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1 **Recognising the potential role of native ponies in conservation management**

2

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11

12 *Running title: Native ponies and conservation*

13

14 **Abstract**

15 Population control of feral horses has been the subject of public debate in many parts of the
16 world in recent years due to wide-reaching ecological and societal impacts. However, the
17 feral populations in these high-profile cases are not 'native' but are instead descended from
18 animals which escaped from or were released by settlers. This paper considers i) the
19 potential role of indigenous equids as conservation grazers within native ecosystems
20 currently in poor condition, and ii) the value of supporting semi-wild native ponies
21 specifically. We argue that the high ecological overlap between ponies and cattle reported
22 in a range of studies means that they should be considered as alternative tools for
23 conservation management, particularly in scenarios where there is a need to reduce the
24 dominance of plant species avoided by more-selective small ruminants such as sheep. Semi-
25 wild ponies could be particularly suited to conservation grazing because their genomes have
26 been predominately shaped by natural and not artificial selection, meaning they may have
27 adaptations no longer present in domesticated equids. With agricultural and environmental
28 policy in the EU and UK under major review, it is anticipated that the wider delivery of
29 public goods, rather than primary production, will be prioritised under future subsidy
30 payment schemes. Recognising the value of native ponies as conservation grazers would
31 broaden the range of routes by which land managers could achieve biodiversity gain, while
32 simultaneously supporting at-risk equine genotypes.

33

34 *Keywords:* horses; equids; semi-wild; conservation grazing; agri-environment; genetic
35 adaptation

36

37 **1. Background**

38 Grazing continues to be a major driver of land use change worldwide and can be both
39 beneficial and detrimental to wildlife habitat. In recent years a link between feral horse
40 (*Equus ferus caballus*) overpopulation and environmental damage has become a
41 contentious issue due to public protests at proposals to cull large numbers (Driscoll, 2018;
42 Scasta et al., 2018). However, the populations in these high-profile cases are not 'native',
43 but are instead for the most part descended from animals which escaped from, or were
44 released by, European settlers in the 16th century (National Research Council, 2013), and are
45 thus categorised as 'feral' (defined as living in a wild state after escape from captivity or
46 domestication). Ecologically, they are alien species, and there is mounting evidence that
47 they are putting ecosystems at risk through trampling and vegetation community change
48 (Davies et al., 2014; Nimmo, 2018; Rogers, 1991).

49

50 What, then, is the role of indigenous equids within their native ecosystems? In such
51 situations, can targeted grazing by horses (taller than approx. 148 cm at the withers) and
52 ponies (less than approx. 148 cm at the withers) achieve conservation gains? These
53 primitive horses or ponies have lived as free-ranging populations for thousands of years
54 with little human intervention. Such herds are classified by the EU as 'semi-wild' and have
55 related derogations which exempt them from legislation relating to e.g. animal
56 identification and treatment. Whilst overall population increase is commonly a concern
57 with feral equids, semi-wild horse and pony populations are more generally under threat.
58 Within the UK very few pony herds that can be designated as semi-wild remain. Two
59 examples of semi-wild native ponies thought to have been *in situ* since the Bronze Age are
60 Dartmoor Hill Ponies and Carneddau Mountain Ponies (Fig 1). In both cases ponies have

61 been removed to make way for domestic livestock in response to economic pressures on
62 farmers, and there is now a serious risk that they may die out. Census data from the 1960s
63 onwards estimate the Dartmoor Hill Pony population has declined from a maximum of
64 12,250 to 1,200 (*J. Hibbs, personal communication*); while there are around 300 Carneddau
65 Ponies found on Snowdonia's Carneddau Mountains today (*H. Kehoe, personal*
66 *communication*). The UK government criterion which defines semi-wild ponies (i.e. that
67 they remain outside of human control for their survival and reproduction) also means they
68 are not protected by societies or registers. As a result, they fall outside of initiatives on the
69 sustainable use of farm animal genetic resources incentivising the conservation of rare or 'at
70 risk' breeds (including breeds of horses and ponies), and the genetic variation within them.
71 Rather short-sightedly the conservation of animal genetic resources has been considered
72 primarily in relation to their potential contribution to agricultural productivity and
73 sustainability (Hall & Bradley, 1995; Rege & Gibson, 2003), with little or no regard given to
74 ecological resilience.

