. The deep subsurface water treatment will supplement subsurface water at constant, monitored rate at a depth of 0.8m. Ambient (aka “dry”) conditions will serve as the third treatment.



| | | | | | |
|---|---|---|---|---|---|
| ▢ | 🌱 | 🌱 | 🌱 | 🌱 | ▢ |
| 🌱 | *Achillea millefolium*<br>Perennial forb | *Oreostem. alpigenum*<br>Perennial forb | *Agrostis stolonifera*<br>Perennial grass | *Artemisia rothrockii*<br>shrub | 🌱 |
| 🌱 | *Holcus lanatus*<br>Perennial grass | *Acroptilon repens*<br>Perennial forb | *Carex nebrascens.*<br>Perennial grass | *Leucanth. vulgare*<br>Perennial forb | 🌱 |
| 🌱 | *Cirsium vulgare*<br>Perennial forb | *Calamogr. canadensis*<br>Perennial grass | *Centaurea stoebe*<br>Perennial forb | *Cirsium scoparium*<br>Perennial forb | 🌱 |
| 🌱 | *Agrostis pallens.*<br>Perennial grass | *Senecio triungularis*<br>Perennial forb | *Bromus tectorum*<br>Ann. grass | *Rubus armeniacus*<br>shrub | 🌱 |
| ▢ | 🌱 | 🌱 | 🌱 | 🌱 | ▢ |

**Figure 3.** Suggested plot layout for replicate block. Native plant species are shown in blue type and non-native plant species are shown in black type. Locations are randomly assigned. All perimeter grid cells are planted with one common native species (e.g., *Carex nebrascensis*) to reduce edge effects. The gray cell represents a grid cell left unvegetated (but covered with organic material) to measure soil moisture and carbon without plant cover. Native and non-native species should be placed adjacent to one another where possible to minimize unevenly distributed neighborhood effects.

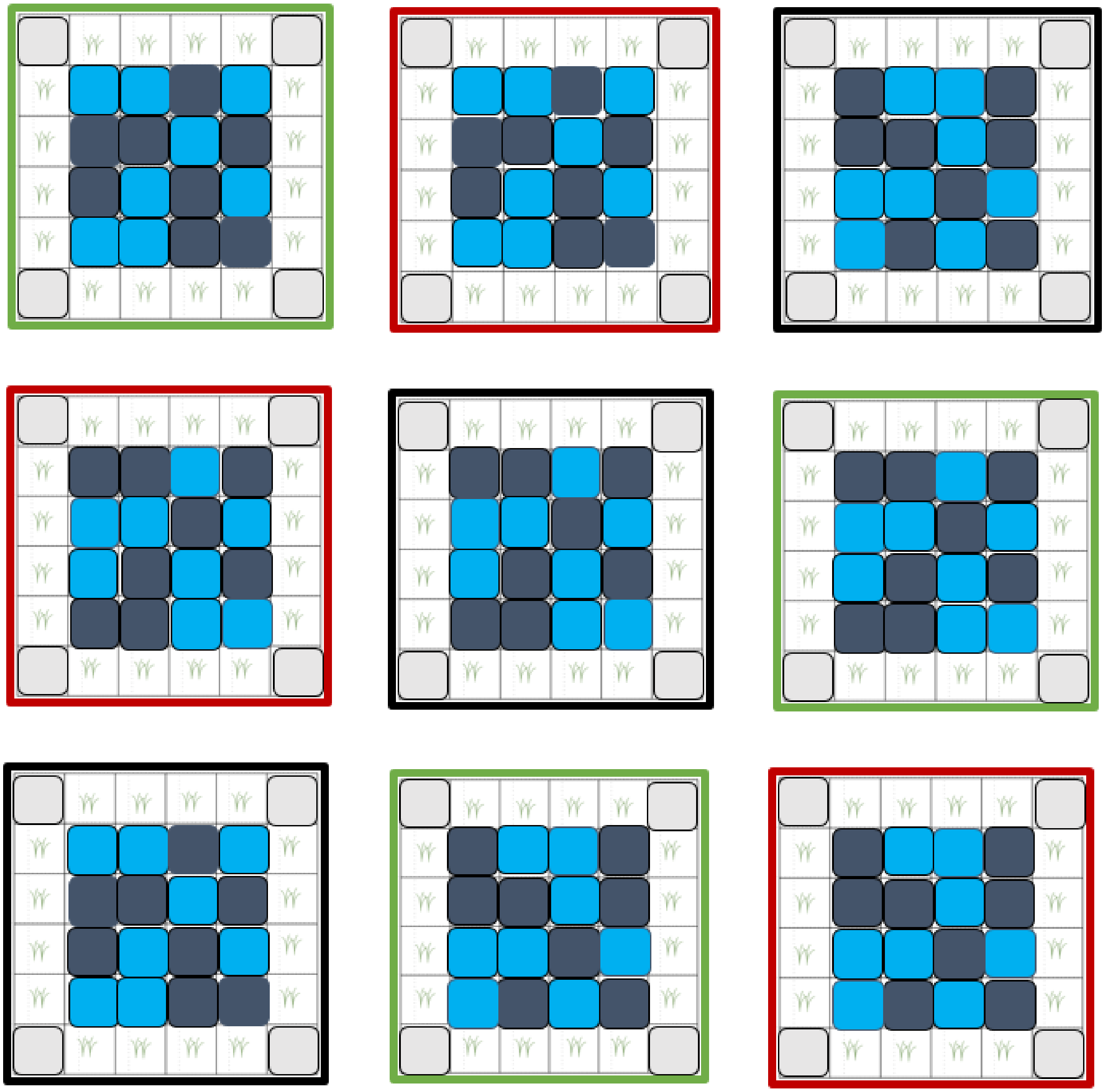


**Figure 4.** Hypothetical nested randomized complete block treatment design with ambient conditions (red outline), 0.5m subsurface supplementation (green) and 1m subsurface supplementation (black). Blue = native; Dark gray = non-native; light gray = non-vegetated soil moisture and soil carbon controls. Species should be positioned in each replicate block randomly. Small 0.25m pathways between grid cells are recommended.

