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Review

Potential environmental effects of pack stock on meadow ecosystems of the Sierra Nevada, USA

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Abstract. Pack and saddle stock, including, but not limited to domesticated horses, mules, and burros, are used to support commercial, private and administrative activities in the Sierra Nevada. The use of pack stock has become a contentious and litigious issue for land management agencies in the region *inter alia* due to concerns over effects on the environment. The potential environmental effects of pack stock on Sierra Nevada meadow ecosystems are reviewed and it is concluded that the use of pack stock has the potential to influence the following: (1) water nutrient dynamics, sedimentation, temperature, and microbial pathogen content; (2) soil chemistry, nutrient cycling, soil compaction and hydrology; (3) plant individuals, populations and community dynamics, non-native invasive species, and encroachment of woody species; and (4) wildlife individuals, populations and communities. It is considered from currently available information that management objectives of pack stock should include the following: minimise bare ground, maximise plant cover, maintain species composition of native plants, minimise trampling, especially on wet soils and stream banks, and minimise direct urination and defecation by pack stock into water. However, incomplete documentation of patterns of pack stock use and limited past research limits current understanding of the effects of pack stock, especially their effects on water, soils and wildlife. To improve management of pack stock in this region, research is needed on linking measurable monitoring variables (e.g. plant cover) with environmental relevancy (e.g. soil erosion processes, wildlife habitat use), and identifying specific environmental thresholds of degradation along gradients of pack stock use in Sierra Nevada meadows.

Additional keywords: cattle, Forest Service, horses, mules, National Park Service, pack animals, wilderness.

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Introduction

Montane, sub-alpine, and alpine meadows of the Sierra Nevada are important for biological diversity, providing key ecosystem services and supporting varied recreational activities. They are also fundamental ecological components of wilderness areas within mountainous regions of western North America. Meadows are characterised by surface water and/or shallow groundwater, have fine-textured soils, which sometimes contain significant amounts of organic matter, and are dominated by herbaceous plant communities with woody species sometimes locally

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abundant (Weixelman *et al*. 2011). Estimating meadow area is difficult because there is not a single comprehensive spatial dataset for the entire Sierra Nevada (see Viers *et al*. 2013). However, in recent analysis Viers *et al*. (2013) estimated meadows to cover 77 039 ha (191 900 acres). And while they only occupy ~3% of the landscape of the Sierra Nevada, they contribute disproportionately to productivity and species diversity (Allen 1987; Jones 2011; Viers *et al*. 2013; USGS, unpubl. data). They provide critical habitat for sensitive species, such as the Yosemite toad (*Anaxyrus canorus*), which has been federally listed as threatened (USFWS 2014) under the United States Endangered Species Act. Meadows also historically contributed a substantial proportion of the available forage and habitat for wildlife (Thomas *et al*. 1979; Allen 1987) and domestic livestock (Roath and Kruger 1982) in national forests, national parks and other areas.

Pack and saddle stock (hereafter referred to as pack stock), including domesticated horses, mules, and burros, are used to support both recreational (commercial and private) and administrative (land management agency) activities in the Sierra Nevada. The historic distribution and intensity of pack stock use has not been systematically documented, but the first recorded crossing of the Sierra Nevada that was facilitated by pack stock occurred in 1827 and, after the mid-century gold rush, use of pack stock became increasingly common. Trips consisting of as many as 200 pack animals did occur beginning with the first Sierra Club sponsored trip in 1901 (McClaran 1989). In the national forests of the central and southern Sierra Nevada and in Yosemite National Park, single trips are currently limited to 25 animals each, although most are typically made up of far fewer than 25 animals (M. Fincher, National Park Service, pers. comm.). Sequoia and Kings Canyon National Parks limit stock parties to 20 animals. In Yosemite National Park, annual stock use between 2004 and 2012 averaged 1571 pack animal nights per year, whereas in Sequoia and Kings Canyon National Parks, where pack stock use has been systematically tracked since 1985, annual stock use between 1985 and 2012 averaged 8482 pack animal nights per year.

Meadows are often the focus of pack stock activities because they provide desirable camping locations, and provide forage and water sources for pack stock (McClaran and Cole 1993). However, the presence of pack stock in and adjacent to meadows has generated significant controversy, both because of disagreements regarding the appropriateness of pack stock in wilderness areas and concerns about their potential environmental effects (USDI 1986; Cole and Landres 1996). These concerns have led to litigation (e.g. USCA 2004; USDC 2008), and the exposure of land management agencies to litigation is promoted in part by the limited scientific literature on effects of pack stock on the meadows of the Sierra Nevada.

The management of pack stock in meadows is an important component of land management and of plans for wilderness stewardship in the Sierra Nevada. Although McClaran and Cole (1993) provided a comprehensive summary describing pack stock use, impacts, monitoring, and management in wilderness areas of the United States, there remains a need for a review focussed on known and potential effects of pack stock in the Sierra Nevada that includes additional information from the past two decades. Plan development requires detailed information related to the timing and duration of use, opening and closing dates, group sizes, use of supplementary feed, and associated handling activities. Although these variables are often included in use permits issued by land management agencies, they are not consistently recorded and, for some factors, compliance with permit specifications is unclear. In addition, the behavioural patterns of pack stock within meadows have not been systematically evaluated, especially during the overnight hours when they are typically turned out to feed, rest, and roam with minimal or no human oversight.

The purpose of this review is to provide a summary of potential effects of pack stock on broad response categories, including water, soils, plants and wildlife in the meadows of the Sierra Nevada. We evaluated potential effects across categories of broad-ecosystem response within the context of the meadow ecosystem for two main reasons. First, there are a limited number of studies on pack stock and nearly all report the effects of presence versus absence of pack stock, and second, these studies do not provide any information about the effects of variations in levels of use in space and time which constitute the foundation of best management practices and standards.

Our focus is on a comprehensive review of the pack stock literature, but we also draw upon some livestock literature to infer potential mechanisms of the effects of pack stock. Inferences from cattle studies are always placed in the appropriate context relative to potential effects of pack stock, recognising that the characteristics of disturbance of the two (i.e. cattle versus pack stock) differ. This is particularly the case in relation to duration and intensity of disturbance caused by pack trains compared with cattle herds, which lead to differing magnitudes of ecosystem response.

A recent review of the effects of livestock took the approach of evaluating effects in the context of standard rangeland practices (Briske 2011). However, this approach is only effective when there is sufficient literature linking specific practices with measureable effects, which is not the case for pack stock.

All effects that have been evaluated and published in available literature are considered in this review. Topics not covered in published literature and, therefore, not addressed here include soil enrichment, meadow/stream bank erosion and dust baths. A summary of the studies reporting environmental effects of pack stock is provided in Table 1. Published studies do not address effects across frequency, duration, or intensity gradients (i.e. levels of use by pack stock) but rather report only effects of pack stock presence versus absence. In our treatment of pack stock, we refer to horses and mules collectively unless specifically noted in text, although it should be noted mules comprise most of stock used in the Sierra Nevada.

