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Feral horse activity reduces environmental quality in ecosystems globally

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ABSTRACT

Feral horses occur on several continents, across a wide range of terrestrial biomes, and have had marked impacts on ecosystems worldwide. Despite their oft-reported negative impacts on plants and soils, a global synthesis of their effects has not been attempted. Here we present a meta-analysis of the global impacts of feral horses on ecosystem structure, function and composition using data from 78 studies across five continents. Two-thirds of these studies were from North America (47%) and Oceania (21%), and most studies examined feral horse effects on plants (58%) or soils (35%). Feral horse activity reduced environmental quality by 13% overall, and the magnitude of this decline increased with increases in the intensity of horse activity. Feral horse activity strongly reduced measures of ecosystem function by 19% on average, and had variable effects on composition, with measures of composition most strongly increased (by 21%) at arid sites. There were no overall effects of feral horse activity on ecosystem structure, with insufficient data to assess effects on plant height and cover. We found that feral horse activity had negative effects on soil, increasing erosion (by 31% on average) and reducing plant biomass and litter cover (by 25% and 31% on average respectively). Increases in soil physical properties generally intensified with increasing aridity. Given the generally negative effects of feral horses on ecosystems worldwide, resource managers and governments need to balance the needs of maintaining healthy functional ecosystems and their biota with social- and cultural-driven commitments to maintaining free-ranging herds of feral horses.

1. Introduction

Biological invasions have had profound effects on ecosystem properties and processes worldwide (Hooper et al., 2005). Introduced herbivores can have significant negative effects on ecosystems, both directly, by altering plant community structure and composition, such as the destruction of kelp forests by sea urchins (Johnson et al., 2005), or indirectly, by changing soil and microbial processes that feed back to alter ecosystem functions and biotic communities (Callaway et al., 2004). This can reduce environmental quality, which we define as the status of ecosystem characteristics in natural or human constructed systems that are important for sustaining all living organisms. For example, soil carbon and nitrogen pools have been severely reduced by introduced feral deer in New Zealand's native forests (Wardle et al., 2001). Managing introduced populations to minimise ecological damage can also be difficult because public perception is often organism- and culture-dependent (Coates, 2007). A classic example of an introduced herbivore is the feral horse (*Equus caballus*), which has presented considerable ecological and social problems for land managers on several continents (Nimmo and Miller, 2007; Davies and Boyd, 2019). While the scientific opinion is generally unified on the damaging role that feral horses have on a range of ecosystems (Robertson et al., 2015; Davies and Boyd, 2019; Driscoll et al., 2019), there have been few attempts to assemble a global synthesis of their net impacts on ecosystem processes worldwide. Here we attempt such a synthesis.

Feral horses are extremely adaptable and now occupy a wide range of terrestrial biomes including drylands (Symanski, 1994), wetlands (Turner, 1987), and riparian (Nimmo and Miller, 2007) and alpine (Dyring, 1990) environments. There is an extensive body of literature documenting their impacts on plant community structure and composition (Prober and Thiele, 2007), soil biology, stability and nutrient networks (Dyring, 1990; Davies and Boyd, 2019), and alterations to landscape hydrology via structural changes to the soil and vegetation (Worboys and Pulsford, 2013; Worboys et al., 2018). Feral horses threaten native wildlife directly by competing for resources, or indirectly, by reducing resource quality and thus altering the availability of food, water and habitat (e.g. polluting streams, reducing grass cover, trampling nests; Hall et al., 2016; Eldridge et al., 2019; Davies and

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Boyd, 2019). Evidence suggests that horses disproportionately use some landscape positions such as streambeds and open areas more intensively than others, thereby heavily concentrating their impacts in riparian areas and grasslands or meadows (Crane et al., 1997; Hampson et al., 2010). Horse-induced changes to vegetation structure in a range of systems, including streambank stability in riparian areas, have been shown to facilitate the invasion of exotic plants and impact multiple species including aquatic fauna (Levin et al., 2002), invertebrates (Ostermann-Kelm et al., 2009), small mammals (Beever and Brussard, 2004) and birds (Zalba and Conzzani 2004). Given their widespread impacts on a range of systems, it is important to synthesize the breadth and depth of feral horse impacts globally.

Studies of feral horses impacts to date have been restricted to specific regions or systems such as the semi-arid rangelands of the western United States (Baur et al., 2017) or the Australian Alps (Robertson et al., 2015), areas where their impacts have garnered substantial political and community attention (Garrott, 2018). As with any large exotic herbivore (Hobbs, 1996), there are likely to be a range of direct and indirect effects of horses on ecosystem structure, function and composition. For example, trampling by horses has been shown to cause irreversible damage to soils and streambanks in alpine riparian systems in Australia (Driscoll et al., 2019). In sagebrush (*Artemisia* spp.) steppe systems in Nevada (USA), there were no differences in perennial grass, biocrust or litter cover between horse grazed and ungrazed exclosures five years after horses were removed (Davies et al., 2014). These conflicting effects of horse activity make it extremely difficult to reach a general consensus of the extent to which they contribute to the degradation of terrestrial systems. It is likely that their impacts vary with changes in abiotic variables such as soil type and climate (Hobbs, 1996). Riparian areas appear to be particularly susceptible to horse impacts year-round (Ostermann-Kelm et al., 2008), but in drylands (rangelands), the magnitude of their effects is likely to be strongly dependent on animal densities (grazing intensity), plant community and annual rainfall (Milchunas et al., 1988). Furthermore, at the global scale, there are large gaps in our understanding of their impacts, with many studies from North America (Beever and Brussard, 2000; Scasta et al., 2016; Davis and Boyd 2019), but relatively few published studies from other continents (though see Turner, 1988; Linklater et al., 2004; Zalba and Cozzani, 2004; Mallon and Zhigang, 2009; Hampson et al., 2010; Odadi et al., 2011).