### 3.1.1 Measuring impacts on carbon sequestration

Meadows, can store a substantial amount of carbon from the atmosphere by means of extensive underground root systems, rhizome networks, and, under appropriate wet, anoxic and acidic conditions, peat formation. Carbon stored below ground in root systems, collected organic matter and rhizomes is more persistent in meadows and less likely to be released again via fire or other mechanisms. Key to understanding the impacts of invasive species is understanding carbon budget impacts of type conversion from existing meadow vegetation (rhizomatous grasses and perennial forbs) to annual forbs or grasses that store proportionally more resources above-ground. Whereas whole-meadow greenhouse gas budget measurements have been calculated and are prioritized under California's Greenhouse Gas Emission Reductions Fund (California Air Resources Board 2018), single-species evaluations have not been made.

Above-ground and below-ground contributions of invasive species belonging to other functional plant groups have not been compared sufficiently to be able to draw conclusions as to their relative contribution to carbon budgets. As a surrogate for estimates of carbon fixed per area, above-ground biomass accumulation and percent soil organic carbon accumulation can be estimated across species and moisture regimes. Ecosystem exchange measurements would also be possible at the 1m$^2$ scale using a chamber equipped with an infrared gas analyzer (e.g., Wolf 2017) but may not be necessary to estimate compare species' above-and below-ground net carbon input and would be difficult to execute for all species under similar ambient conditions.

**Questions:** How do key invasive plants of mountain meadows affect soil and above-ground carbon accumulation in comparison to the native vegetation that they may be displacing? How does biomass accumulation vary with subsurface moisture depth?

**Data collection:** Prior to planting, initial biomass and size will be recorded for each species (10-30 plants will be destructively sampled, separated by roots and shoots, dried, and weighed to estimate starting conditions). At end-of-season, each 1m$^2$ species patch will be harvested. Before harvest, percent vegetative cover and number of leaves per area will be estimated by grid cell. Above-ground biomass will be dried at 60°C and weighed. Soil carbon will be sampled at the same time by taking three 5cm-wide sectioned soil cores to a depth of 0.7m following O'Neill (2005). Three depths will be sampled: 0-10cm, 10-20, and 60-70 cm. Samples for each depth will be pooled within species grid and processed using a loss on ignition (LOI) method (see USDA Natural Resource Conservation Service, Soil Survey Laboratory Methods Manual, Burt 2004) to provide estimates of percent soil organic matter accumulation. Unvegetated controls should be similarly sampled and values should be subtracted from species' grid values to remove effects of pre-existing soil carbon. Temperature, humidity, photosynthetically-active radiation (PAR), and rainfall should be monitored at the site level throughout the season by the field station.

**Supplemental data and experiments that could enhance the study:**

- Locate a subset of the eight invasive and native species in extant meadows and collect end-of-season first-year above-ground biomass to compare with experimental data. Differences can be compared to experimental results to determine whether growth patterns are similar.
- Conduct germination trials and/or track on-site spring emergence of all species being studied in order to gauge potential competitive advantage from pre-emption.
- Track differences in carbon loss through decomposition across species by installing litter bags with plant material from each species in an ambient location (e.g., along the planted perimeter of the plot). See Coleman *et al.* (2004) for methodology.
- Individual plants can be bagged to track relative growth rate on a per plant (rather than per area) basis.

- Install Phenocams to track changes in plant growth at a whole plot scale over the course of a growing season to provide an indication of differences in growth rate across species. Or alternative measure growth rates (height and number of leaves) for each species grid to obtain a more precise estimate of biomass accumulation over time/RGR.

### 3.1.2 Measuring impacts on meadow water retention

Meadows can serve to recharge groundwater supplies by retaining water, releasing it into the ground. Meadow drying can be caused by erosion and reductions in snowpack. Vegetation change can further drive changes in water retention. Deep rooted plants may deplete water resources from lower in the soil profile. Shallow-rooted plants and annual plants in particular may alter both the available soil surface moisture for germination and can leave thatch that increases surface flammability and reduces light penetration. This experiment will be able to explicitly compare: (1) differences in soil water draw down across species, (2) differences in transpiration rates and water use efficiency.

**Questions:** How do key invasive plants of mountain meadows differ in their soil moisture depletion rates when compared to common native species? Are they interchangeable?

- **Data collection:** Soil moisture will be measured at three intervals and three depths (10cm, 20cm and 70cm) within each species patch (minimum of three probe samples per patch) and in unvegetated controls across the three moisture treatments to determine differences in soil draw down between species and relative to controls. Soil moisture can be measured effectively at multiple depths using a hydroprobe moisture neuron depth gauge (DiTomaso *et al.*, 2003). Rainfall, temperature, PAR, and humidity should be recorded for the field station. Prior to conducting the experiment, test soil at field site for clay, silt, and sand composition as well as major and minor nutrients and soil residues. Water use efficiency can be measured indirectly by analyzing plant tissue for CN and C isotope rate ($\delta^{13}C$) using isotope ration mass spectrometry (see Valliere 2019).

**Supplemental data that could enhance study:**

- Soil moisture availability can be concurrently monitored in extant meadows at the same depths and over the same timespan for a subset of the species studied. Neighbor species, plant density and cover, and other site conditions will be recorded as covariates.
- Additional moisture measurements can be made along the soil profile.
- Transpiration rates can be measured by species using a photometer.

### 3.1.3 Measuring impacts on wildlife and biodiversity

Meadows harbor many animals, including Sierra garter snake, Sierra and mountain yellow-legged frog, Sierra chorus frog, willow flycatcher, Lincoln’s, and white crowned sparrow, as well as a rich arthropod fauna. Change in vegetation can significantly impact associated animal communities.