75

76 Agricultural abandonment of grasslands and heathlands across the EU due to changes in
77 farming practice has been identified as a specific threat to related habitats and species
78 (Hermoso et al., 2018; Keenleyside & Tucker, 2010), particularly in areas that are marginal
79 for agricultural production due to environmental challenges. Left unmanaged, many of
80 these vegetation communities have become dominated by plant species rejected by stock
81 (e.g. *Juncus* spp., *Molinia caerulea*, *Deschampsia cespitosa*, *Pteridium* spp, *Ulex* spp.). This
82 degradation of native plant communities limits the value of these areas for achieving
83 biodiversity conservation objectives. Consequently, government agencies and conservation
84 charities are resorting to mechanical cutting of vegetation (Talle et al., 2018; Valasiuk et al.,
85 2018), as a substitute for grazing, to ensure the long-term survival of Europe's most valuable
86 and threatened habitats and species (as listed under both the EU Birds Directive
87 2009/147/EC and the EU Habitats Directive 92/43/EEC; i.e. sites with NATURA 2000 status).
88 This is however costly, does not create the same degree of structural heterogeneity as
89 grazing, and over time leads to nutrient depletion.

90

91 Farming systems in areas designated by the EU as less favoured have for many years been
92 supported by specific agricultural subsidies. It is anticipated that under future support
93 schemes the wider delivery of public goods, rather than primary production, will be
94 prioritised. Crucially this could allow the grazing outcomes of stock types other than sheep
95 and cattle to be eligible for support payments. The biodiversity benefits of mixed-low-
96 intensity grazing systems have been well documented (Critchley et al., 2008; Fraser et al.,
97 2014; Liu et al., 2015; Lopez et al., 2017b) (Table 1), yet in countries including the UK semi-
98 natural grassland and heathland communities continue to be managed predominately under
99 sheep-only systems. A policy change which recognised the role of native ponies could have
100 multiple benefits; improved biodiversity, diversification of income streams, and
101 conservation of threatened genotypes of grazer. However, to date there have been little
102 robust data collected regarding the comparative impacts of equid grazing, largely because of
103 proportionately low levels of research funding compared to those with domesticated stock.
104 Unless addressed, this will continue to compromise our ability to optimise deployment of
105 conservation grazing tools, undermining our ability to meet conservation targets.

106

107 To explore these issues further we evaluated i) the potential role of native ponies as

108 conservation grazers, and ii) the value of supporting semi-wild ponies specifically. Firstly,
109 we examined the comparative foraging strategies and dietary preferences of equids, and
110 identified situations where grazing by ponies could be particularly beneficial. Secondly, we
111 considered the behavioural ecology of ponies in the context of conservation grazing
112 schemes and free-living populations, highlighting both the merits of using ponies as
113 conservation grazers and behavioural factors that must be considered when using ponies in
114 these contexts. Finally, we explored the population genetics of UK native ponies and
115 associated evidence of adaptation.