In this study, we combined a structured, qualitative search of global literature with a quantitative meta-analysis to explore the net effects of feral horses on ecosystems worldwide. We retrieved 4261 observations from 78 publications that reported quantitative data on the effects of feral horses on 64 ecosystem response variables such as plant community composition and cover; soil chemistry and soil stability, that together give us a measure of environmental quality. Studies of feral horse impacts are unevenly distributed across continents affected by feral horses, with a strong emphasis on a few ecosystems. We expected that sites subjected to a higher intensity of horse activity would show the greatest changes in ecosystem structural, functional and compositional variables. Similarly, we expected that, as horse impacts vary widely among widely different ecosystems, any impacts would likely be mediated by changes in soils (clay content) and climate (aridity). Erosion, for example, might be expected to be more severe on finer-textured soils (Robertson et al., 2015). Similarly, changes in plant composition would likely be more pronounced in drier (more arid) systems where plant cover is sparse and their recovery is more protracted (Noy-Meir, 1982). Understanding the general trends in horse impacts improves our understanding of how horses might affect ecosystems and therefore how they can be managed more effectively, helping land managers, administrators, governments and policy advisers to make appropriate decisions to mitigate their impacts.

2. Methods

2.1. Database construction

To compile a comprehensive list of publications on ecosystem impact of feral horse across the globe, we searched multiple databases (e.g., Web of Science, Scopus, Proquest Science & Technology, Infromit Online, Environment Complete, Biosis and Geobase/georef) for studies of ecosystem impacts by feral horse populations. We used the following search string to search for relevant papers by searching for key terms that fell within five words (NEAR/5) of the word horse: Topic = (horse NEAR/5 ecosystem OR horse NEAR/5 environment OR horse NEAR/5 ecolog* OR horse NEAR/5 soil* OR horse NEAR/5 plant* OR horse NEAR/5 vegetation OR horse NEAR/5 hydrolog* OR horse NEAR/5 crust OR feral NEAR/5 horse). We supplemented this dataset by including unpublished government reports (e.g. National Research Council, 1980) and student theses. This resulted in 1182 unique studies, which were then screened using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) procedure (Liberati et al., 2009) in the revtools package (Westgate, 2018) within R (R Core Team, 2018) (Appendix A). Revtools allows bibliographies to be systematically and efficiently screened based on the frequency of keywords within abstracts, titles and keywords (Westgate, 2018). Studies that were included were based on the following criteria: 1) a focus on wild, free-roaming, introduced horses occurring within the environment unrestrained or uncontained; 2) quantitative data were reported; 3) data were relevant to ecosystem responses to feral horse activity, including grazing (i.e., herbivory, consumption of plant material) and disturbance (i.e., non-trophic, engineering effects associated with changes in the physical environment of the soil or plant structure, such as defecation pollution, trampling disturbance); 4) reported values represented feral horse impacts only (i.e. not combined with additional herbivore impacts); and 5) comparison data were provided for different levels of feral horse activity (i.e., no activity, low activity, moderate activity and high activity). By activity, we refer to any effects of horses that influence environmental quality including soil disturbance, pugging, vegetation destruction, and herbivory. Based on these criteria, studies were refined to 78 publications (Appendix B).

2.2. Data collection

From each study, we recorded the location, the intensity of horse activity (i.e., no activity, low, moderate or high activity as described in relative terms by the data source), sample size, the mean and the standard deviation for each ecosystem-related attribute, for all available measures of feral horse activity treatments. We also extracted data on environmental variables that were indicative of increases or declines in environmental quality in order to explore potential ecological impacts of feral horses under different environmental contexts. The Aridity Index (AI = precipitation/potential evapotranspiration) was derived from the Consortium for Spatial Information (CGIAR-CSI) means of the 1950–2000 period (Zomer et al., 2008) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database) and soil properties were obtained from the Harmonized World Soil Database (1 km resolution) (http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). In this study, we defined aridity as 1 minus Aridity Index so that increases in aridity corresponded to greater dryness. Numeric data from figures were extracted using the software Engauge Digitizer V 4.1. Our final database consisted of 64 ecological response attributes, which were categorised into 12 broad categories (animal richness, animal abundance, bacterial abundance, plant biomass, litter cover, plant abundance, plant cover, plant richness, soil physical, soil chemistry, soil organics, soil erosion; Appendix C).