Effects on water quality

Defecation and urination by pack stock may introduce and/or redistribute nutrients and microbial pathogens from one location to another. Because most water bodies at high elevation are extremely oligotrophic, even small increases in their nutrient loading have the potential to cause detectable ecosystem effects. The main categories of potential effects include changes in nutrient dynamics, microbial pathogens, sedimentation and temperature (Table 2).

Table 1. Studies that describe environmental effects of pack stock (horses, mules, and/or burros), or evaluate the role of pack stock in causing environmental effects (e.g. as vectors for invasive plants or human pathogens), in meadow ecosystems in North America

Note that the description of each study does not include information on levels of pack stock use (e.g. frequency, duration and intensity) but rather only reports of presence/absence effects. This reflects the fact that multi-level or gradient studies of pack stock use do not exist in the literature. Note that all locations shown below are within the USA

Ecosystem component	Effect categories	Type of study and approach for discerning pack stock effects	Location	Citation
Water	Nutrient dynamics	Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Derlet *et al*. (2012)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Hayden *et al*. (2010)
		Observational study, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Ursem *et al*. (2009)
	Microbial pathogens	Descriptive survey, and described frequency of pathogens in pack stock animal feces	Sierra Nevada	Atwill *et al*. (2000)
		Descriptive survey, and compared frequency of pathogens in pack stock animal compared with wild animal feces	Sierra Nevada	Derlet and Carlson (2002)
		Descriptive survey, and described frequency of pathogens in pack stock animal feces	Colorado	Forde *et al*. (1998)
		Descriptive survey, described frequency of pathogens in pack stock animal feces	Sierra Nevada	Johnson *et al*. (1997)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Derlet and Carlson (2004)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Derlet and Carlson (2006)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Derlet *et al*. (2004)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Derlet *et al*. (2008)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Hayden *et al*. (2010)
		Observational study, compared presence with absence of pack stock use, and could not distinguish backpacker/pack stock combined effects from pack stock effects alone	Sierra Nevada	Ursem *et al.* (2009)
	Sedimentation	N/A	Sierra Nevada	No representative study found
	Temperature	N/A	Sierra Nevada	No representative study found
Soils	Compaction	Observational study, compared soil compaction between backpacker and/or pack stock sites to control sites, greater soil compaction in 'camp' sites compared with control sites, and pack stock sites had greater soil compaction compared with back packer sites	Bob Marshall Wilderness, Montana	Cole (1983)
		Experimental study, compared vegetation trampling by horses, motorcycles and hikers, former two groups more damaging than latter most, soil compaction increased with increasing number of passes and was greater on slopes	Northern Rocky Mountains	Weaver and Dale (1978)
		Observational study, compared soil strength among pack stock meadows and non-stock control meadows in Sequoia National Park, and pack stock meadows demonstrated significantly greater soil strength in a reed grass and sedge vegetation association type	Sierra Nevada	Holmquist *et al.* (2014)
	Nutrient cycling	N/A	N/A	No representative study found

(*continued next page*)

Table 1. (*continued*)

Ecosystem component	Effect categories	Type of study and approach for discerning pack stock effects	Location	Citation
Plants	Plant individuals, populations, and communities	Experimental study, compared changes in plant productivity by picketed horses/mules, and pack stock reduced mean plant productivity between 17–22% and between 7–13% greater bare soil, depending on meadow type after 4 years of grazing	Sierra Nevada	Cole *et al*. (2004)
		Observational study, compared grazed and ungrazed meadow by pack stock, and reported lower litter cover and depth, and greater bare ground in grazed sites	Sierra Nevada	Holmquist *et al*. (2013*a*, 2013*b*)
		Observational study, compared grazed and ungrazed meadows by pack stock, and reported lower litter cover and depth in grazed sites	Sierra Nevada	Holmquist *et al*. (2010)
		Observation study, compared ungrazed, lightly and heavily grazed patches, reported negative effects on vegetation structure in heavily grazed patches	Yosemite NP	Holmquist *et al*. (2014)
		Experimental study, compared foraging behaviour by picked horses, and found grasses were preferred to forbs initially, but forb preference increased with time grazing and plant height, whereas grass use was independent of plant height	Northern Rocky Mountains	Olson-Rutz *et al*. (1996*a*)
		Experimental study, and failed to find effects of grazing by picketed horses on bare soil, litter, vegetation, rock, moss cover and stem counts the year following grazing	Northern Rocky Mountains	Olson-Rutz *et al*. (1996*b*)
		Observational study, and reported little evidence that pack stock produced compositional changes	Sierra Nevada	Hopkinson *et al*. (2013)
	Non-native invasive species	Targeted surveys, reported non-native species in select meadows, and several species known to be dispersed in horse digestive tracts were also present along trails	Sierra Nevada	Gerlach *et al*. (2003)
	Non-native invasive species	Targeted dung collections, and over 20 non-native species germinated from horse dung	California – various	Quinn *et al*. (2008)
	Non-native invasive species	Targeted dung collections along trails and trailheads, seeds of non-native species where found in horse dung, and 85% of the seedlings reordered where non-native	Western Colorado	Wells and Lauenroth (2007)
	Encroachment by woody species	N/A	N/A	No representative study
Wildlife	Population	Bird point counts and literature review, and reported cowbird occurrence in Sierra Nevada may have been facilitated by human activities and presence of horse corrals	Sierra Nevada	Rothstein *et al*. (1980)
		Radio-telemetry of cowbirds, and reported travelling from nesting sites to forage in horse corrals	Sierra Nevada	Rothstein *et al*. (1984)
		Stratified permutation test evaluating the occurrence of Yosemite toad breeding with pack stock use patterns, reports no known relationship among use patterns. Suggesting pack stock do not negatively influence breeding by Yosemite toads	Yosemite NP	USGS, unpubl. data
	Communities	Observational study, and no effect of long-term pack stock use was detected on arthropod communities	Sierra Nevada	Holmquist *et al*. (2010)
		Observational study, and reported lower arthropod abundance across morphospecies and lower canopy fauna from mid-season pack stock grazing	Sierra Nevada	Holmquist *et al*. (2013*a*)
		Observational study, and reported greater arthropod for Orthoptera and Coleoptera, but year and vegetation type considered were also important	Sierra Nevada	Holmquist *et al*. (2013*b*)
		Observation study, compared ungrazed, lightly and heavily grazed within meadow patches, and reported heavily grazed patches had low species diversity and positive effects on arthropod community structure in lightly grazed patches	Yosemite NP	Holmquist *et al*. (2014)

Nutrient dynamics

Derlet *et al*. (2012) considered algae as indicators of aquatic eutrophication in the central and southern Sierra Nevada. Of the 64 sites in their study, 9% were in 'cattle' sites grazed by cattle that were trucked in for 90–100-day grazing durations; 56% were in 'recreational' sites with moderate to heavy use by humans and variable use by pack stock; and 25% were in 'wildlife' sites with little or no human or domesticated animal traffic. Periphyton were found at 48 sites including 100% of the cattle sites, 89% of the recreational sites, and 25% of wildlife sites. Mean benthic cover of algae was 66% at cattle sites, 41% at recreational sites, and 2% at wildlife sites. These data suggest that eutrophication was

Table 2. Potential effects of pack stock on water quality summarised from the literature presented in the text