116

117 **2. Dietary preferences of equids**

118 *2.1 Physiological factors influencing foraging*

119 A variety of factors influence the foraging choices and grazing behaviour exhibited by large
120 herbivores. One of the key determinants of foraging behaviours is body size, since energy
121 requirements scale to 0.75 rather than 1 (Demment & Van Soest, 1985). Consequently,
122 larger animals are generally less selective grazers than their smaller counterparts (Sensenig
123 & Demment, 2010), and tend to prioritise maintaining their intake rate rather than the
124 nutritional value of what is consumed when resources become limited. These differences
125 are evident when the dietary preferences of cattle and sheep are compared (Critchley et al.,
126 2008; Cuchillo-Hilario et al., 2018; Fraser et al., 2009; Grant et al., 1985). Gut morphology
127 and function also have a role to play in influencing diet composition. While ruminants are
128 fore-gut fermenters (with fermentation taking place in the reticulorumen), equids are hind-
129 gut fermenters (fermentation occurs in the caecum and colon). A mainly post-gastric site of
130 fermentation (i.e. after the stomach) means they can digest and absorb available soluble
131 carbohydrate and protein directly, without the potential inefficiencies associated with the
132 synthesis of microbial protein (Santos et al., 2011). Evidence suggests that equids achieve
133 higher nutrient extraction rates than bovids on all forages, whether housed or at pasture
134 (Duncan et al., 1990; Illius & Gordon, 1992; Santos et al., 2011). Without selective retention
135 of large particles in the rumen, digesta passes relatively quickly through the equine
136 fermentation zone. This faster throughput is an advantage which outweighs their lower
137 digestive efficiency, particularly on poor quality forages, allowing them to ingest large
138 amounts of fibre-rich forage.

139

140 *2.2 Comparative foraging strategies*

141 Studies of natural grazing systems in Africa were among the first to identify differences in
142 foraging strategies of large grazers, and categorised the equid present (the zebra) along with
143 ruminants of a similar size as generalist (rather than specialist) feeders (Jarman & Sinclair,
144 1979). There is consensus from a range of ecosystems that equids prefer graminoids to
145 browse species (Celaya et al., 2011; Ferreira et al., 2013; Gordon, 1989; Lopez et al., 2017a;
146 Menard et al., 2002; Pratt et al., 1986; Scasta et al., 2016). However, as generalist feeders,
147 they will switch to alternative plant species and plant parts when preferred items become
148 depleted. Thus, like cattle, equids will incorporate woody vegetation into their diets as
149 high-quality grassland availability declines (Putman et al., 1987; Scasta et al., 2016).
150 However, equids have been found to be more reluctant to browse on *Calluna* spp. (a plant
151 species that heathland grazing prescriptions are frequently designed to protect) than are
152 cattle (Celaya et al., 2011; Ferreira et al., 2013) or sheep (Ferreira et al., 2013). Instead,
153 ponies prefer to consume *Ulex* spp. (Putman et al., 1987) (a plant species that grazing
154 prescriptions are often aiming to control), with dietary inclusion rates higher than for cattle

155 or sheep (Ferreira et al., 2013).

156

157 Studies in areas with mixed habitats found that the summer diet of ponies, like that of
158 cattle, consisted primarily of grasses (80-90%) (Putman et al., 1987). However, *M. caerulea*,
159 a species scarcely eaten by cattle, contributed to 20% of their diet at this time. In the UK,
160 increased *M. caerulea* abundance has frequently been at the expense of more diverse
161 upland heath and mire habitats (Yeo & Blackstock, 2002); a situation exacerbated by sheep-
162 only grazing since sheep strongly avoid consuming this species. To counteract this, agri-
163 environment schemes have offered incentives for cattle grazing, since as less selective
164 feeders they are more likely to switch to consumption of *M. caerulea* as preferred resources
165 decline (Critchley et al., 2008; Fraser et al., 2011). However, loss of cattle from many less
166 favoured areas in response to economic and social challenges (poor returns, aging farmer
167 populations, lack of labour) has meant that there in many regions there are insufficient
168 cattle numbers to deliver recommended grazing prescriptions. Despite the potential for
169 targeted pony grazing to also reduce *M. caerulea* dominance through increased utilisation
170 this has not been fully explored or exploited. Indeed, the high dietary overlap between
171 ponies and cattle shown by a range of studies (Celaya et al., 2011; Gordon, 1989; Menard et
172 al., 2002; Pratt et al., 1986; Scasta et al., 2016) suggests that these animals could be
173 considered broadly as alternative tools for conservation management, eligible for similar
174 agri-environmental scheme payments based on the outcomes of their grazing.