2.3. Estimating mean effect size and constructing the variance matrix

We calculated a log response ratio as the effect size to determine the effect of feral horse on ecological attributes: LnRR = $\ln(\overline{x}_t / \overline{x}_c)$ (Hedges et al., 1999) where $\overline{x}_t$ is the mean value of the ecological variable in the horse activity plot (i.e. treatment), and $\overline{x}_c$ is the mean value of the ecological variables in either the plot with no horse activity or the plot with the lower intensity of horse activity (i.e. control). Thus, positive values indicate an increase in the measure of environmental quality with greater feral horse activity and vice versa. The LnRR is used as the response in calculating the overall effect size of the ecosystem responses and the interaction with moderators in the meta-regression models. Our final dataset contained 4261 contrasts between intensity levels of horse activity (i.e. several treatments and controls). Where increases in an ecological response indicated a reduction in ecosystem function (e.g. increases in soil erosion, greater surface runoff, etc.), the LnRR values were multiplied by −1 (i.e. 'coined', Eldridge et al., 2016b) to allow consistency among positive values and to place all values in a common direction. We realise that this approach might have potential shortcomings given our assumption that increases in a given attribute (e.g. shrub cover, soil carbon) indicate an increase in functionality and therefore greater environmental quality. However, in the absence of the additional information on how an increase in a particular attribute affects function, we assume increases lead to greater ecosystem function.

We used random effects models to estimate mean effect sizes for feral horse impacts. All of our models had an intercept of zero and included random factors to structure a variance matrix to account for three potential sources of non-independence: i) data collected from the same study, ii) residuals of each observation from calculations of the variance and the potential bias from sample size, and, iii) shared controls among observations from a single study that reported multiple levels of feral horse activity but only a single control (e.g., lower activity level or no activity plot). To control for any potential lack of independence within and among studies we included a unique ID for each reference as a random factor. To account for non-independence in the construction of our model and the potential bias from sample size, we included another random factor to account for the order of the data within the data file. To control for the potential influence of shared controls, we included a coded group used to identify shared controls (Nakagawa and Santos, 2012).

2.4. Calculating measures of ecosystem structure, function and composition

We used a relatively novel approach of pooling a number of related ecological attributes into three categories that provide measures of ecosystem structure (landscape architecture), function (measures that support ecosystem processes), and composition (measures of diversity, richness etc). This allowed us to pool attributes that would otherwise occur at different spatial or measurement scales to calculate a meaningful, scaled up assessment of the response of ecosystems to feral horse activity. For example, we pooled together plant cover and density as structure, and biota diversity and richness as composition, while soil organics, soil physics and plant biomass were pooled into function. This approach has been used elsewhere to examine ecosystem effects of shrub encroachment (Eldridge et al., 2013; Ding and Eldridge, 2019), soil disturbing animals (Mallen-Cooper et al., 2019) and mammalian herbivores (Eldridge et al., 2016a) on structural, functional and compositional attributes in global and regional studies.

2.5. Meta-regression model approach

Our modelling approach involved three stages. First, we ran four intercept-only (null) models for 1) the total dataset, and its separate components of ecosystem 2) structure, 3) function, and 4) composition. We then ran 12 separate models for their subset of attributes (i.e. for the individual measures, or categories, that comprised structure, function and composition) using LnRR as our response variable, and included the variance matrix and random factors described above. The null models allowed us to estimate the mean effect sizes for an overall ecological response. The significance of the estimated effect sizes was examined using a *t*-test, testing whether the estimated effect size was significantly different from zero in the random effect model at $P < 0.05$. Secondly, to explore the influence of the intensity of feral horse activity on different ecosystem response variables, we ran meta-regression models that included the variance matrix described above for the total dataset, with LnRR as the response variable and a comparison of different intensities of horse activity (i.e., no activity to high activity, low to high, no activity to medium, medium to high, low to medium, no activity to low) as fixed effects. We then used the modified version of I^2, a heterogeneity statistic based on intra-class correlation, to determine the total level of heterogeneity among effect sizes (Nakagawa and Santos, 2012). Our high I^2 (0.983) indicated significant heterogeneity within our model despite accounting for data variance and random factors, and justified the inclusion of moderators to explain this variance. We selected the aridity as explanatory variables that might account for the observed heterogeneity. Aridity gives us insights into whether effects are consistent from mesic to arid areas, and clay is the soil fraction that is most susceptible to compaction, most sensitive to pugging (indentations in damp soil resulting from hoof action), and contains most of nutrients. Thus the consequences of erosion of clay soils is likely to be more pronounced. Thirdly, to explore which explanatory variable might explain the observed heterogeneity, we ran two separate meta-regression models that included the variance matrix described above, with LnRR as the response variable and each explanatory variable separately (i.e. aridity, soil clay content) as the fixed effects for the total dataset, and datasets for ecosystem structure, function, composition, and, 12 subset attributes. Meta-analyses were performed using the 'metafor' package (Viechtbauer, 2010) in R 3.4.1 version (R Core Team, 2018). To assess any potential publication bias, we used funnel plots, Egger regression and 'trim and fill' approaches (Nakagawa and Santos, 2012) across the whole dataset, and for ecosystem structure, function and composition subsets (Appendix D). An important caveat from our publication bias results was the inconsistent evidence from publication bias tests, with two of the three tests suggesting some publication bias in the ecosystem function dataset. These tests indicated that our results for the ecosystem function may be overestimated to some extent, despite including 78 publications and 4261 rows of data from across the world. The possibility of publication bias would likely result from heterogeneity in the unexplained residuals from our data such as other measures of environmental factors (climate variability, soil fertility, topography), horse populations, plant communities and interactions with livestock (e.g. cattle, sheep, goats, etc). Our results therefore require conservative interpretation.