Categories	Potential effects
Nutrient dynamics	Increased nutrient levels may occur but vary with pack stock density, duration of use, season of use, and location of feces and urine deposition. Defecation and urination can alter aquatic nutrient levels, and levels may spike following runoff events
Microbial pathogens	*Giardia* and *Cryptosporidium* are human pathogens that can be present in pack stock manure and the former can remain viable in cold water for many years. However, these pathogens are typically present in only 1–5% of pack stock, and at higher levels with increased animal density. About one-tenth of pack stock manure samples contain bacteria pathogenic to humans, but manure from wildlife, such as deer, can also contain these pathogens. Coliform bacteria (including *E. coli*) can be prevalent at most sites used by cattle, about half of sites used by pack stock and humans, and about one-tenth of sites with minimal anthropogenic influences
Sedimentation	Removal of streamside vegetation by grazing, especially reductions in vegetation height, can increase suspended sediments
Temperature	Removal of streamside vegetation by grazing may increase water temperatures but other factors may have equal or greater influence (e.g. air mass characteristics, elevation gradient, adiabatic lapse rate, stream channel width and depth, water velocity, surrounding landscape, and interflow inputs)

highest at sites grazed by cattle, moderate at the recreational sites with human and/or pack stock use and lowest at sites used by wildlife but with minimal human impact. However, it is unclear if the differences among the three contrasting land-use categories may have alternatively been due to other systematic factors such as elevation and time since last use by cattle, humans, and/or pack stock. The design of this study also did not distinguish between effects by humans backpacking versus humans travelling with pack stock (Table 1). Similar results were reported by Hayden *et al*. (2010) where biomass of periphyton was higher at mixed-use sites used by both backpackers and pack stock than at sites used only by backpackers in the Sierra Nevada. However, that study had the same limitations in study design as described above for Derlet *et al*. (2012) and is further limited because it does not account for the possibility that mixed-use sites may have also experienced higher use by backpackers because they tend to be closer to major trails to accommodate access by pack stock.

A similar study was conducted by Roche *et al*. (2013) with somewhat differing results from those reported above. Concentrations of nitrogen (N) and phosphates were recorded within streams across 12 United States Forest Service cattle grazing allotments in the Klamath, Coast, Cascade, and Sierra Nevada mountain ranges within California. Of the 155 sampling sites, 63% were within 200 m of 'key grazing' areas within meadows and riparian areas that cattle were known to occupy frequently and/or for extended periods of time during the grazing season, 17% were within 200 m of 'recreation' areas including camping grounds, swimming areas, and trailheads used by hikers and pack stock, and 20% were in areas of 'no concentrated use activities' at perennial flow tributary confluences that did not have concentrated cattle or recreational uses. Mean concentrations and standard errors of total N and phosphates were both significantly higher in key grazing (61 ± 4 and $7 \pm 0.3\ \mu g\ L^{-1}$, respectively) than recreational areas (38 ± 3 and $5 \pm 0.2\ \mu g\ L^{-1}$), consistent with the studies reported above. In contrast to those studies, concentrations in areas with no concentrated use (64 ± 6 and $8 \pm 0.6\ \mu g\ L^{-1}$) were as high as the key grazing areas (Roche *et al*. 2013; Table 4). Concentrations of nitrates were also significantly higher in areas with no concentrated use ($25 \pm 2\ \mu g\ L^{-1}$) than in recreational areas ($16 \pm 1\ \mu g\ L^{-1}$), but not in key grazing areas ($17 \pm 4\ \mu g\ L^{-1}$). Concentration of total phosphorus (P) did not vary among the three areas. These data suggest that common nutrient drivers of eutrophication can be higher in areas grazed by livestock compared with areas used for multiple recreational uses, including pack stock. However, the reason that areas without (or with very low levels) of these anthropogenic factors had similar concentrations of some nutrients as areas experiencing cattle grazing is unknown. Roche *et al*. (2013; Table 5) reported significantly higher concentrations of phosphate when cattle were present at the time of sampling, but lower levels of phosphates and total N when recreational activities (i.e. swimming, bathing, camping, hiking, fishing and horse riding) were present when sampling but do not attribute a reason for the pattern. Similar to the other studies cited above, it appears that the three land-use categories compared by Roche *et al*. (2013) may have had other systematic differences than simply differing by the identified land use.

While pack stock and livestock can potentially be positively associated with indicators of eutrophication, the ultimate question is whether eutrophication is significantly affected. Roche *et al*. (2013) provide key information by comparing the aquatic nutrient concentrations that they detected with regulatory and background benchmarks of water quality. They found that mean and median concentrations of N and P in water were one order of magnitude or more lower than levels recommended to avoid eutrophication and were at or below estimated background levels (Roche *et al*. 2013). For example, they reported that total N concentrations for all their land-use categories (Roche *et al*. 2013; Table 4) were at the low end or below the estimates of the USA Environmental Protection Agency for background concentrations in their study region (60–530 $\mu g\ L^{-1}$). When evaluating effects of use of pack stock on water nutrient levels it may be useful to consider absolute concentrations relative to benchmarks of ecological significance in addition to noting a statistically significant effect. Also, factors, as well as recreation, can influence nutrient dynamics at a site; for example, the area of forested cover and lake area in the watershed can affect N levels and chemical species composition (see Brown *et al*. 2008).

Microbial pathogens

Pack stock may influence aquatic levels of microbial pathogens directly through manure and urine deposition into water bodies or indirectly by deposition along trails, in campsites, at grazing

areas, and adjacent to streams and lakes. Subsequent introduction to water bodies then occurs via overland flow following summer thunderstorms and snow melt (Derlet and Carlson 2004) (Tables 1 and 2). Among the best documented pathogens in both cattle and pack stock are *Giardia* and *Cryptosporidium*, each of which is pathogenic to humans (Atwill *et al*. 2000). Derlet and Carlson (2002) postulated that these pathogenic organisms can remain present and potentially be infectious for extended periods of time, such as *Giardia*, which can survive for many years in cold water.

The prevalence of human pathogens in pack stock appears to be relatively low, although not negligible. Among 91 horses used for wildland recreation in a study from California, none were positive for either *Giardia* or *Cryptosporidium* (Johnson *et al*. 1997). Only 0.7% of horses using public trails in Colorado had detectable concentrations of *Giardia* and 0.3% had detectable concentrations of *Cryptosporidium* (Forde *et al*. 1998). Fecal specimens taken from 305 pack stock (i.e. horses and mules) in the Sierra Nevada revealed that 4.6% of them were shedding *Giardia* and the prevalence at a herd level ranged between 0% and 22% (Atwill *et al*. 2000). The total number of corralled pack stock, their density and corral size influenced the prevalence of *Giardia* and *Cryptosporidium* (Atwill *et al*. 2000). In a study to evaluate various human pathogens in manure, Derlet and Carlson (2002) found that ~10% of the samples collected in manure from pack stock from popular high Sierra Nevada trails contained enteric bacteria that may have pathogenic potential for humans. It should also be noted that bacteria pathogenic to humans do not only occur in domesticated stock, as they have also been found in scat from deer and other wild animals (see Derlet and Carlson 2002).