175

176 Given that between-species comparisons of dietary preferences and grazing behaviour
177 involving ponies are rare, it is not surprising that there is a complete lack of evidence as to
178 similarities and differences in the diet composition of different pony breeds or types.
179 Studies with cattle have found few differences between the diets selected by contrasting
180 traditional and modern breed types (Fraser et al., 2009; Fraser et al., 2013), with utilisation
181 of *M. caerulea* similar among breeds. However, results from cattle breed comparisons also
182 highlight that adaptations to adverse environments as well behavioural responses to
183 topographical/climactic conditions must also to be considered. Since such factors affect
184 energy requirements and nutrient use efficiencies they can potentially influence both
185 grazing patterns and welfare (Fraser et al., 2009; Ricci et al., 2014).

186

187 **3. Behavioural ecology**

188 *3.1 Social organisation*

189 Ponies show a relatively high level of social complexity compared with grazers such as sheep
190 or cows, which can have certain implications for conservation grazing schemes. Free-living
191 horses live mostly in either family bands or bachelor bands. Family bands are comprised of
192 between two and 35 mares, along with one to two stallions and all immature offspring
193 (Boyd & Keiper, 2005). These often show patterns of fission and fusion, where groups split
194 up and reform frequently (*CS, personal observation*). Bands also show seasonal fluctuations
195 in the relative level of social cohesion, most likely due to a combination of food availability
196 and stallion herding frequency (Stanley et al., 2017). Whilst foals can be nutritionally
197 independent of their mothers at the age of around six months old, youngsters of both sexes
198 only naturally disperse from the group in which they are born between the ages of two and
199 five years old (Boyd & Keiper, 2005). These social factors must be taken into account, in
200 addition to grazing capacity, when considering stocking densities and sex ratios of ponies in
201 conservation grazing schemes; for example if there are no neighbouring groups to which

202 youngsters can disperse, they will need to be removed from the group to avoid them being
203 the targets of aggression (Stanley & Shultz, 2012). Strong social bonds exist between
204 females and their band stallion, but social bonds between females are also important;
205 mares are known to remain together after the death of their band stallion (Keiper, 1985).
206 Existing social bonds and opportunities for their maintenance should therefore be a key
207 consideration for both the selection of individuals and their management in both
208 conservation grazing schemes and free-living populations.

209

210 Horses are polygynous, meaning they show high levels of reproductive skew (Rubenstein &
211 Nunez, 2009). Since not all males can hold harems at any one time, yet the sex ratio is most
212 commonly 1:1 in free-living populations (Ransom & Kaczensky, 2016), surplus males
213 commonly form bachelor bands. These are known to number up to 16 individuals (McCort,
214 1984) and are thought to be mostly unstable in terms of membership (Boyd & Keiper, 2005).
215 If the number of breeding stallions is controlled in feral populations, conservation grazing
216 schemes elsewhere could provide a potential sink for these excess bachelor males.

217

218 *3.2 Home ranges*

219 Horse bands do not generally defend discrete territories (Boyd & Keiper, 2005); instead,
220 they occupy overlapping but well-defined home ranges that can persist for a number of
221 years (McCort, 1984) and vary significantly in size, both within and between populations
222 (Boyd & Keiper, 2005). Such site fidelity could make ponies more suited to targeting specific
223 locations within a larger habitat for conservation grazing. Whilst hefting (selective breeding
224 to instil a specific home range) has traditionally been used to achieve this in sheep, reduced
225 flock sizes in recent years has reduced the effectiveness of this strategy. A herd (a group of
226 horse bands living in same geographical area) can show significant social structure, where
227 bands follow similar movements and have an inter-band dominance hierarchy (Miller,
228 1979). Home range size can vary seasonally in feral horse populations, although there
229 seems to be no consistent trend as local conditions seem to have a significant influence
230 (Boyd & Keiper, 2005). Habitat utilisation does, however, appear to vary seasonally in most
231 populations; in mountainous regions, vertical migrations may occur to benefit from
232 changing vegetation quality and abundance (Berger, 1986; Linklater et al., 2000), whilst
233 water availability (Berger, 1977) and tabanid fly abundance (Keiper & Berger, 1982) can also
234 influence home range use. It is important to note that whilst the factors affecting home
235 range use have been studied across a variety of feral populations, our understanding of the
236 influence of herd composition on grazing behaviour is lacking.