3. Results

Most observations of feral horse effects on ecosystems were from North America (47%), followed by Oceania (21%), Europe (17%) and South America (12%; Fig. 1). Fifty-eight percent of observations were of plants (58%), followed by measures of soil (35%) and fauna (7%; Fig. 2a & 2b). Averaged across all 4261 observations, the mean log response ratio (LnRR) was close to zero (−0.044 ± 0.025; mean ± SE), indicating a 4% decline over all attributes. However, when our data were coined to place all response variables in the same direction to represent an increase in environmental quality (e.g., erosion and runoff multiplied by −1), the overall effect of feral horses was strongly negative (−0.121 ± 0.132) and left skewed (skewness = −0.24, kurtosis = 8.94). The mean LnRR for the coined data represented a 13% decline in overall environmental quality due to horse activity (Fig. 3). Our coined data also indicate that the log response ratio declined with increasing contrast between any two levels of horse activity (Fig. 3). The effects of feral horse activity on ecosystem composition and

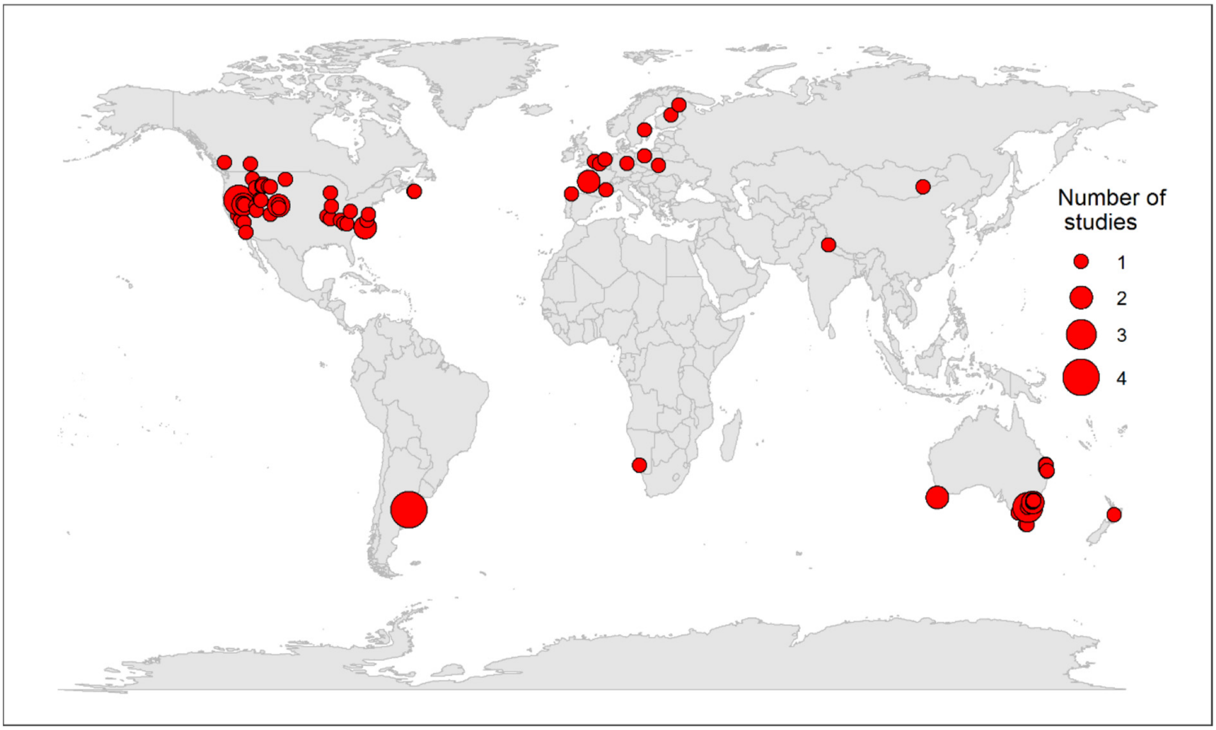

Fig. 1. Global distribution of studies of feral horse activity on ecosystem properties.

structure did not differ significantly from zero, but feral horse activity reduced ecosystem function by 19% (LnRR = −0.21, P = 0.020, 95% CI: −0.39 to −0.03, Fig. 4).

When we examined the individual responses to increasing horse activity, we found consistent negative outcomes on environmental quality (Fig. 4). For example, microbial abundance declined by 78% (LnRR = −1.511, P = 0.004, 95% CI: −2.536 to −0.485, n = 31), animal richness by 59% (LnRR = −0.886, P = 0.092, 95% CI: −1.917 to 0.144, n = 42), plant biomass by 25% (LnRR = −0.294, P = 0.071, 95% CI: −0.613 to 0.025, n = 324) and litter cover by 31% (LnRR = −0.378, P = 0.056, 95% CI: −0.766 to 0.010, n = 115; Fig. 4). Predictably, soil erosion increased by 31% compared with treatment plots (LnRR = 0.377, P < 0.001, 95% CI: 0.190 to 0.565, n = 627). We also detected some interactions with aridity, with greater increases in composition (LnRR = 0.239, P < 0.001, 95% CI: 0.432 to 0.047, n = 1087) and soil physical properties (LnRR = 0.336, P = 0.002, 95% CI: 0.548 to 0.124, n = 202) due to feral horse activity at more arid sites (Fig. 4). However, we found no significant interactions with soil clay content.