The contribution of each plant species in the experiment to community and trophic complexity will be measured by sampling the arthropod fauna on each. Arthropods assemblages can vary dramatically at a fine spatial scale based on plant characteristics, genotype, and even provenance (e.g., Pratt *et al.*, 2016), and are therefore good study organisms to measure plant-based differences. Although the arthropods associated with each plant may not all occur in the varied meadows across the sierra, both the abundance and richness of species associated with specific plants will provide an indicator of its suitability to harbor or host them in the field. Diversity and abundance of arthropods is a good indicator for other levels of diversity as well as for food resources that are available to other organisms. In addition, each species will be tested for the presence of a functional tradeoff that could allow greater species coexistence, by comparing RGR (biomass increase over study period):WUE across species.

**Question:** Which species support the greatest biomass, diversity and number of arthropods? How do arthropod guilds vary across species? Which species do/do not show evidence of a functional RGR:WUE tradeoff?

**Data collection:** Arthropods can be sampled for each species patch using a modified blower vacuum (see Bioquip®) that is capable of sampling single plants and small spaces. Vacuum samples can be collected twice over the course of the growing season and bulked across time period for each species in each replicate block to decrease sampling variance. Evidence of feeding and visual observations can also be included in this assessment. Arthropods in each of the 48 bulked samples will be identified, where possible to Family and functional group (herbivore-sucking, herbivore-chewing, herbivore-galling, predator, parasitoid, scavenger, pollinator, detritivore) and given a size classification. Assemblages will be compared between and within native and non-native plant species groups. RGR and WUE data collection was described in earlier sections.

**Supplemental data to complement study:**

- Researchers may consider sampling arthropod fauna on a subset of species from the experiment at meadow field sites. Observational data would complement experimental data collected.
- Biomass of samples can be estimated (using size classes) and compared across species to estimate food resources.
- Other sensitive-species-specific observational studies could be conducted in the field when specific information for a particular animal species is needed. For instance, habitat patch use could be tracked by logging time spent by bird species in different plant types (native and non-native) in meadows. Similarly, target study animals could be tracked with radio transmitters in order to determine whether they avoid particular plant species.

### 3.2 Analysis

Species can be compared to one another on the basis of their function in a mountain meadow system. Variables to compare include: (1) above-ground carbon assimilation (and potential competitive superiority) via weight of dried above-ground biomass, (2) below-ground soil carbon accumulation via % soil carbon estimations from incineration method, (3) water use efficiency, (4) relative growth rate versus water use efficiency, (5) soil water draw-down, (6) arthropod family-level richness (and evenness), and (7) arthropod functional group richness and abundance.

The study can be analyzed as a full factorial nested randomized complete block experiment, with moisture serving as the whole plot effect and plant species (or species[origin]) serving as the nested effect. Arthropod richness, evenness, and functional group richness can be analyzed by multiple regression or using multivariate ordination techniques. Similarly, the diverse array of plant growth soil water use measurements can also be compiled in an ordination. When plotted in multi-dimensional space, species that are fundamentally different due to a combination of these traits will appear as distinct clusters or outliers, while species that are similar in their functional traits will overlap. Thus any outlier species are more likely to be potential ecosystem transformers. Differences can also be compared in a multivariate analysis of variance, with moisture level and species being independent variables the various measurements being dependent variables.

### 3.3 Summary

Research to characterize carbon assimilation, water use and biodiversity support of native and non-native plant species found in Sierra meadows will help land managers anticipate the potential impact of individual plant species invasions into meadow systems. As a result, we will be better be able to prioritize prevention, early detection/rapid response, and when species expand, long-term management. Study results will also create a strong research-based foundation for management actions. The study outlined here is designed to be modular and scalable, based on available resources and capacity. Studies are strongest when conducted together to provide a more comprehensive picture of the function of individual species in the Sierra meadows system. As with all conservation research, they also function best when conducted as a collaboration between management and research. We should aim toward such a collaboration around protecting Sierra Nevada meadows.

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## Appendix 1. Non-Native Species of Concern in Sierra Meadows

A selection of non-native species considered to be potentially impactful to meadows in the Sierra Nevada. Species highlighted in bold were considered priority candidates for the experiment because they were: identified as problematic by more than one source, were representative of a distinct functional group to be tested, and presumed able to persist at mid-elevation latitudes. Creeping bentgrass was included in the study because it was particularly called out by restoration practitioners as being problematic.