A study conducted by Derlet *et al*. (2012) in the Sierra Nevada, described in the section above on nutrient dynamics, also compared the presence of coliform bacteria, and *E. coli* in particular, in aquatic areas grazed by cattle, recreational areas frequented by humans and pack stock, and wildlife areas with minimal impacts by humans or domesticated animals. The authors found suspended aquatic coliform bacteria (*E. coli*) at 100% (91%) of the cattle sites, 24% (8%) of recreational sites, and 0% (0%) of wildlife sites. Coliform bacteria (and *E. coli*) were associated with algal mats at 100% (100%) of the cattle sites, 53% (24%) of the recreational sites, and 12% (0%) of the wildlife sites. Similar results using the same basic design of studies were reported by Derlet and Carlson (2004, 2006), Derlet *et al*. (2004, 2008), Derlet (2008), Ursem *et al*. (2009), and Hayden *et al*. (2010). These results suggest that areas used by both backpackers and pack stock can be associated with an increased prevalence of coliform bacteria, and *E. coli* in particular, in aquatic habitats of the Sierra Nevada. However, as discussed above in the section on nutrient dynamics, it is unclear if the differences among the three contrasting land-use categories may have been influenced by other systematic factors, such as elevation, and it is impossible to separate specific effects of backpackers from pack stock (see Table 1 for the types of data available).

Roche *et al*. (2013) found that concentrations of fecal coliforms were significantly lower in recreational areas (55 ± 9 cfu 100 mL^{-1}) than either key grazing (87 ± 12 cfu 100 mL^{-1}) or no concentrated use areas (90 ± 12 cfu 100 mL^{-1}), and found similar patterns for *E. coli* (29 ± 7 versus 42 ± 6 or 43 ± 8 cfu 100 mL^{-1}). They also found that both measures of fecal indicator bacteria were significantly higher when cattle were present, but lower when recreational activities were present at the time of sampling (Roche *et al*. 2013). As with their results for concentrations of N and P, it is unknown why recreational areas had lower levels of fecal indicator bacteria than the other two land uses.

Clow *et al*. (2013) conducted a similar type of study comparing mixed (pack stock and backpacker), backpacker, and minimal use sites at Sequoia and Kings Canyon National Parks and concluded that mixed-use sites had significantly higher levels of *E. coli* (2.8 cfu 100 mL^{-1}) and total coliform (214 cfu 100 mL^{-1}) than either of the other two types of sites. Other factors, however, may be responsible for the differences in coliform levels. They support this caveat with corroborating data (Clow *et al*. 2013; Table 1) showing that, compared with the other two types of sites, especially minimal use sites, mixed-use sites are at much lower elevations, draw from much larger watershed basins, have higher adjacent forest cover, and have water with higher levels of alkalinity, specific conductance, and concentrations of calcium, magnesium, sodium, potassium, silicon, chloride, and sulfate. These differences are consistent with the conclusion that mixed-use sites were associated with lower-elevation meadows adjacent to forests where longer water residency time and greater interactions between water, soil, and vegetation were potentially the primary reasons why *E. coli* and total coliform concentrations were highest in those areas. They also reported the results of a stepwise General Linear Model, which indicated that two characteristic variables (i.e. length of longest flow path and basin relief) of basins explained 33% of the variance in *E. coli* concentrations and, when the three visitor-use categories were added to the analysis, explanatory power increased by 11% (to 44%). Clow *et al*. (2013) reported high levels of *E. coli* and coliform bacteria below compared with above the mixed-use sites but that could have been due to factors other than pack stock use, such as humans, wildlife, or hydrologic characteristics within the mixed sites. Thus, because higher levels of *E. coli* and total coliform bacteria at mixed-use sites are dictated mostly by factors other than visitor use, it is almost impossible to evaluate the much smaller potential effects of mixed use, much less the individual effects of pack stock use at these sites.

Similar to the effects on nutrient dynamics, the effects of pack stock on levels of fecal coliform and *E. coli* appear to be less than those of livestock. However, absolute levels reported by Roche *et al*. (2013) were still lower on average for each of their three land-use areas than the national USA Environmental Protection Agency standards of 190 and 235 cfu 100 mL^{-1}, respectively. That study found 16% of cattle sites and 15% of recreational sites contained water samples that exceeded the lower national standard of 190 cfu 100 mL^{-1} (Roche *et al*. 2013). However, more stringent regional regulatory standards were exceeded at the majority of their sites.

Sedimentation

Effects of pack stock on sedimentation have not been specifically studied. There has been work to suggest cattle grazing increases sediment loads in water bodies by reducing the ability of stream-side vegetation to filter sediment, debris, and other nutrients during runoff events (Winegar 1977; Kauffman and Krueger

1984; Platts 1991). Vegetative cover, plant height and density, aboveground biomass, surface roughness, sediment texture, bare ground, distance down slope, and species composition also influence sediment detachment, movement and filtration (Pearce *et al*. 1998). All of these variables are potentially affected by use by pack stock, although links to pack stock have not yet been evaluated.

Temperature

Effects of pack stock on water temperature also have not been specifically studied although reduced vegetation, and hence increased solar insolation, that could result from use by pack stock may lead to increased water temperature (Table 2). Both average water temperature and temperature fluctuations can change with altered vegetative structure, thereby altering the aquatic ecosystem (Meehan *et al*. 1977). Although this has only been documented for cattle (Maloney *et al*. 1999), the mechanism of change is also possible for pack stock.

Loss of shade, and subsequent changes in water temperature, has been directly linked to small-scale disturbances such as cattle grazing (Beschta 1991; Anderson *et al*. 1993). However, small-scale watershed attributes, such as air mass characteristics, elevation gradient, adiabatic lapse rate, stream channel width and depth, water velocity, surrounding landscape, and river/groundwater exchange may be of equal or greater importance on stream temperature (Larson and Larson 1996; Loheide and Lundquist 2009). The magnitude of some of these factors (e.g. river/groundwater exchange) may be decreased in channels degraded by pack stock (loss of riparian vegetation, incision or widening) with concomitant reductions in water quality (Loheide and Lundquist 2009).

Effects on soil

Two studies have reported the effects of pack stock on soils, and both evaluated effects on soil compaction (Weaver and Dale 1978; Cole 1983) (Table 1). Effects of pack stock on soils are likely to be similar to the effects of cattle, but the degree of impact may be lower due to the shorter duration and lower intensity of disturbance from pack stock compared with cattle.

Potential effects on soils other than compaction include changes in nutrient cycling but these changes are likely to be small. Pack stock may influence nutrient cycling over the long-term by reducing levels of soil nutrients by incorporating nutrients into animal biomass and removing them from the system. However, the limited literature suggests that off-site transfers may not measurably affect soil N and P levels (Berg *et al*. 1997). Pack stock also redistribute nutrients within a site by transferring them from grazing to resting areas where they are deposited as feces and urine. In areas with a long-term history of livestock husbandry, such transfers may lead to significant nutrient enrichment of nearby areas. Although there is no quantitative evidence on the magnitude of such a process in the Sierra Nevada, visual evidence suggests that meadows are the principal focus of herbivory and adjacent forested areas, which serve as shade, are often a major repository of feces for both pack stock (R. Blank, pers. obs.) and cattle (Huber *et al*. 1995) (Table 3).