4. Discussion

We examined the global published literature on the effects of feral horse activity on a range of ecosystem response variables and found that their overall effect was a 13% decline in environmental quality, which we interpreted as a decline in the status of ecosystem characteristics that are important for sustaining living organisms. Furthermore, the magnitude of this decline increased markedly with

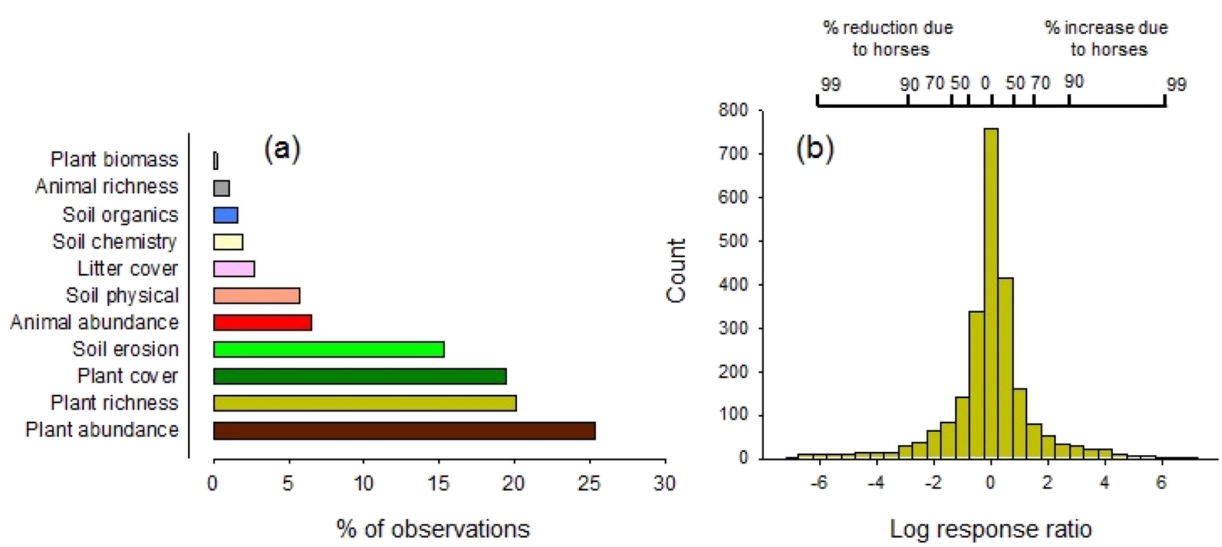

Fig. 2. (a) Percentage of observations for each of the 11 main attributes and (b) frequency distribution of all effect sizes using coined data. Note the greater number of observations of LnRR < 0.

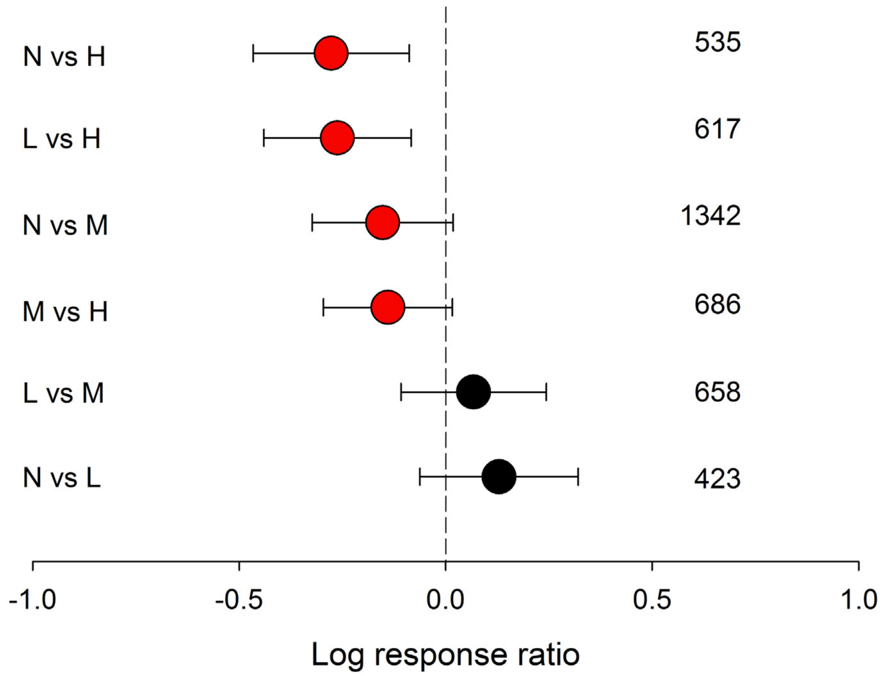

Fig. 3. Estimates (± 95% CI) of the log response ratio for all coined data arranged in order of increasing horse activity contrast, i.e. for the lowest contrast (no activity to low activity) to the highest difference in the intensity of horse activity. N = no activity, L = low activity, M = moderate activity, H = high activity. Red symbols represent a significant decline in the log response ratio for those activity contrasts ($P < .05$); grey symbols indicate no significant effect ($P > .05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