| **Species** | **Common Name** | **Cal-IPC**[1] | **Stillwater 2012**[2] | **NPS 2018 Work plan**[3] | **Cal-IPC Rating**[4] | **Functional Group** |
|---|---|---|---|---|---|---|
| ***Acroptilon repens*** | **Russian knapweed** | **√** | **√** | **MOD** | **MOD** | **per. forb** |
| ***Agrostis stolonifera*** | **Creeping bentgrass** | √ | | | **LIMITED** | **rhiz. grass** |
| *Aegilops triuncialis* | Barbed goatgrass | √ | | | HIGH | ann. grass |
| *Ailanthus altissima* | Tree-of-heaven | √ | √ | | MOD | tree |
| *Alhagi maurorum* | Camelthorn | | √ | | MOD | shrub |
| *Arundo donax* | Giant reed | √ | √ | MOD | HIGH | rhiz. grass |
| *Atriplex semibaccata* | Australian saltbush | | √ | | MOD | per. forb |
| *Bromus inermis* | Smooth brome | | | MOD | *not reviewed* | ann. grass |
| ***Bromus tectorum*** | **Cheatgrass** | √ | | **HIGH** | **HIGH** | **ann. grass** |
| *Carduus nutans* | Musk thistle | √ | | | MOD | ann. forb |
| *Carduus pycnocephalus* | Italian thistle | √ | | HIGH | MOD | ann. forb |
| *Centaurea diffusa* | Diffuse knapweed | √ | | | MOD | per. forb |
| ***Centaurea solstitialis*** | **Yellow starthistle** | **√** | | **HIGH** | **HIGH** | **ann. forb** |
| ***Centaurea stoebe*** | **Spotted knapweed** | **√** | **√** | **HIGH** | **HIGH** | **per. forb** |
| ***Chondrilla juncea*** | **Rush skeletonweed** | **√** | | **HIGH** | **MOD** | **per. forb** |
| *Cirsium arvense* | Canada thistle | √ | | | MOD | per. forb |
| ***Cirsium vulgare*** | **Bull thistle** | **√** | **√** | **HIGH** | **MOD** | **per. forb** |
| *Conium maculatum* | Poison hemlock | √ | √ | | MOD | per. forb |
| *Cortaderia selloana* | Pampasgrass | √ | √ | | HIGH | rhiz. Grass |
| *Cynosurus echinatus* | Hedgehog tailgrass | √ | | | MOD | ann. Grass |
| ***Cytisus scoparius*** | **Scotch broom** | **√** | | **HIGH** | **HIGH** | **Shrub** |
| *Dactylis glomeratus* | Orchardgrass | √ | | | LIMITED | rhiz. Grass |
| *Dipsacus fullonum* | Common teasel | √ | √ | | MOD | biennial forb |
| *Dittrichea graveolens* | Stinkwort | √ | √ | | MOD | ann. Forb |
| *Elymus caput-medusae* | Medusahead | √ | | HIGH | HIGH | ann. Grass |
| *Fallopia japonica* | Japanese knotweed | √ | √ | | MOD | per. Forb |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Fallopia sachalinense* | Sakhalin knotweed | √ | √ | | MOD | per. Forb |
| ***Genista monspessulana*** | **French broom** | **√** | | **HIGH** | **HIGH** | **Shrub** |
| *Hedera canariensis* | Algerian ivy | √ | √ | | HIGH | Vine |
| *Hedera helix* | English ivy | √ | √ | | HIGH | Vine |
| *Hieracium murorum* | Wall hawkweed | | | MOD | *Not reviewed* | per. Forb |
| ***Holcus lanatus*** | **Common velvetgrass** | **√** | **√** | **HIGH** | **MOD** | **rhiz. grass** |
| *Hordeum murinum* and *marinum* | Mediterranean barley | √ | √ | | MOD | ann. grass |
| *Isatis tinctoria* | Dyer's woad | √ | | | MOD | ann. forb |
| *Lepidium latifolium* | Perennial pepperweed | √ | √ | | HIGH | per. forb |
| ***Leucanthemum vulgare*** | **Ox-eye daisy** | √ | **√** | **MOD** | **MOD** | **per. forb** |
| *Linaria genistifolia and L. vulgaris* | Dalmation and yellow toadflax | √ | | | MOD | per. forb |
| *Lithrum salicaria* | Purple loosestrife | √ | | | HIGH | per. forb |
| *Onopordum acanthium* | Scotch thistle | √ | √ | | HIGH | per. forb/biennial |
| *Phalaris arundinacea* | Reed Canarygrass | | | | *Not reviewed* | rhiz. grass |
| *Phleum pratense* | Timothy | | | | *Not reviewed* | rhiz. grass |
| *Poa pratensis* | Kentucky bluegrass | √ | | | LIMITED | rhiz. grass |
| ***Rubus armeniacus and R. laciniatus*** | **Himalayan cut-leaf blackberry** | **√** | **√** | **HIGH** | **HIGH** | **shrub/vine** |
| *Rumex acetosella* | Sheep sorrel | | √ | | MOD | per. forb |
| *Sesbania punicea* | Scarlet wisteria | √ | √ | | HIGH | shrub |
| *Spartium junceum* | Spanish broom | √ | √ | | HIGH | shrub |
| *Tamarix parviflora* | Smallflower tamarisk | √ | √ | | HIGH | tree |
| *Tamarix ramosissima* | Saltcedar | √ | √ | | HIGH | tree |
| *Taraxacum officinale* | Common dandelion | | | MOD | Not listed | per. forb |
| *Vinca major* | Big periwinkle | √ | √ | | MOD | vine |

[1] A selection of species identified as being containment or eradication targets in the Sierra Nevada based on Cal-IPC (2011), a climate adaptation management opportunities report for the Wildlife Conservation Society (Cal-IPC 2014) and on current containment opportunities for the Sierra Nevada region (calweedmapper.cal-ipc.org).

[2] Non-native species called out as a potential concern for Sierra Meadows in Stillwater (2012).

[3] Species highlighted as 'high' or 'moderate' priority for control in the 2018 Yosemite National Park Workplan (National Park Service 2018). Includes species not occurring in meadows.

[4] Invasive plant rating from Cal-IPC Inventory.

## Appendix 2. Common Native Plant Species in Sierra Meadows

Common native meadow species (primarily derived from Ratcliff 1985, Jones 2011, and Demetry 2017) that are suggested candidates for comparison to non-native species targeted for study. Species highlighted in bold are common members of mid-elevation meadow communities throughout the Sierra Nevada, represent similar functional groups as non-native candidate species, and could be candidates for the experiment.