Compaction

There is often a period following snowmelt when meadow and riparian soils of the Sierra Nevada are saturated and chemical-reducing (redox) conditions can change soil chemistry and affect vegetation. The duration and magnitude of reducing conditions are predicated on many factors, including snowpack variables, soil texture, landscape slope, and internal hydrology. Trampling by both pack stock and cattle can compact the soil and potentially increase the severity and length of time of such soil conditions.

The direct effects of trampling include localised fragmentation of sod, trailing, roll pits, stream bank and lake shore erosion, increased amounts of unvegetated soil and, over longer time scales, soil compaction and shearing (Liddle 1975*a*, 1975*b*, 1991) (Table 3). Soil compaction promotes increased bulk density, which effectively reduces intra-soil particle pore space, lowers water infiltration rates, and increases runoff (Ratliff 1985; McClaran and Cole 1993).

In the Sierra Nevada, stock camps are not permitted in meadows but are often located nearby and/or adjacent to meadows in forested or similar upland habitat. The direct effect of increased compaction through greater trampling at stock camps has the potential to translate to increased erosion, increased runoff and associated hydrological effects at the meadow/forest interface.

Most of the literature on the impacts on soil compaction and hydrologic processes in meadows focuses on livestock, specifically trampling effects by cattle (e.g. Kauffman and Krueger 1984; Trimble and Mendel 1995; Belsky *et al*. 1999). Effects of trampling by herds of cattle are likely to be more severe than that of pack trains, although the mechanism of impact is the same. However, the greater potential intensity and duration of cattle trampling may cross thresholds of impact that lead to hydrologic changes in meadows more frequently than the less intense and continuous levels of use typically exhibited by pack stock.

Table 3. Potential effects of pack stock on soils summarised from the literature presented in the text

Categories	Potential effects
Nutrient cycling	Pack stock use can potentially reduce soil nutrient levels, redistribute nutrients within a site (e.g. a meadow), promote compensatory plant growth, which can secondarily affect soil nutrient levels, and increase nutrient turnover rates through the facilitative process of digestion
Compaction	Most research has focussed on livestock effects on hydrology through the direct effects of trampling, including localised fragmentation of sod, trailing, roll pits, stream bank and lakeshore erosion, increased amounts of unvegetated soil, and, over longer time scales, soil compaction and shearing. The degree of impact is primarily tied to the intensity and duration of disturbance, and although pack stock have the potential for similar effects the intensity and duration of their disturbances are much lower than that of cattle

Effects on plants

Meadow vegetation can change due to the direct effects of vegetation removal and trampling or the indirect effects on meadow hydrology and soils. Studies that specifically evaluate effects of pack stock on plants are more numerous than those focussed on effects on water, soils and wildlife combined. These studies provide information on how pack stock affect individual plants, populations and communities of plants (Weaver and Dale 1978; Olson-Rutz *et al*. 1996*a*, 1996*b*; Cole *et al*. 2004; Holmquist *et al*. 2013*a*) and invasive plants species (Campbell and Gibson 2001; Gerlach *et al*. 2003; Couvreur *et al*. 2004; Wells and Lauenroth 2007; Gower 2008; Quinn *et al*. 2008) (Table 1). Effects of pack stock on vegetation are likely to be similar to effects of cattle, but the degree of impact may be lower due to the smaller intensity and duration of pack stock compared with cattle disturbance. Some differences may be due to different foraging behaviour, including forage selection, between pack stock and cattle. Potential effects of pack stock on vegetation can be summarised based on (1) the responses of individual plants, and populations and communities of plants to vegetation removal and trampling, (2) non-native invasive species (i.e. colonisation and spread) and (3) encroachment by woody species (Table 4).

Plant individuals, populations and communities

Most published material on the effects of pack stock and cattle describes responses to vegetation removal and trampling. These two effects are discussed separately below in terms of their effects on plant individuals, populations, and communities, including plant productivity, cover, density, reproductive output, species composition and diversity, and other related responses such as cover of litter and bare ground.

Vegetation removal

The duration, intensity, frequency, and timing of vegetation removal are all components of the disturbance regime that affect individual plants, population dynamics, and composition of plant communities (Belsky 1986; Mazzu 1987; Stohlgren *et al*. 1989; Turner *et al*. 1993; Fahnestock and Detling 2000; Pierce *et al*. 2007). These effects can vary spatially and temporally (Belsky 1986), especially across environmental gradients (Bakker *et al*. 2006). In some cases, vegetation removal can reduce productivity (Stohlgren 1986), plant size (Miller and Donart 1981), leaf and culm length, tiller production (Fahnestock and Detling 2000), and reproductive output (Edwards 1985).

A single period of heavy pack stock grazing (18 h per picket circle) or moderate (8 h) repeated grazing throughout the summer can reduce plant and litter cover, increase bare soil, and reduce stem counts of grasses (Olson-Rutz *et al*. 1996*b*). Holmquist *et al*. (2010, 2013*a*, 2013*b*) reported lower litter cover and depth, and greater bare ground, in sites grazed by pack stock. Vegetation removal by pack stock has been shown to affect patterns and interactions among plant communities including diversity and competitive outcomes in an Argentinean montane grassland (Carilla and Grau 2010). Changes in plant communities of meadows following grazing by pack stock may be minimal after unsustained, infrequent, or relatively light seasonal use (Cole *et al*. 2004). Low grazing intensities actually led to increased plant cover due to compensatory growth in three common meadow types; shorthair sedge (*Carex filifolia*), shorthair reedgrass (*Calamagrostis breweri*) and tufted hairgrass (*Deschampsia cespitosa*) in Yosemite National Park, USA (Cole *et al*. 2004). In a study of five paired meadows in Sequoia and Kings Canyon National Parks, Hopkinson *et al*. (2013) found very little evidence for grazing-related compositional differences over a 25-year period. In contrast, sustained, frequent, or relatively high intensity grazing can produce substantive decreases in plant productivity, although there might be initial increases in productivity before declines (Stohlgren *et al*. 1989). Generally, experimental evidence with pack stock and artificial clipping treatments suggests that plant productivity declines with increased grazing pressure (Pond 1961; McLean *et al*. 1963; Stohlgren *et al*. 1989; Fahnestock and Detling 2000; Cole *et al*. 2004). Moreover, grazing utilisation (i.e. intensity) and number

Table 4. Potential effects of pack stock on plants summarised from the literature presented in the text

Categories	Potential effects
Plant individuals, populations, and communities	Due to vegetation removal. Increased removal can lead to decreased plant cover and increased bare ground, although effects may be minimal after unsustained, infrequent, or relatively light seasonal use. Early season grazing may have more lasting effects on productivity during subsequent years; however, it may also lead to compensatory growth among some species. Grazing may decrease plant diversity on poor or arid soils but increase it on rich soils. Pack stock removal of plant species may be selective when productivity is high, but more generalised when productivity is low due to vegetation trampling. Trampling can decrease vegetation cover, increase soil compaction, and have variable effects on bulk density. Resilience to trampling declines with elevation, slope, soil wetness, and prevalence of shrubs, and increases with growing season length, graminoid dominance, and prevalence of plants with protected buds
Non-native invasive species	Incidence of non-native invasive plants is relatively low in meadows, but the combination of high resource availability and the potential of propagule dispersal from human activities render them potentially invasible, likely most true for relatively lower sites in elevation and those near corrals. Propagules can be transported within the gut of pack stock or via supplemental feed, or through adhesion to animals and equipment. Localised pack stock disturbances and deposited feces create conditions that favour establishment of invasive plants
Woody species encroachment	Moderate levels of livestock grazing may facilitate meadow encroachment by woody plants but it is unclear if pack stock have similar effects. Vegetation removal and soil disturbance due to grazing can reduce competition at the microsite scale for sagebrush seedlings

of years grazed have been shown to interact, suggesting that inter-annual variation in vegetation removal may be important in determining plant responses (Cole *et al*. 2004).