237

238 *3.3 Influence of contraception*

239 Contraceptive vaccines are being increasingly used to control female fertility and therefore
240 limit population sizes in feral horses. Since natural predators are frequently absent from
241 habitats in which feral horses thrive, management interventions are often required to
242 control population sizes (Ransom et al., 2016; Saltz, 2002). However, the use of
243 contraception can influence both behaviour and range use (Nunez et al., 2009; Ransom et
244 al., 2010), and this could have implications both for the welfare of free-living populations
245 and range use in conservation grazing schemes. Gelding excess colts is another approach to
246 population control, but again the potential impacts on subsequent resource utilisation are
247 poorly understood. Of course, such approaches to meeting sustained external pressures to
248 control numbers also pose additional risks to already rare populations such as the

249 Carneddau and Dartmoor Hill Ponies, including a reduction in genetic diversity and the
250 introduction of artificial selection to these populations. Interventions such as removal of
251 stallions, gelding of stallions, and mare contraception all result in management decisions
252 being imposed upon the herds, threatening their semi-wild status and potentially impacting
253 upon the selection of specific genes and traits correlated with adaptation to the harsh
254 environments they have evolved in.

255

256 Males used in conservation grazing schemes are frequently castrated (gelded) to avoid
257 breeding. Gelding is also commonly carried out to facilitate handling and management
258 (McDonnell, 2005). However, groups of geldings likely differ in home range use to the more
259 well-studied family bands, or even compared with non-castrated bachelor bands. This could
260 have implications for the management of gelding groups, specifically in terms of predicting
261 their seasonal movements.

262

263 **4. Population genetics**

264 *4.1 How genetically distinct are breeds?*

265 Science has only recently begun to address the question of how distinct free-living,
266 unmanaged populations of horses and ponies are from their registered counterparts.
267 Factors such as adaptation, artificial selection (in the registered breeds) and inbreeding
268 must be considered. Genetically speaking, there is no universally accepted definition of a
269 'breed', which is an artificial human concept based on a closed (or restricted) breeding pool
270 of individuals which share a common phenotype (typically purely morphological i.e. height,
271 coat colour). In cattle, for example, the primary distinction between Red and Black Angus is
272 due to a mutation in a single coat colour gene (Matukumalli et al., 2009). In the case of
273 semi-wild pony populations then, the question of how distinct they are from their registered
274 relatives is perhaps not as important as the reason for any differences (i.e. are they
275 signatures of adaptation?).

276

277 *4.2 How do native pony breeds differ?*

278 In the first studies of their kind, several studies of population diversity and relationships in
279 both registered and semi-wild UK pony populations were undertaken (Winton et al. 2013;
280 McMahan et al. 2015; Hegarty et al. 2017). Genotype data of semi-wild populations were
281 generated using 15 simple sequence repeat markers (SSR) and 162 single nucleotide
282 polymorphism (SNP) markers on samples from 16 herds of Welsh Mountain Hill Pony
283 (McMahan et al., 2015) and 19 herds of Dartmoor Hill Ponies (Hegarty et al., 2017). These
284 data were compared to existing genotypes (Winton et al., 2013) of Section A Welsh Ponies
285 and Section D Welsh Cobs (breed society registered), the Carneddau Pony (semi-wild),
286 Connemara Ponies (breed society registered), Irish Draught horse (breed society registered)
287 and Dartmoor Ponies (breed society registered) (Fig 2).