| Species | Functional group |
|---|---|
| ***Achillea millefolium*** | **Perennial forb** |
| *Agrostis hallii* | Rhizomatous grass |
| ***Agrostis pallens*** | **Rhizomatous grass** |
| ***Artemisia rothrockii*** | **Shrub** |
| *Calamogrostis breweri* | Rhizomatous grass |
| ***Calamogrostis canadensis*** | **Rhizomatous grass** |
| *Cardamine breweri* | Perennial forb |
| *Carex amplifolia* | Rhizomatous grasslike |
| *Carex exserta* | Rhizomatous grasslike |
| *Carex heteroneura* | Rhizomatous grasslike |
| ***Carex nebrascensis*** | **Rhizomatous grasslike** |
| *Carex rostrata* | Rhizomatous grasslike |
| ***Cirsium scariosum*** | **Perennial forb** |
| *Deschampsia caespitosa* | Rhizomatous grass |
| *Dodecatheon redolens* | Perennial forb |
| *Eleocharis pauciflora* | Rhizomatous grasslike |
| *Eriogonum umbellatum* | Perennial forb |
| *Gentiana newberryi* | Perennial forb |
| *Hypericum anagalloides* | Annual/perennial |
| *Juncus sp,* | Rhizomatous grasslike |
| *Kalmia polifolia* | Shrub |
| *Lupinus breweri* | Perennial forb |
| *Mimulus primuloides* | Perennial forb |
| *Muhlenbergia filiformis* | Rhizomatous grass |
| *Muhlenbergia richardsonis* | Rhizomatous grass |
| *Olypolis occidentalis* | Perennial forb |
| ***Oreostemma alpigenum*** | **Perennial forb** |
| *Penstemon heterodoxus* | Perennial forb |
| *Salix sp.* | Tree |
| *Scirpus microcarpus* | Rhizomatous grasslike |
| *Senecio scorzonella* | Perennial forb |
| ***Senecio triungularis*** | **Perennial forb** |
| *Solidago canadensis* | Perennial forb |
| *Trifolium longipes* | Perennial forb |
| *Trifolium monanthum* | Perennial forb |
| ***Vaccinium caespitosum*** | **Shrub** |

## Appendix 3. Report on “Potential impacts of invasive plants on Sierra Nevada wet meadows” by Evan Wolf, 2019

See following pages.

# Potential impacts of invasive plants on Sierra Nevada wet meadows

By Evan Wolf
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Report prepared for the California Invasive Plant Council

Partially funded by the National Fish and Wildlife Foundation (Grant # 0103.15.049976 Assessing Invasive Plant Vulnerability for Sierra Nevada Meadows)

31 January 2019

## Introduction

Invasive species have been identified as one of the major threats to ecosystems around the world (IUCN 2018). However, the effect of invasive plants on native ecosystems varies widely on a case-by-case basis and depending on the impact of concern (Didham *et al.* 2005; Pyšek *et al.* 2012). Many of the world's invasive plants are wetland species, possibly as a result of two primary factors. First, the typical low-topographic position of wetlands provides a collection point for plant propagules carried by wind and water. Second, wetland-dominant plants often employ a clonal growth strategy and are effective at growing quickly below-ground to forage for nutrients and above-ground to compete for light. This set of traits is associated with high invasive potential  (Zedler & Kercher 2004). However, not all wetland types are equally invaded or prone to invasion.

Most plants, including invasive species, have difficulty colonizing and thriving in the stressful environment of wetlands with high stable water levels, persistent soil anoxia, limited nutrient availability, toxic levels of metals and acidity, and infrequent disturbance (Zefferman *et al.* 2015). However, plants adapted to these stresses in their home range can establish in similar nonnative environments (Rejmánek 2000). In addition, a common human impact to perennially saturated wetlands is to drain them via direct ditching or water diversion, or indirectly by causing gully formation (effectively ditching) through poor land management. Disturbance can remove or weaken the environmental filters or competitive constraints that limit the number of invasive (and native) plants species capable of establishing at a site (Funk *et al.* 2008).

Approximately one-third of Earth's wetland area has been eliminated by humans (Hu *et al.* 2017). In the lower 48 United States half of the wetland area has been lost, with about 90% loss in California (Dahl 1990). About 13% of the remaining 6,210 km$^2$ of freshwater non-lake wetlands in California (SFEI 2016) are located in the Sierra Nevada (Viers *et al.* 2013). These mountain wetlands are collectively referred to as meadows.

Sierra Nevada meadows formed during the past 10,000 years as sediment and organic matter was deposited and remained in place (Wood 1975). However, unregulated grazing from the 1860s to the 1940s removed much of the meadow vegetation and lead to the formation of erosion gullies in some sloping meadows (Sumner Jr. 1941; Armstrong 1942; Wolf & Cooper 2016). Gullies rapidly drain water from meadows, lowering the water table (Hammersmark, Rains & Mount 2008), altering vegetation composition and cover (Loheide II & Gorelick 2007; Lowry *et al.* 2011) and exposing soil organic matter to decomposition (Chimner & Cooper 2003; Schimelpfenig, Cooper & Chimner 2014). It is estimated that over half of Sierra meadows require management intervention to recover natural hydrologic, geomorphic, and vegetative states and processes (Odion, Dudley & D'Antonio 1988; Kattelmann & Embury 1996).

Meadows occupy less than 3% of the land area of the Sierra Nevada (UCD & USFS 2017), but are hot-spots of floral biodiversity (Jones 2011) and ecosystem services (Hammersmark 2008; Loheide *et al.* 2009; Norton *et al.* 2011). They provide important habitat for birds (Van Riper & Van Wagtendonk 2006), insects (Simonson *et al.* 2001; Hatfield & LeBuhn 2007), amphibians (Morton & Pereyra 2010; Liang & Stohlgren 2011), and mammals (Grenfell & Brody 1986). (Jones 2011). In addition, mountain meadows can attenuate flood peaks (Hammersmark 2008), store and transform carbon and nitrogen (Norton *et al.* 2011), and retain shallow groundwater and soil water (Loheide *et al.* 2009).

For all of these reasons, preservation and restoration of Sierra Nevada meadows is a top priority for land managers and funding agencies in California. Although hydrolo6rtgic impacts are the focus of most meadow research and restoration efforts, it is clear that changes to vegetation can have both direct and indirect impacts to ecosystem function as well. What is less clear is the role that invasive plant species may play in altering the vegetation, hydrology, soils, and wildlife habitat of these mountain wetlands. This report will summarize the current state of knowledge about invasive plants in Sierra Nevada meadows and the effects they may have on water and carbon storage and wildlife habitat. Very little research has directly examined the effect of invasive species on carbon or water storage in meadows. Therefore, a summary of related work is provided, and broad patterns that are likely to affect these processes are discussed.