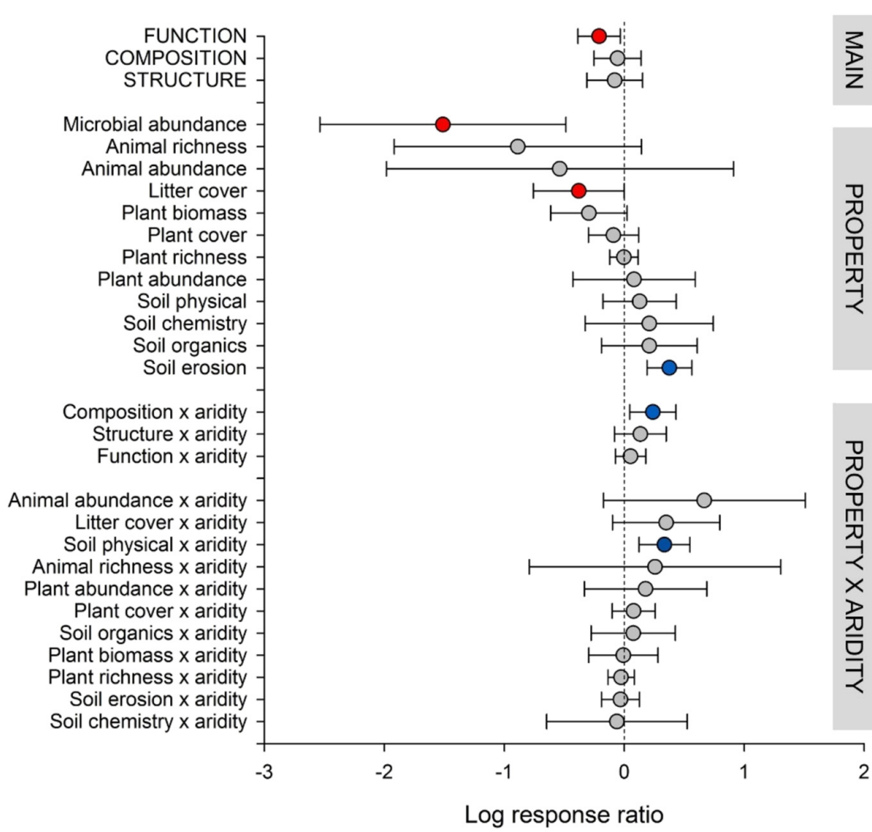

Fig. 4. Results of meta-regression with three moderators (aridity, ecosystem property and the interaction of property and aridity. Blue circles represent response attributes that increase significantly ($P < .05$) under greater horse activity, red points those that decline ($P < .05$), and grey points represent insignificant responses ($P > .05$). Error bars represent 95% confident intervals. As all of the observations of microbial abundance came from the same section of the aridity gradient, there are no interactions with aridity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increases in the intensity of horse activity and became strongly negative with comparisons between low and moderate horse stocking rates. We found three main results. First, low activity (i.e. comparing no activity with low activity scenarios) had neither positive nor negative environmental outcomes (i.e. the log response ratio was not significantly different from zero), though the mean effect of feral horse activity was highly variable, and overall had an insignificant positive effect (13% increase compared to lower horse activity). However, the difference between moderate and high activity contrasts resulted in clear and significant reductions (~15%) in environmental quality, suggesting that increases above moderate activity likely result in marked reductions. Our study results are largely consistent with recent reviews indicating substantial reductions in soil, vegetation, and ecosystem health in areas grazed by feral horses (Nimmo and Miller, 2007; Beever and Aldridge, 2011, Worboys et al., 2018; Beever et al., 2019; Davies and Boyd, 2019). Our results also demonstrate the fact that the global effects of feral horses are consistent with the results of more regional or local impacts.

Notwithstanding these results, we acknowledge that additional data might reveal a significant positive effect of very low levels of activity compared with no activity, consistent with the literature on ungulate grazing activity elsewhere (e.g. cattle; Scasta et al., 2016), particularly in areas where large-bodied, hard-hooved ungulates have co-evolved with soils and vegetation (Beever and Brussard, 2000) such as in Europe or the Americas. Such a scenario is unlikely, however, in continents with a short evolutionary history of grazing or that lacked large ungulates (e.g. Australia), which were under-represented in our data. Similarly, an important caveat from the results of the publication bias tests is that our results may underestimate the effects of horses, given the relatively small number of global studies. Second, the main effects of feral horse activity were related to reductions in plant biomass and litter cover, and increases in soil erosion, with some evidence that feral horse activity reduced microbial abundance and animal richness. Declines in microbial biomass are likely to have marked cascading effects to ecosystem functions associated with nutrient availability and the processing of organic matter. Thirdly, we found that, although individual components of ecosystem composition were unaffected by changes in aridity, the effect of feral horse activity on overall composition became more positive as aridity increased. The most parsimonious explanation is an increase in grazing-insensitive plants (e.g. exotic plants, forbs) with increasing horse activity. Similarly, soil physical effects became more positive, indicating a greater increase in bulk density due to horse activity with increases in aridity.