288

289 These analyses demonstrated that the Carneddau Pony is genetically distinct from the
290 Section A Welsh Pony (Winton et al., 2013), despite the Carneddau Ponies generally being
291 thought of as being either an offshoot or an ancestor of the Welsh Section A. Population
292 structure analysis showed that the two types are related, but distinct, and mitochondrial
293 DNA analysis identified several rare variants present at high frequency in the Carneddau
294 Ponies but not any of the other types. High levels of deviation from Hardy-Weinberg
295 equilibrium were detected which are indicative of selective pressure, and it was argued that

296 conservation or further study of the Carneddau Ponies was important to avoid losing useful
297 genetic adaptations.

298
299 Similar results were observed in studies of the Welsh Mountain Hill Pony (McMahon et al.,
300 2015) and Dartmoor Hill Ponies (Hegarty et al., 2017). In both cases, the populations can be
301 distinguished from their registered counterparts. Thus, whilst both semi-wild populations
302 are related to their registered cousins, there are key genetic signatures which are common
303 across animals from the same group and can be used to distinguish them. The largest
304 genetic difference observed was that between the Carneddau and the Section A Welsh, with
305 a Wright's F_{st} (Wright, 1965) measure of genetic distance 0.157 when all datasets were
306 compared. This value is comparable to the difference seen between established horse
307 breeds in studies in France (Leroy et al., 2009) and Poland (Stachurska et al., 2014). Whilst
308 we continue to argue that genetic degrees of difference should not be a hard limit on what
309 humans consider a 'breed', the Carneddau Pony is clearly a distinct population far older
310 than the Welsh Section A. Interestingly, other close relationships are apparent between the
311 'upland' types, suggesting the possibility of a shared 'upland' signature linked to adaptation,
312 though other factors such as common ancestry may be in play. These studies were the first
313 in the world to explore the comparative population genetics of different breeds and types of
314 equine, and clearly show there is much to be learned about adaptation and related
315 environmental impacts.

316 317 **5. Conclusions**

318 At a time when the ecological role of feral horses is under considerable scrutiny this paper
319 presents evidence that grazing by native horse and ponies could play an important role in
320 restoring and maintaining habitats of conservation importance. Semi-wild populations
321 could be particularly suited to conservation grazing schemes due to both physiological and
322 behavioural adaptations to a free-roaming lifestyle. They might also have a particular
323 genetic value; their genomes have been shaped by natural and not artificial selection,
324 meaning these ponies may have ecological adaptations no longer present in domesticated
325 ponies. These populations are also highly valued on a cultural basis and are an important
326 part of their regions' heritage. Conservation grazing schemes could provide an important
327 sink for excess individuals from these populations, allowing satellite populations to be
328 maintained as an 'insurance policy' against catastrophic events to founder populations.
329 Such factors should be taken into account as new policies and prescriptions are being
330 developed to meet revised targets for biodiversity gain.