The effects of vegetation removal on productivity differ between mesic and xeric meadows. Long-term herbage removal reduced productivity more in mesic, tufted hairgrass/beaked sedge (*Deschampsia cespitosa*-*Carex rostrata*) sub-alpine meadow communities than in a relatively xeric shorthair sedge (*Carex exserta*) type (Stohlgren *et al*. 1989). In contrast, Cole *et al*. (2004) reported that the effect of grazing intensity by pack stock on plant productivity was greatest for the relatively xeric shorthair sedge meadow type (highest elevation and lowest productivity of meadow types considered) when compared with the more mesic shorthair reed grass and tufted hairgrass types. Decreases in vegetative cover led to an increase in bare ground as the duration of pack stock grazing increased in a mesic montane Idaho fescue-slender wheatgrass meadow (Olson-Rutz *et al*. 1996*a*). Results of various grazing and herbage removal treatments in meadow ecosystems are variable but generally indicate reduced productivity and increased bare ground with increasing grazing or herbage removal (Table 4).

Mechanisms by which grazers affect plant diversity include the modification of competitive relationships among plants through removal of competitively dominant species. When the nutritive value of forage, and its availability, are high, horses are highly selective grazers (Mayes and Duncan 1986) and show marked preferences for grasses (Reiner and Urness 1982; Gudmundsson and Dyrmundsson 1994; Olson-Rutz *et al*. 1996*a*; Cole *et al*. 2004). Selective grazing may promote associational effects among plants growing in mixed-species stands. Removal or reduction of preferred forage species can facilitate an increase in other less preferred or less grazing-tolerant species. Results from an Icelandic mire (similar to wet meadow or fen) indicate that species richness was minimally affected by differences in grazing intensity at low and moderate levels by horses, but differed markedly under high intensity horse grazing (Magnússon and Magnússon 1990, 1994). Intense horse grazing was associated with substantial increases in bare ground, preferential removal of highly preferred species, and increased species richness (potentially indicating competitive release).

Vegetation trampling

Many factors can influence the degree of trampling in meadows, including animal liveweight, hoof size, pack animal behaviour, pack animal management, plant community composition, substrate conditions, and other aspects of the physical setting (Weaver and Dale 1978; Vallentine 1990; Thurow 1991; McClaran and Cole 1993). Even if vegetation removal is minimal, pack stock can still cause disturbance by physical trampling of meadow vegetation and soil by passing through, accessing water, or engaging in other behaviours such as rolling. Various studies, evaluating effects of trampling by horses or humans on herbaceous vegetation types, have shown decreased plant cover and diversity, increased bare ground and soil compaction, and variable effects on soil bulk density (Table 4).

Resistance to penetration by plant roots can increase with an increased number of passes by pack stock (Cole 1987). Site characteristics that influence the severity of trampling effects in meadows include elevation, slope, and hydrology (Ratliff 1985). Steeper slopes result in increased soil disturbance and vegetation damage from trampling because force is exerted at an angle to the substrate surface. Moist or wet site conditions can lead to greater levels of soil shearing and severing of roots (Vallentine 1990). Although horses may prefer to graze on dry compared with wet sites (Magnússon and Magnússon 1990, 1994), trampling of wet sites may be inevitable if the spatial patterns of vegetation and water funnel passage of stock through wet soil areas for access to water or preferred forage.

Life form and plant stature influence plant resistance to trampling and may have a greater influence on trampling effects than physical site characteristics (Cole 1995*b*). Soil compaction can have a greater negative effect on the root penetration of plants with fibrous roots, and this can indirectly facilitate dominance of compaction-tolerant tap rooted and shallow-rooted species (Liddle 1975*b*, 1991). An evaluation of 18 montane meadow and non-meadow community types found that resistance to trampling effects was positively related to cover of shrubs and graminoids and negatively related to cover of forbs (Cole 1995*b*). Erect herbs are less resistant than tufted and matted graminoids (Cole 1995*b*). Small plants survive better in trampled sites, and plants with non-rosette, creeping or prostrate habits do not survive trampling impacts well (Pryor 1985; Liddle 1991). Cryptophytes (plants that hold their developing buds below ground) and plants with folded leaves are better able to persist in trampled environments (Liddle and Greig-Smith 1975; Liddle 1975*a*, 1975*b*, 1991). Species with protected rather than exposed meristems survive trampling better (Bates 1938). Taller dicotyledonous species are reduced by trampling which may allow for increased dominance of small graminoid monocotyledonous species (Pradhan and Tripathi 1983). Sites found to be most resilient after several seasons of trampling were those that had long growing seasons and high proportions of grasses (Cole 1987).

Because there is a decline in the amount of vegetation that can be affected by trampling as intensity increases, one may expect a curvilinear relationship between disturbance and trampling (Cole 1987; Kuss and Hall 1991). However, other more recent studies (Cole 1995*a*, 1995*b*) suggest a linear relationship, particularly in more resistant and tolerant vegetation types (i.e. those dominated by graminoids). Vegetation types may have thresholds of vulnerability and may be resilient while trampling intensity remains low (Cole 1995*a*) but, when trampling intensities exceed these thresholds, change can occur and increase linearly with continued trampling (Cole 1995*a*).

The ability of a vegetation type to tolerate recurrent trampling appears to be associated with its ability to recover from damage more than its ability to resist being damaged. Resilience (i.e. recovery rate) to trampling varies by trampling intensity, vegetation type, species composition, mean temperature, and soil moisture (Cole 1987, 1995*b*). In general, resilience is reduced with increasing elevation, possibly due to decreasing length of the growing season. Recovery patterns can also be complex. For example, in a fescue (*Festuca* spp.)-dominated montane grassland, the maximum recovery after the second and third trampling seasons generally occurred in areas receiving less trampling (40–300 passes per year after the third trampling season), whereas the greatest overwinter recovery did not

necessarily coincide with lowest trampling frequency (Cole 1987). In addition, Cole (1987) found that the return of vegetative cover after a single year was greatest in areas subjected to the highest levels of trampling (>600 passes per year). Resilience to trampling can be positively related to abundance of tufted graminoids and geophytes and negatively related to abundance of shrubs and chamaephytes, particularly those that are matted (Cole 1995*b*).

Non-native invasive species

Pack stock can influence processes that promote introduction and establishment of non-native species into meadow ecosystems. The factors affecting plant invasions include propagule availability and dispersal, disturbance, competitive release and nutrient availability (Davis *et al*. 2000; Brooks 2007).