The word "meadow" is a broad and poorly defined term that encompasses several different treeless ecosystem types. This report focuses on wetland ecosystems, and the use of the term meadow refers to wet meadows where wetland conditions exclude trees, except where other dry meadow types are specifically referred to.

## Plant community impacts and competition

As plant resource availability increases and site stress decreases, both native and nonnative wetland species richness increases. In a study of 58 Ontario, Canada wetlands, nonnative invasives were as likely to dominate wetlands as native dominant plants, with similar effects on native rare plants. Community dominants, regardless of origin (native or not) caused similar reductions in native wetland plant community diversity (Houlahan & Findlay 2004). Wetland plant communities with highly dominant species were typically less diverse than those without.

In the Sierra Nevada both native and nonnative plant richness are higher at lower elevations, where numerous environmental stresses are ameliorated (Keeley, Lubin & Fotheringham 2003). Only 12% of high elevation meadows (2,200 – 3,400 m; 7,200 – 11,150 ft) had nonnative plant species present, and in all cases the nonnative cover was less than 5% (D'Antonio, Berlow & Haubensak 2004). In addition, native and nonnative plant species richness is higher in dry portions of meadows with similar grazing histories (Dwire, Kauffman & Baham 2006). Drier meadow edges are often less stressful than the permanently saturated and anoxic soil conditions in the wettest areas of meadows.

In a study of management challenges in Sierra meadows, all of the mid-elevation (6,000 – 9,000 feet) pack stock meadows within Yosemite and Sequoia and Kings Canyon National Parks were found to contain two nonnative species: Kentucky bluegrass (*Poa pratensis*) and common dandelion (*Taraxacum officinale*) (Gerlach Jr. et al. 2003). Half of the pastures contained only those two species, and the other half contained those two plus one to three other species. Nonnative richness and frequency were greatest near areas of human and livestock use, such as trails, roads, campgrounds, corrals, and pastures. Animal dung is an effective vector for nonnative plants, and the species used for animal forage have often been bred or genetically engineered to be hardy, drought tolerant, or herbicide resistant. As a result, transmission of propagules into meadows via animal feces risks introducing difficult-to-remove species (Quinn *et al.* 2008; Ostoja *et al.* 2014).

Genetic contamination is also an important concern for native species. Reed canarygrass (*Phalaris arundinaceae*) is a native wetland plant that has interbred with repeatedly-introduced Eurasian genotypes (Lavergne & Molofsky 2007). This hybrid has invaded wet meadows in the upper Midwest, dominating some sites to the detriment of native plant cover (Maurer *et al.,* 2003; Annen *et al*., 2008). Light availability is the primary limiting factor to the survival and spread of *Phalaris arundinaceae*, but in nutrient-rich conditions, established *Phalaris* can clonally expand into shady areas and replace native plant communities (Maurer & Zedler 2002).

Prevention of initial colonization can be key to minimizing invasion, because once established, populations can be very resilient. For example, young individuals of *Phalaris arundinaceae* are growth-limited by shade and flooding, but established clones can spread rhizomes into unfavorable areas by providing nutrient subsidies to flooded and shaded shoots (Maurer & Zedler 2002). Common velvetgrass (*Holcus lanatus*) is an established nonnative invasive of mid-elevation Sierra Nevada meadows. Hand-pulling is an ineffective treatment. Similarly, velvetgrass cover returns to pre-treatment levels after one year following a single glyphosate application (Jones *et al.* 2015).

Of particular concern for meadows are yellow star thistle (*Centaurea solstitialis*), medusahead (*Elymus caput-medusae*) perennial pepperweed (*Lepidium latifolium*), and purple loosestrife (*Lythrum salicaria*) (D'Antonio *et al.* 2004). Several woody species can also establish in riparian areas: Russian olive (*Eleagnus angustifolia*), and saltcedar (*Tamarix parviflora*, and *T. ramosissima*). These species are all present in the lower elevations and valleys surrounding the Sierra Nevada and have only made small or temporary incursions into the montane and higher zones. Sierra invasions by these potentially problematic plants are not large or widespread at this point, so early detection and eradication are still feasible. Disturbance is the most likely facilitator of further invasion or expansion.

## Disturbance effects

Domestic livestock grazing has been a widespread disturbance to Sierra Nevada meadows since the mid-1800s (Gross & Coppoletta 2013). In nutrient-poor sites, grazing disturbance tends to decrease species richness, while the reverse tends to be true for nutrient-rich sites (Proulx & Mazumder 1998). Dense cover in these productive sites often limits establishment of newcomers. In a low elevation coastal

California meadow, established invasive annual grasses suppress native and nonnative broadleaf meadow plants via live stem and leaf competition for light and shading from accumulated grass litter, not via competition for water (Coleman & Levine 2007).

Disturbance can provide an important establishment opportunity by allowing propagule access to bare soil and reducing shading of small seedlings. Soil disturbance by burrowing rodents and/or cattle grazing facilitates the invasion of even wet meadow sites by the upland native woody shrub sagebrush (*Artemisia rothrockii*). Undisturbed dense vegetation prevented shrub establishment, and the exclusion effect was strongest at the wettest sites. Shading from dense vegetation reduced the growth and survival of post-seedling sagebrush (Bauer, Berlow & D'antonio 2002; Berlow, D'Antonio & Reynolds 2002; Berlow, D'Antonio & Swartz 2003).

However, grazing disturbance effects on invasive plant cover differ between meadow types. In low-elevation riparian areas embedded within oak savanna/annual grasslands of the coastal mountains of California, across actively restored, passively restored, or unrestored sites, invasive plant cover increased with seasonal grazing duration (Gornish *et al.* 2017). However, at wetter and higher elevation sites this correlation between grazing and invasive cover was not observed. Ten and three-year grazing treatments (ungrazed to moderately grazed) in groundwater-fed wetlands in the Sierra foothills resulted in no change in the relative amounts of native and nonnative plant species diversity (Allen-Diaz *et al.* 2008). Over a decade-long study in National Forests across the western US, grazing intensity was correlated with reduced wetland species but did not affect nonnative plant frequency. However, both nonnative species frequency and native wetland species frequency increased in relatively wetter years (Oles *et al.* 2017).