For those studies that also reported specific rates, feral horse stocking rates varied from approximately 6.7 horses ha^{-1} in mesic environments in Poland (Chachaj and Seniczak, 2005) to as few as 0.002 horses ha^{-1} for a range of environments in Europe (Belgium and France; Cosyns and Hoffmann, 2005) and the USA (Baur et al., 2017). However, estimates of free-ranging horse numbers can vary substantially due to problems of access and therefore animal detection. For example, aerial surveys over extensive areas (2860 km^2) of grassland and forest in the Australian Alps have assessed feral horse numbers to be about 2.7 horses km^{-2} (Cairns and Robertson, 2015), though these densities are likely to be larger given the remoteness, nature of the terrain and therefore the difficulty of detection. Poor detection can make surveys of large areas problematic and can be a major issue when dealing with free-ranging animals. However, free-ranging feral horses tend to congregate in favoured locations such as riparian areas and grasslands, so that average densities are not indicative of the true stocking rate and impacts in habitats favoured by horses. In our study, we could not ascribe exact stocking rates to much of our data, either because these data were not provided in the studies we accessed, or studies were conducted across large areas and therefore average stocking rates would be misleading. Rather, we relied upon the subjective assessment of the intensity of feral horse activity reported by individual authors to assign rates to each study. This technique has been shown to be highly correlated with empirical measures of stocking intensity in other grazing studies (e.g. Eldridge et al., 2016a).

4.1. Feral horse activity leads to substantial reductions in biomass

We found a significant and relatively large (19%) reduction in ecosystem function associated with feral horse activity, and smaller, yet highly variable, non-significant declines in composition (5%) and structure (8%; Fig. 4). Our functional declines indicate a reduction in the capacity to support critical ecosystem functions such as the plant biomass production or carbon and nitrogen sequestration in soils (soil organic matter), and analyses of individual functions revealed that this decline is driven strongly by reductions in plant production of about 25% overall. This result is not unexpected, given that a major impact of horses would be plant removal either directly by herbivory (e.g. Wood et al., 1987; Seliskar, 2003; de Villalobos and Zalba, 2010) or indirectly by trampling-induced soil damage (Turner, 1987; Beever et al., 2008). For example, using sites across a rainfall and temperature gradient, Baur et al. (2017) showed that feral horses reduced biomass by > 47% in Nevada and Utah (arid) but only 6% in North Dakota (humid) and Colorado (dry subhumid). Most of the effects were due to changes in the biomass of grasses (Baur et al., 2017), the preferred food item of horses (McInnis and Vavra, 1987; Scasta et al., 2016). Feral horses have a stronger preference for graminoids than forbs and shrubs (Scasta et al., 2016), and grazing can lead to a conversion of grasslands to shrublands because shrubs are generally not consumed (Van Rees and Holmes, 1986). Reductions in grass cover could also lead to long-term reductions in grass production (e.g. de Villalobos et al., 2011).

Reductions in plant biomass, height and structure resulting from increasing horse activity (Turner, 1987; de Villalobos and Zalba, 2010) could lead to a number of potential outcomes such as: 1) alteration to plant cover, richness and composition (Lopez et al., 2017); 2) reduced vegetation structure and therefore habitat quality (Martin and Fahrig, 2012), which has been shown to alter ant community composition for example (Beever and Herrick, 2006), 3) reduced capacity for production of litter and organic matter, and thus increased soil erosion risk (Weaver and Dale, 1978), and 4) reduced organic matter inputs into the soil, with feedback effects on soil biota, microbially-mediated decomposition and therefore soil nutrient pools (Six et al., 2004). Although there are some studies of the impacts of horses on plant height and structure (e.g. de Villalobos and Zalba, 2010; Lopez et al., 2017), we did not find significant evidence of feral horses reducing plant cover or height in our database largely because there were insufficient data to undertake a global assessment. However, declines in plant biomass have been linked to changes in vegetation height, which have been shown to affect habitat quality for a range of grassland-dependent biota. For example, broad-toothed rats (*Mastacomys fuscus mordicus*) are highly dependent upon large, dense, native grasses for habitat and foraging, particularly in winter (Carron et al., 1990). Increasing feral horse activity has been shown to reduce habitat quality for broad-toothed rats by reducing grass height (Schulz and Green, 2018; Eldridge et al., 2019). Horses may also influence larger herbivores such as elk by displacing them at watering points (Hall et al., 2016). Feral horse activity has also been shown to affect invertebrates (Ostermann-Kelm et al., 2009), small mammals (Beever and Brussard, 2004), birds (Zalba and Cozzani, 2004) and estuarine fauna (Levin et al., 2002), some through changes in vegetation structure.

Reduced biomass likely equates with lower litter levels, which we found declined by 31% under feral horse activity (Fig. 4), consistent with other studies (Freedman et al., 2011; though see Davies et al., 2014). In functional ecosystems, litter plays a critical role by regulating soil temperature, protecting the soil surface against raindrop action, and providing organic compounds, enzymes and nutrients to the soil (Facelli and Pickett, 1991). Livestock grazing has been shown to redistribute surface litter (Daryanto et al., 2013), increasing the connectivity of bare patches and the potential for overland flow to move sediment, organic material and nutrients off-site. The depth of litter is also important for a range of biota. Scheele and Foster (2018) showed that horse activity reduced litter depth to a level that was sub-optimal for nest construction for the endangered corroboree frog (*Pseudophryne pengilleyi*), potentially exacerbating any effects of egg desiccation that lead to reproductive failure (Scheele et al., 2012).