Non-native plant propagules can be transported from areas of summer and winter use, transfer locations and trailhead corrals via feces and adhesion to animals and equipment (Couvreur *et al*. 2004; Couvreur *et al*. 2005). Non-native plant propagules can also be transported via contaminated feed. Gerlach *et al*. (2003) reported that non-native species were detected within 0.5 km of stock corrals in Yosemite National Park suggesting pack stock as a likely dispersal agent. Some of those species, such as silver European hairgrass, poverty brome, and Kentucky bluegrass (*Aira caryophyllea*, *Bromus sterilis* and *Poa pratensis*, respectively), are found on nearby trails and/or in the corrals and are known to be successfully dispersed in horse dung. Twenty-three non-native species for which horses are known to be endozoochorus dispersers were found during plant surveys along trails in Sequoia and Kings Canyon and Yosemite National Parks (Gerlach *et al*. 2003). Among these, eight species are listed by the California Invasive Plant Council as invasive in wildlands (Cal-IPC 2006). Also among the 23 species, one is invasive in meadows [common velvetgrass (*Holcus lanatus*)], one in pastures [horehound (*Marrubium vulgare*)], and four in mesic sites [sheep sorrel (*Rumex acetosella*), toothed dock (*R. dentatus*), Johnsongrass (*Sorghum halepense*), and common chickweed (*Stellaria media*)]. In eastern USA forest systems, Gower (2008) found no difference in the incidence of non-native species between trails used by horses (2–6% non-native) and those used by hikers (1–7% non-native).

Disturbance, such as that produced by moderate to heavy pack stock or cattle use, has the potential to promote species invasions (Hobbs and Atkins 1988; Burke and Grime 1996; Smith and Knapp 1999) by creating safe sites for germination (Oesterheld and Sala 1990; Jutila and Grace 2002; Cosyns *et al*. 2006) and reducing competition from native species, both associated with increased resource availability (Gross *et al*. 2005). Non-native species may have increased competitive abilities for limiting resources and increased growth in novel habitats (Blossey and Notzold 1995), and they may successfully compete in a novel environment when herbivores preferentially graze more preferred native species (Carpenter and Cappuccino 2005; however, also see Keane and Crawley 2002; Colautti *et al*. 2004; and Levine *et al*. 2004) or when non-native plants are more competitive in response to non-native herbivore grazing (Parker *et al*. 2006). For example, some non-native species may be better adapted than other species to a regime of pack stock or cattle grazing. Kentucky bluegrass, a common non-native species of montane (and to a lesser extent, sub-alpine) meadows in the Sierra Nevada, is more tolerant of continuous, close grazing than any other cool-season grass and is particularly tolerant of close grazing by horses and sheep (Wedin and Huff 1996). Germinable seed production of non-native Kentucky bluegrass can be 10 times greater under grazed than ungrazed conditions (Willms and Quinton 1995).

Non-native grazers can facilitate both the local increase and the spatial spread of non-native plant species through selective grazing and propagule transport (Best and Arcese 2009). In a meta-analysis of 63 published studies across a wide range of biomes, Parker *et al*. (2006) found that the relative abundance of non-native plants was 52% higher in communities grazed by non-native herbivores than in communities grazed by native herbivores. Grazing by non-native herbivores also increased the species richness of non-native plants. However, Stohlgren *et al*. (1999) found no difference in native and non-native plant species composition between native ungulate-grazed and long-ungrazed sites in Rocky Mountain grasslands.

Encroachment by woody species

Many montane and sub-alpine meadows in the Sierra Nevada exhibit various degrees of colonisation by native woody species typically associated with upland habitat, such as sagebrush (*Artemisia* spp.) and conifers [e.g. lodgepole pine (*Pinus contorta*)] (Helms and Ratliff 1987; Vale 1987; Bauer *et al*. 2002; D'Antonio *et al*. 2002; Millar *et al*. 2004). Encroachment by lodgepole pine, in particular, has been a focal management issue at numerous times in the past century (e.g. Sharsmith 1961; Cooper *et al*. 2006), and, at higher elevations, native woody species encroaching into meadows may play a larger role in changing meadow habitats than non-native plant species (D'Antonio *et al*. 2002). It is thought that grazing can lead to increased drying of meadows thereby promoting encroachment of non-meadow species including shrubs and trees; however, detailed information linking effects of pack stock to encroachment by woody species does not exist.

Grazing, primarily by livestock, and trampling in general, have been implicated among possible causes of encroachment by woody species that include natural ecological succession, climate, physical disturbance, fire suppression, biotic interactions and enhanced seed dispersal (Friedman and Orshan 1975; Wood 1975; Vankat and Major 1978; Vale 1987; Odion *et al*. 1988; Wambolt *et al*. 1989; Schoenherr 1995; Knapp and Matthews 1996; Kirchner *et al*. 1998; Dull 1999; Bauer *et al*. 2002; Berlow *et al*. 2002; Millar *et al*. 2004; Norman and Taylor 2005). Observational studies in the Sierra Nevada and other areas suggest that these factors interact in complex, but somewhat predictable, ways (see Vale 1987; Miller and Halpern 1998; Millar *et al*. 2004; Norman and Taylor 2005).

Effects on wildlife

Meadows provide essential habitat for a diverse suite of native wildlife species including several with special status, such as the great grey owl (*Strix nebulosa*), willow flycatcher (*Empidonax trailii*) and the Yosemite toad (*Anaxyrus canorus*). These ecosystems are also used by bighorn sheep (*Ovis canadensis sierrae*), mule deer (*Odocoileus hemionus*) as well as numerous

Table 5. Potential effects of pack stock on wildlife summarised from the literature presented in the text

Categories	Potential effects
Individuals, populations, communities – vertebrates	Special status species, such as the Yosemite toad, willow flycatcher, and great grey owl, may be indirectly affected by pack stock through habitat modification of soils, water, and/or vegetation (cover). Potential direct impacts from pack stock could occur if wildlife species are trampled. Reduction in vegetation cover, and the concomitant increase in bare ground, may be detrimental to small vertebrates by increasing risk of predation, promoting behavioural shifts, or affecting habitat use patterns, and these changes in prey may secondarily affect predators as well. Increased soil compaction from trampling can reduce infiltration rates and alter hydrologic patterns, potentially affecting fossorial, aquatic and semi-aquatic species
Individuals, populations, communities – invertebrates	The several pack stock studies that have been conducted on invertebrates showed no to slight effects of pack stock use in the Sierra Nevada at the meadow scale but reported negative community responses on heavily grazed patches and positive responses on lightly grazed patches within meadows

species of birds, small mammals and invertebrates. Since the duration and intensity of pack stock use are considered the most influential aspects of disturbance from the perspective of water, soil, and vegetation effects (see sections above), they are also potentially the most influential factors affecting wildlife (Table 5).