Where invasives are already dominant, disturbance may play a key role in allowing native plants opportunities to establish and thrive. In low elevation California grasslands, oak savannas, and meadows, grazing during years with low-precipitation springs reduced medusahead (*Taeniatherum caput-medusae*) cover, but had no effect on yellow star thistle (*Centaurea solstitialis*). A complete absence of grazing for 10 years resulted in a shift in dominance from medusahead to other invasive grasses more tolerant of the accumulated litter layer (Davy *et al.* 2015). In Central Valley vernal pool wetlands dominated by nonnative annual grasses, grazing reduced nonnative cover and allowed increased native species richness and cover (Marty 2005).

## Wildlife impacts

Outside of the Sierra Nevada there are numerous examples of invasive plants displacing native plants, altering invertebrate and fungal communities, affecting wildlife habitat (Dukes & Mooney 2004), and degrading ecosystem services (Funk *et al.* 2014). Several invasive species with documented impacts to wildlife occur in or near Sierra Nevada meadows and may pose a similar threat.

A native subspecies (ssp. *americanus*) and nonnative subspecies (ssp. *australis*) of the perennial grass *Phragmites australis* are found in the US and it is unclear which form or forms are present in California. *P. australis* (ssp unidentified) is found in the Sierra Nevada, up to about 7000 ft elevation. Throughout

North America *P. australis* ssp. *australis* can become a wetland community dominant with generally positive effects on salt-marsh aquatic wildlife (shrimp and fiddler crabs), freshwater amphibians (American toads and green frogs), and small mammals (muskrats, shrews, voles) and negative effects on birds, although this may depend on the patchiness of the *P. australis* cover (Destefano 2013). In marshes on the east coast of the US where invasive *Phragmites australis* ssp. *australis* has replaced *Spartina alterniflora* as a salt marsh dominant, the herbivorous arthropod community that fed on *Spartina* has been largely replaced by detritovores or consumers of benthic microalgae (Gratton & Denno 2005, 2006).

A set of palustrine emergent wetlands in the Sierra Foothills, which were all co-dominated by nonnative invasive grasses, supported populations of the threatened bird, the California black rail. Rail site occupancy was positively correlated with wetland size, with wetter irrigation-fed hydrology, and denser vegetation. They also occupied sites with a greater percentage of native rush dominants compared with invasive grass dominants, but this is likely due to the preference of both rushes and rails for wetland hydrology rather than a direct effect of the invasive grasses (Richmond *et al.* 2010). In wetlands around Boston, MA the abundance of wetland bird species responded in varied and unpredictable ways to purple loosestrife (*Lythrum salicaria*) cover (Tavernia & Reed 2012).

In low elevation valley wetlands in Oregon, the abundance of *Phalaris arundinacea* was negatively correlated with native amphibians in actively and passively managed agricultural wetlands (Rowe & Garcia 2014). However, there was no difference between native and nonnative dominated wetland habitats in New York state with respect to amphibian growth. Differences in plant traits that controlled soluble phenolics, litter C:N ratio, and litter N:P ratio did impact the survival of young amphibians (Cohen, Maerz & Blossey 2012).

## Soil and carbon storage impacts

As with impacts to wildlife, invasive plant effects on soil are likely tied to specific plant traits. At a low elevation wetland in northeast California the nonnative perennial pepperweed (*Lepidium latifolium*) altered surface soil properties by concentrating calcium and magnesium in its aboveground biomass (Blank & Young 2002). Areas of meadows in the Rockies invaded by leafy spurge (*Euphorbia virgata*) and Canada thistle (*Cirsium arvense*) have lower plant species richness, lower arthropod density, and lower decomposition rates of certain litter fractions (Pritekel *et al.* 2006).

Plant traits can significantly affect greenhouse gas sequestration and emission (Ward *et al.* 2009). Production of acetate, a root exudate, drives methanogenesis in native arctic wetland species (Strom *et al.* 2003). In addition, the aerenchyma tissue in wetland plants that provides aeration to roots also serves as a conduit for rapid transport of methane from its origin in the soil to the atmosphere (Shannon *et al.* 1996). Little to no research has been conducted describing the differences between natives and nonnatives with regard to many plant traits. However, one broadly applicable trait-based observation is that invasive plants tend to grow faster, allocate more resources to leaves and stems, and contain more biomass than native neighbors (Van Kleunen, Weber & Fischer 2010).

These traits indicate that invasives have high photosynthetic rate and gross primary production (GPP). GPP quantifies the amount of carbon dioxide transferred from the atmosphere to the ecosystem and ecosystem respiration (ER) is a measure of the movement of $CO_2$ in the opposite direction, from the ecosystem back in to the atmosphere. The sum of these opposing processes (GPP + ER, by convention GPP is always a negative number, ER always positive) yields net ecosystem exchange (NEE). Therefore the high-GPP traits exhibited by many invasive plants may indicate a tendency for invaded ecosystem to increase their net storage of carbon dioxide in aboveground biomass.

However, despite fast growth and large stature, invasive plants that invest heavily in aboveground growth may not contribute much to soil carbon storage. Belowground growth of roots and rhizomes is the primary mechanism for carbon storage in organic-rich meadow soils (Chimner, Cooper & Parton 2002; Rasse, Rumpel & Dignac 2005; De Deyn, Cornelissen & Bardgett 2008). The dominant native plants that typify Sierra meadows are densely rooted clonal monocots (Manning & Padgett 1995; Potter 2005; Fites-Kaufman *et al.* 2007). Clonal reproduction and high below- to above-ground biomass ratios are common traits in wetland plants (Moor *et al.* 2017). Invasive plants that successfully dominate hydrologically intact wetlands are often clonal monocots as well (e.g. *Phragmites australis, Phalaris arundinacea* and *Holcus lanatus*).