Despite their preference for graminoids (Scasta et al., 2016), we found highly variable effects of feral horse activity on measures of plant composition such as richness, evenness or diversity, yet no significant net effect as grazing-induced declines in one species are typically accompanied by compensatory increases in other species. Grazing by feral horses might lead to the persistence of prostrate plants or unpalatable plants or species with short life cycles, rosette-forming habits, or species associated with grazing lawns at the expense of more erect and palatable, often native species. For example, in the Australian Alps, feral horse grazing has been shown to be associated with increases in lightdependent herbs, particularly exotic species, and exotic European grasses such as *Holcus lanatus*, but marked declines in the native perennial sedge *Carex gaudichaudiana* (Prober and Thiele, 2007). Thus, although we found no significant changes in richness, a component of composition, overwhelming evidence suggests major changes in composition with prolonged horse grazing such as declines in dominant perennial grasses or sedges and increases in short stature plants (e.g. Fahnestock and Detling, 1999; Bai et al., 2001). Plant community richness has been shown to increase under horse grazing in the coastal grasslands in France (Loucougaray et al., 2004; Marion et al., 2010), but declines in more arid environments in the western United States (Beever and Brussard, 2000; Davies et al., 2014). In gorse shrublands in northern Spain, feral horse grazing led to a reduced abundance of woody species, which was compensated by an increase in herbaceous species (Lopez et al., 2017).

4.2. Feral horse activity increases erosion risk

The impacts of horses on erosion are highly variable and, like the effects of cattle, are likely to vary with factors such as vegetation type, stocking rate, soil properties, slope and level of utilisation, to name a few. We found evidence that feral horses increased erosion by pugging and streambed widening in riparian areas (Robertson et al., 2015; Prober and Thiele, 2007) and that high levels of recreational horse activity lead to considerable erosion (e.g. Summer, 1986; Newsome et al., 2002). Overall, our analyses showed that soil erosion increased by 31% (Fig. 4), which is likely to lead to instability and further declines in function.

Patch creation by large-bodied herbivores is an important process driving plant community composition and leading to increases in spatial heterogeneity (Bakker and Olff, 2003). However, the extent to which large patches of disturbed soil such as dust baths and wallows created by feral horses lead to positive ecosystem benefits is unknown. These effects are likely to be predominantly negative in environments with a short evolutionary history of grazing by horses. The effects of horses on erosion are also likely to be indirect, by reducing plant cover and biomass or increasing bare ground, which lead to substantial declines in soil aggregate stability (Davies et al., 2014). Erosion also has flow-on effects to ecosystem functions, reducing the capacity of the soil to produce biomass, or changing plant composition by altering soil seed banks. We did not find that erosional effects varied with aridity, though the implications of erosion are likely greater in more sensitive alpine areas (e.g., alpine bogs) where soil formation rates are extremely low in the production of peat, the main component of alpine soils (Hope and Nanson, 2015).

Finally, the effect of feral horse activity on animals was highly variable. We did not test for feral horse effects on mammals specifically because most research has focused on plants and soils (Fig. 2a), and animal effects have focused mainly on specific iconic species such as the greater sage-grouse (*Centrocercus urophasianus*; Davies et al., 2014), corroboree frog (Scheele et al., 2012), mountain pigmy possum (*Burramys parvus*; Bates, 2018), a range of vertebrates and invertebrates (Davies and Boyd, 2019), or behavioural interactions between horses and other vertebrates (Ostermann-Kelm et al., 2008), to name a few. However, studies from the Australian Alps have documented substantial negative effects of feral horses on a range of threatened fauna from reptiles to fish and amphibians (Worboys et al., 2018). There are some specific environments where it is likely that the reductions we observed in biomass, litter cover and erosion would translate into reduced richness and abundance of other unstudied biota. Future studies need to consider how functional and structural shifts in ecosystems will alter biotic communities. Further work could also benefit from exploring the large variation we found surrounding some results and consider potential sources that led to positive publication bias test results for our models. Future work may consider different measures of environmental quality (climate, soil texture, topography) or account for horse populations, specific plant communities and interactions with other herbivores.

5. Concluding remarks

Our results provide strong evidence that feral horses have marked effects on ecosystems and are associated with reductions in overall function, but also specific reductions in soil health associated with reduced litter cover and greater erosion. Our data do not allow us to provide specific grazing or activity rates that could be advocated to prevent declines in environmental quality due to feral horse activity, largely because of the paucity of data on specific grazing rates for many of these studies due to an emphasis on large scale studies of free-ranging horses. There are three clear conclusions that arise from our review. First, there are surprisingly few empirical data on horse effects on vertebrates, particularly those associated with riparian areas. Second, we know little about whether a sustainable level of feral horse activity is possible or even feasible, but given that total control is unlikely in most areas, this should be a high priority for resource managers. Finally, the feral horse issue is as much a social and political issue as it is an ecological issue. We echo a call by others (e.g. Nimmo and Miller, 2007) to involve the community and stakeholder groups in feral horse management. It is only by engaging all sectors of the community that we can hope to find a balance between the needs of maintaining healthy functional ecosystems and their biota, and societal needs of supporting free-ranging herds of feral horses to meet cultural and social outcomes.

Author contribution

DJE designed the study and methods. DJE and SKT wrote the manuscript drafts. JD and SKT collected the data and built the database. JD performed the data analyses and revised manuscript drafts.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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