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337

338

339

340

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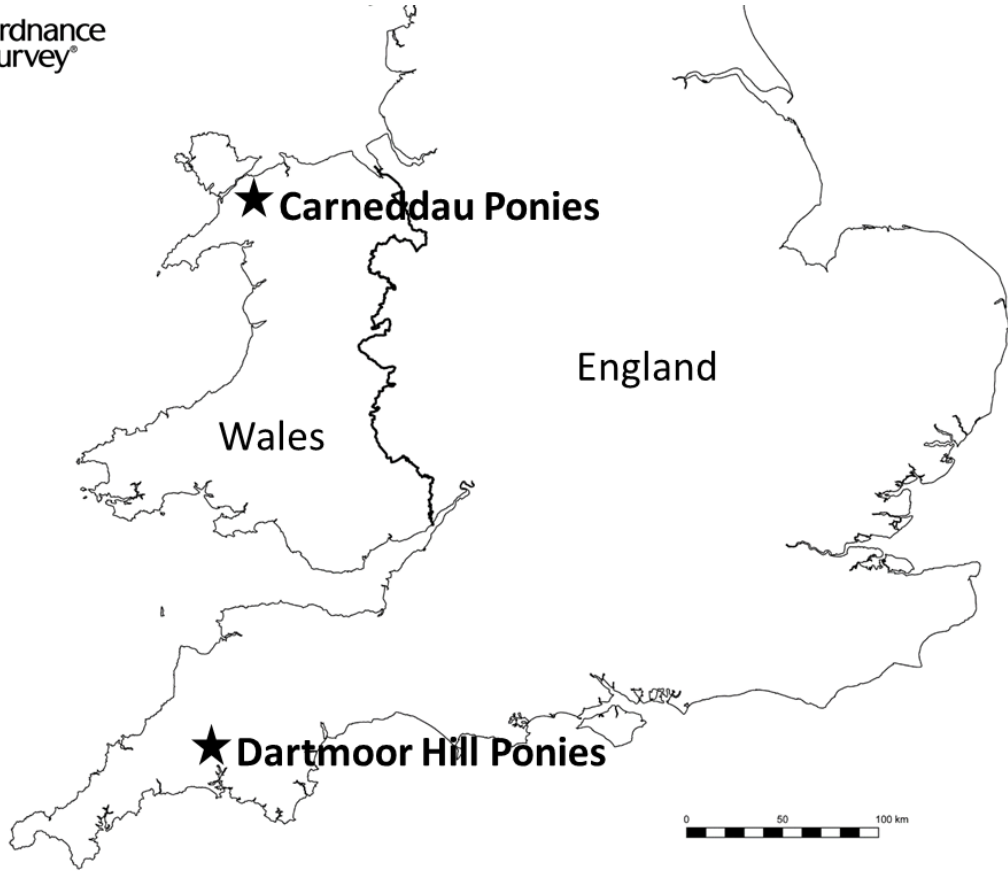
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505

Group		Genus/species	Livestock species	Response to mixed grazing	Country	
Plants	Tracheophyta	Combined	Cattle + sheep	+	UK China	(Critchley et al., 2008; Evans et al., 2015) (Liu et al., 2015)
Mammals	Rodentia	Vole (<i>Microtus agrestis</i>)	Cattle + sheep	+	UK	(Evans et al., 2006a; Evans et al., 2015)
	Carnivora	Red fox (<i>Vulpes vulpes</i>)	Cattle + sheep	+	UK	(Evans et al., 2015)
Birds	Passeriformes	Meadow pipit (<i>Anthus pratensis</i>)	Cattle + sheep	+	UK	(Evans et al., 2006b; Evans et al., 2015)
Arthropods	Araneae	Combined	Cattle + sheep Cattle + goats	+	Spain	(Garcia et al., 2011)
	Opiliones	Combined	Cattle + sheep Cattle + goats	+/-	Spain	(Garcia et al., 2011)
	Coleoptera	Combined	Cattle + sheep	+	UK	(Dennis et al., 2008)