## Hydrology impacts

Invasive plant effects on hydrology are likely to be trait-based in a similar way as their effect on carbon flux. Growth rate and leaf area are both highly correlated with plant transpiration of water (Pagter, Bragato & Brix 2005). Transpiration of water by plants is a major outflow of water from wetlands, and a shift to a faster-growing and/or a greater leaf-area plant community could cause hydrologic impacts (Loheide II & Gorelick 2005; Hammersmark *et al.* 2008; Nash *et al.* 2018). Fast, early-growing annual plants (often a set of traits possessed by invasives) can extract soil moisture from surface layers, leaving a deficit for later-growing plants. Deep-rooting by plants such as yellow star thistle can access water below dry surface layers, allowing for co-occurrence with annuals that depend on shallow soil water (Borman, Johnson & Krueger 1992). In meadow sites where channel incision has caused a dropped in water level, species dependent on shallow water die off, creating establishment opportunities for deep-rooted shrubs like sagebrush (Darrouzet-Nardi, D'Antonio & Dawson 2006).

## Assessing the carbon and water budgets of meadows

Measurement of changes to meadow carbon or water storage involve the development of site balances for these two parameters. In both cases the balances consist of measuring or estimating inputs, outputs, and a change in storage. Carbon balances for the purpose of quantifying warming potential often include a quantification of two other greenhouse gases: methane (CH4) and nitrous oxide (N2O). In most cases the primary contributing greenhouse gas is carbon dioxide (CO2), which is also the most significant gas for the purposes of quantifying the movement of elemental carbon into and out of an ecosystem.

Inputs and outputs of the three greenhouse gases are usually measured by covering a meadow plot with a chamber that seals to the soil surface, including undisturbed live vegetation inside. An initial time zero ambient sample of the chamber headspace is taken, and then samples are drawn from the headspace at regular intervals to quantify a rate of change in gas concentration. Reductions in chamber headspace concentrations of gas (uptake by the meadow ecosystem) are usually expressed as negative rates on a per meadow area basis. Measured increases in chamber headspace gas concentrations (emissions from the meadow) are expressed as positive rates, per area.

Measurements from single plots and single points in time must be interpolated across the gaps in space between sample plots, and the gaps in time between sampling intervals. For spatial interpolation, plots are generally selected and replicated so as to be representative of larger homogenous sections of meadow that share similar vegetation, hydrology, soil, and geomorphic position. For temporal interpolation, environmental variables that drive the primary processes of GPP and ER (such as air and soil temperature, soil moisture, incoming solar radiation, and plant greenness) are recorded at much shorter time intervals. A model is used to estimate GPP and ER using these frequently-measured environmental variables and fill in the gaps between direct field measurements of gas flux. Separate models can be constructed for methane and nitrous oxide if they are measured in quantities that are significant (Strack, Keith & Xu 2014; Millar *et al.* 2016; Wolf 2017).

The size of the soil carbon pool is assessed by collecting soil samples from depth profiles and measuring their organic carbon content. Carbon content can be measured by the loss-on-ignition method, where the dry soil sample is incinerated in a furnace, the organic matter mass loss measured, and a literature-derived carbon content (~50%) is assigned to the incinerated organic matter. Alternatively, carbon content can be measured directly by high temperature chromatography in a CHN analyzer.

An often-cited trait of invasive plants is their high productivity per area, which should in general shift a plant community towards net carbon storage. The strategies of carbon capture are not fundamentally different between native and nonnative plant species, so trait-based assessments of invasive impacts to greenhouse gas flux are likely to be appropriate estimates (Leishman, Thomson & Cooke 2010).

Water balances are measured by quantifying surface inflows and outflows and measuring the change in storage using groundwater monitoring wells. The major challenges in constructing a complete water balance include quantifying groundwater inputs or outflows and evapotranspiration. Similar to the carbon balance, spatial interpolation between spaced measurement points is often necessary. Wells and staff gauges are usually very simple constructions of slotted 1-2” diameter PVC pipe installed vertically that allows water, but minimal sediment, to pass freely into and out of the slotted walls. Well pipes are installed into hand-auger holes in meadow soil and staff gauge pipes are attached to rebar or t-posts pounded into the streambed. Water level data loggers can be suspended within the pipe and used to record water level in wells and stream gauges at short time intervals (Drexler *et al.* 1999; Hammersmark *et al.* 2008; Kitlasten & Fogg 2015).

A large-scale attempt to quantify the water use of nonnative trees compared to shorter stature native vegetation is ongoing in South Africa (Gorgens & Van Wilgen 2004). Initial studies indicate a modest increase in nonnative water use compared with natives in high rainfall areas. Early estimates of high water use by the invasive shrub genus *Tamarix* in the Colorado River Basin have failed to be corroborated by more detailed and sophisticated scientific studies (Stromberg *et al.* 2009).

## Conclusions

Although there are a good number of studies demonstrating the likely response of invasive plant species to various types of disturbance to meadows, relatively little is known about how invasive species themselves impact Sierra Nevada meadows. Important avenues of research would include investigations into competitive exclusion of natives by invasive plants in mountain meadows, the alteration of carbon, nutrients, and water cycling, and broader impacts to insect and larger animal food webs. Lower elevation meadows of the Sierra are more invaded than higher sites, so efforts to prevent spread, detect early colonization, and eradicate invasive populations should start at the tops of watersheds and work down. Livestock grazing in meadows should be more closely examined in relation to invasive plants. This one activity serves as a vector of nonnative plant propagules, produces plant and soil disturbance that provides new plant establishment opportunities, and is also a source of concentrated nutrients that promotes fast-growing species.

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