Several studies, which have evaluated the effects of pack stock on wildlife, have focussed on invertebrate responses (Holmquist *et al*. 2010, 2013*a*, 2013*b*, 2014) and birds (Rothstein *et al*. 1980, 1984) (Table 1). Holmquist *et al*. (2010) found few lasting effects (negative or positive) of long-term pack stock use on arthropods. Holmquist *et al*. (2013*a*, 2013*b*) report a detectable, but minimal, effect of grazing on arthropod communities, which differed among arthropod families and depended on season of grazing and local vegetation assemblage considered. For birds, Rothstein *et al*. (1984) demonstrated that nest–parasitising brown-headed cowbirds used forests for nesting but travelled up to 6.5 km to pack stock corrals to feed. Cowbird expansion into the Sierra Nevada in the 1930s was promoted by human activities, including pack stock corrals, which promoted increased rates of nest parasitism of the warbling vireo (*Vireo gilvus*) potentially threatening the species survival in the affected areas (Rothstein *et al*. 1980).

Pack stock use may lead to soil compaction (see Trampling section above), which may negatively affect small fossorial organisms that use underground burrows (Torre *et al*. 2007). Sustained trampling can reduce infiltration by increasing compaction and potentially reducing the amount of time a site remains wet. Species, dependent on wetness of a site for breeding and other critical activities (e.g. amphibians), could be at risk with heavy pack stock use if it leads to increased site aridity. It is also possible that pack stock may directly interfere with wildlife populations and communities, especially during breeding seasons, so the timing of pack stock use may be influential as well.

Trampling has the potential to directly kill small terrestrial vertebrates, including juvenile frogs and toads and ground-nesting birds that have limited mobility in early developmental stages. Newly metamorphosed amphibians are particularly vulnerable because they often aggregate around the fringe of breeding pools, and cattle-induced mortality has been shown for western toads (Bartelt 1998). Martin (2008) reported that cattle trampled and killed Yosemite toad eggs and new metamorphs. Martin (2008) also witnessed Yosemite toad sub-adult and metamorph deaths during the movement of cattle across a stream channel. Observational data suggest that livestock can negatively affect mountain yellow-legged frogs by altering habitat and trampling of individual frogs (V. Vredenburg, San Francisco State University, pers. comm.).

The presence of pack stock may translate to altered foraging behaviour and use patterns, potentially promoting increased vigilance thereby lowering foraging efficiency. Although effects of pack stock on deer have not been specifically evaluated, small numbers of pack stock present for short periods of time are less likely to disrupt wildlife movements than large numbers of cattle present for long periods of time (McClaran and Cole 1993). For example, native deer have been shown to alter their foraging and habitat use patterns in the presence of cattle (Loft *et al*. 1991), and bighorn sheep in Alberta have been reported to change levels of vigilance, grazing behaviour and distribution in the presence of cattle (Brown *et al*. 2010).

Although detailed investigations have been conducted linking cattle effects to wildlife (Jennings 1996; Knapp and Matthews 1996), the applicability of these studies to pack stock effects is limited (see Introduction above). One can derive some inference of potential effects of pack stock from an understanding of the habitat requirements of wildlife and the effects of pack stock on those variables as described in the previous sections of this review. For example, pack-stock use can promote shifts in species composition, cover and height of vegetation, which could translate to changes in cover for wildlife. Cover in particular has long been noted as an important habitat characteristic for small vertebrates (Elton 1939; Grant *et al*. 1982). Cover may also be especially important for small less agile amphibians that are prone to predation. Changes or reductions in vegetative cover due to grazing may benefit some species but negatively affect small vertebrates by increasing risk of predation, promoting behavioural shifts, and affecting habitat use patterns (Kotler *et al*. 1991). Powers *et al*. (2011) found that cattle-grazed meadows supported greater pocket gopher (*Thomomys monticola* and *T. bottae*) densities than ungrazed meadows. Reductions or changes in the species composition of small vertebrates may indirectly affect predators (e.g. great grey owl) that depend on these organisms as prey. Knapp and Matthews (1996) found that the density and biomass of California golden trout (*Oncorhynchus mykiss aguabonita*) were greater in ungrazed

than in cattle-grazed sites in 75% of comparisons, suggesting that cattle grazing may have compromised stream and riparian system integrity. Pack stock are unlikely to exert effects of a similar magnitude because levels of localised use are most often lower and shorter in duration than those of livestock.

Patterns of Yosemite toad breeding occupancy in the Sierra Nevada were not found to be associated with cattle (Allen-Diaz *et al*. 2010; Roche *et al*. 2012*b*) or pack stock use (USGS, unpubl. data). Cattle were shown to prefer drier meadows, whereas toads preferred wetter meadows, which may have resulted in habitat partitioning that is the reason for the lack of correlation between the two (Allen-Diaz *et al*. 2010). However, cattle have also been shown to prefer riparian habitat over upland habitat in the Sierra Nevada (Kie and Boroski 1996), so cattle may not always avoid meadows where Yosemite toads are present. Although it is often stated by pack stock operators that pack stock avoid standing water and moist soils, which may indicate avoidance of toad habitat, this behaviour has not been systematically evaluated. It should be noted, however, that pack stock has been observed in flooded and saturated portions of Lyell meadow in Yosemite National Park (L. Jones, National Park Service, pers. comm.). A study evaluating the effects of cattle exclosures on Yosemite toads resulted in no detectable effects (Allen-Diaz *et al*. 2010; Roche *et al*. 2012*a*), but it is unclear to what extent legacy effects from past livestock grazing may have influenced the results. If exclosure studies had been also done with pack stock, they would have suffered from similar limitations.

Management implications

The information provided in this review can be used to inform the development of pack stock management plans and management objectives. Considering the information available, the most prudent ecological management objectives could include the following: (1) minimise bare ground; (2) maximise plant cover and maintain species composition of native plants; (3) minimise trampling, especially on wet soils and stream banks; and (4) minimise direct urination and defecation by pack stock animals into water. Protecting meadow vegetative cover and species composition will help ensure resistance and resilience of the meadows in the face of disturbance. Moreover these ecosystem characteristics can be effectively monitored and managed. Effectiveness monitoring can be designed and meadow response(s) tracked along with patterns of pack stock use to provide the foundation of monitoring plans. Ultimately, this will provide the ability to evaluate progress towards meeting pack-stock management objectives.

This review presents the most detailed information available, but clearly more research is warranted on the effects of pack stock use, especially studies focussed on soils and wildlife. Improved documentation of patterns of pack stock use and disturbance regimes (e.g. intensity, duration and frequency) would help inform such research. Not knowing where past impacts have occurred, especially where environmental thresholds may have already been crossed, confounds analyses of cumulative legacy effects and significantly complicates the process of designing new experiments to evaluate contemporary effects. In addition, many past studies have compared the net effect of human recreation, specifically pack stock and backpacker use, with areas lacking those activities, precluding the ability to discern effects of pack stock. Most of studies have been observational (Table 1), which has limited the quantification of the effects of pack stock associated with measured environmental responses, a limitation not shared by manipulative experimental studies. It is also largely unknown how effects of pack stock compare to or may interact with other stressors such as hiker activities, wildlife diseases, pesticide drift from adjacent agricultural areas, or changes in climatic conditions. Potential variation in these effects and interactions across the wide range of meadow types further complicates these analyses. Future studies should focus on linking measurable monitoring variables (e.g. basal plant cover) with environmental relevancy (e.g. soil erosion processes) and identifying specific environmental thresholds of degradation in Sierra Nevada meadows.

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