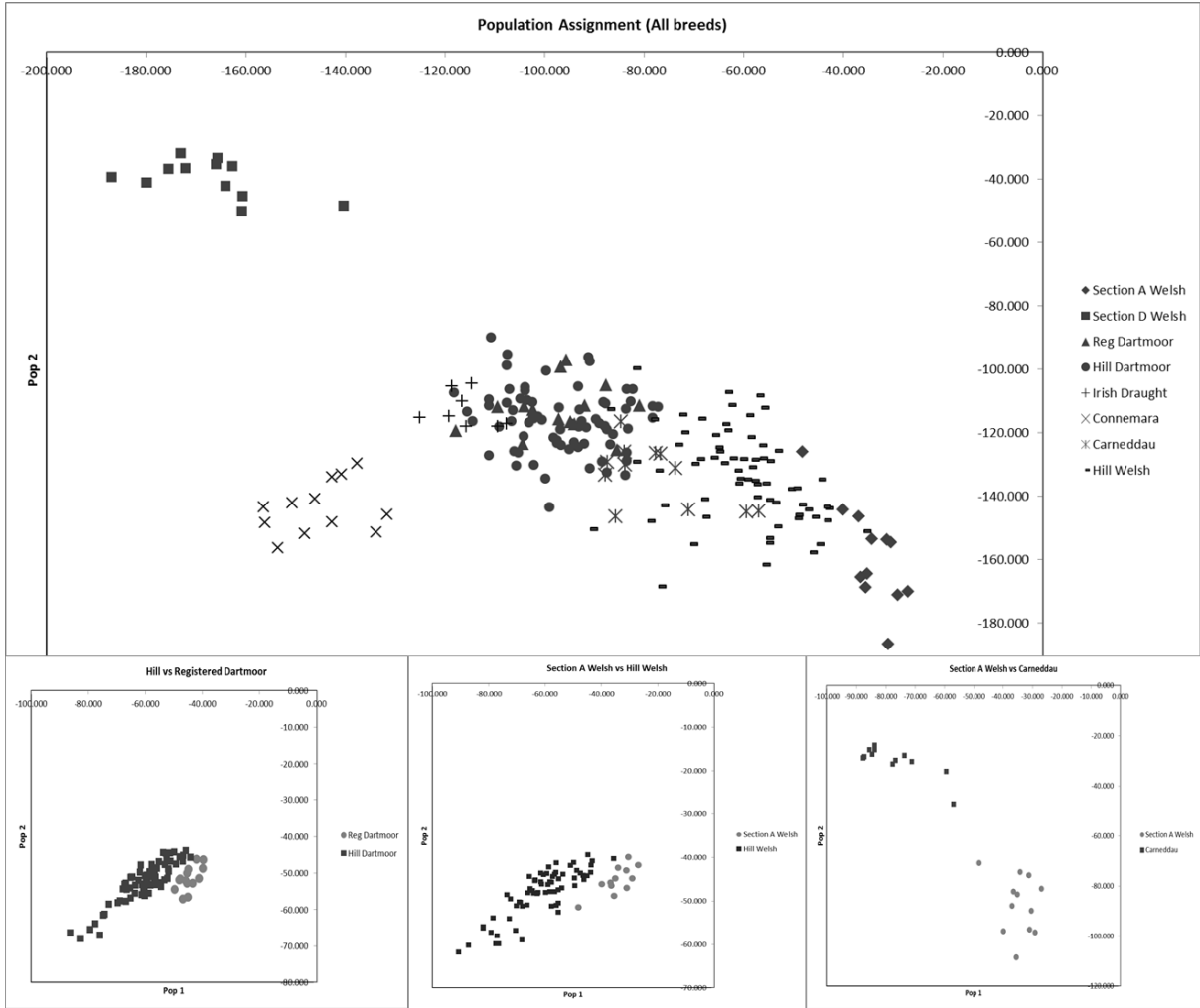


Table 1: Examples of responses of different taxa to mixed grazing of semi-natural vegetation communities; where + = positive effects from mixed grazing, +/- = no response to mixed grazing; compared to single-species grazing treatments. Study duration ranged from 3 to 10 years.

Figure 1: The distinct geographic locations where the semi-wild Carneddau Ponies and Dartmoor Hill Ponies are found. Breeding studs and animals registered with breed societies such as the Welsh Pony and Cob Society and the Dartmoor Pony Society are found throughout the British Isles (map reproduced from Ordnance Survey map data by permission of the Ordnance Survey © Crown copyright 2001).

Figure 2: Results of population assignment clustering for all pony types based on 162 single nucleotide polymorphism markers, highlighting the close relationships of the Hill Welsh, Carneddau and Dartmoor Hill ponies. Subfigures show the results of population assignment for these three types relative to Section A Welsh (for Carneddau and Hill Welsh) and Registered Dartmoor Pony (for Dartmoor Hill Pony) in order to show that deeper levels of resolution enables separation of these types.