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Presenter Information

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Livestock corridors working as pollinator refuges and dispersal hotspots: lessons from Spain

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Key words: herbivore corridors; seed dispersal; pollination; landscape genetics

Abstract

Habitat fragmentation is one of the greatest threats to biodiversity conservation and ecosystem productivity mediated by direct human impact. Its consequences include genetic depauperation, comprising phenomena such as inbreeding depression or reduction in genetic diversity. While the capacity of wild and domestic herbivores to sustain long-distance seed dispersal has been proven, the impact of herbivore corridors in plant population genetics has not been observed previously.

We conducted this study in the Conquense Drove Road in Spain, where sustained use by livestock over centuries has involved transhumant herds passing twice a year en route to winter and summer pastures. We compared genetic diversity and inbreeding coefficients of *Plantago lagopus* populations along the drove road with populations in the surrounding agricultural matrix, at varying distances from human settlements.

We observed significant differences in coefficients of inbreeding between the drove road and the agricultural matrix, as well as significant trends indicative of higher genetic diversity around human settlements. Trends for higher genetic diversity along drove roads may be present, although they were only marginally significant due to the available sample size.

Our results illustrate a functional landscape with human settlements as dispersal hotspots, while the findings along the drove road confirm its role as a pollinator reservoir observed in other studies. Drove roads seem also to function as linear structures that facilitate long-distance dispersal across the agricultural matrix, while local *P. lagopus* populations depend rather on short-distance seed dispersal. These results highlight the role of herbivore corridors for conserving the migration capacity of plants and contribute towards understanding the role of seed dispersal and the spread of invasive species related to human activities. The coupling of traditional pastoralist practices with the phenology of plants and pollinators raises concerns on the environmental effects of current global land use change.

This paper is based on García-Fernández et al. (2019).

Introduction

Increased habitat fragmentation is a major worldwide threat for ecosystems and biodiversity (Fahrig 2003), leading to genetic drift and reduction in within-population genetic diversity. Inbreeding depression impacts biodiversity conservation (Ouborg et al. 2006) or ecosystem productivity (Crutsinger et al. 2006). Measures to connectivity between isolated vegetation patches include boosting dispersal, a key element for reducing extinction risk, and is subjected to strong selective pressures (Cheptou et al. 2017). Large wild herbivores functionally disappearing from ecosystems (Bar-On et al 2018), livestock seed dispersal is a cheap and effective management tool with complementary modes of dispersal that leads to an almost complete representation of the grassland community.

Corridors for mobile livestock can increase multifunctionality of the landscape by increasing landscape heterogeneity at the large scale, translated into higher biodiversity and maintenance of pollination services (Odhiambo and Manzano 2021). But does the proven capacity of livestock in achieving long-distance dispersal translate into effective and determinant vector for gene flow across the landscape? Considering the similarities of corridors used by ancient wild migratory herbivores and livestock mobility routes maintained during centuries (Manzano Baena & Casas 2010) this question is very relevant to understand whether widespread mobile pastoralism can substitute the ecological functions of wildlife.

Livestock mobility corridors area also reported to harbor a significant pollinator community in fragmented agricultural landscapes they cross, which is also a relevant element in the current pollinator crisis in high-income countries (Hevia et al 2016). The effect of either keeping them in use or leaving them just as a landscape element is also key to understand the relevance of mobile pastoralism for ecological functionality.

Methods and Study Site

This study was conducted in the Conquense Drove Road (CDR), one of the major Spanish road droves (ca. 410 km long) that are still used for transhumant sheep and cattle herds that move every year from the cooler and wetter mountains of Teruel, Cuenca and Guadalajara provinces to the wintering dehesas in Sierra Morena at lower altitude (Oteros-Rozas et al. 2012). The area is located between Quintanar de la Orden, Tomelloso and Villarrobledo municipalities, on a plateau (830-900 meters a.s.l.) of sandstones, loams and clay materials under continental Mediterranean climate, with a mean annual rainfall of about 500mm and severe summer droughts. The vegetation is a mosaic of agricultural dry cereal and sunflower croplands, abandoned fields and dry grasslands used by local flocks. Herds still cross the study area twice a year, timing their transit at two productivity peaks in May and October (Manzano-Baena and Casas 2010). Their numbers are significantly lower than they have historically been, shrinking from about half a million heads in the 16th and 17th centuries to ca. 9000 heads of sheep and 1,200 heads of cattle nowadays (Bacaicoa Salaverri et al. 1993). Resident livestock, historically much more irrelevant, are currently relatively common in the landscape. They are kept at stables in urban settlements at night and graze grassland patches that are spread across the landscape. Drove roads tend to avoid urban settlements and run tangentially, so resident livestock do little use of them because of the rather radial pattern of land use, with urban settlements in the center.

For this study we selected *Plantago lagopus* L., an abundant annual or biennial forb that is self-compatible, with both wind and insects as major pollination agents (Sharma et al. 1993). It is estimated that a typical herd of 1,000 sheep would disperse ca. 2 million seeds per transhumance day in spring, or 50,000 seeds in autumn. Such large dispersal, along with the faster dynamics in annual plants (overlapping generations in perennial plants may disturb some genetic descriptors due to the mixture of genotypes), make them particularly suited to test genetic signals of dispersal in fragmented scenarios (Ewers & Didham 2006). Using specifically developed microsatellites, we compared genetic diversity and inbreeding coefficients of 6 *P. lagopus* populations along the drove road with 7 populations in the surrounding agricultural matrix, at varying distances from human settlements

Results

Landscape factors governing genetic descriptors in P. lagopus populations

For two genetic factors analyzed (F_{IS} or inbreeding coefficient, as a measure of inbreeding depression; and A_r , or rarefacted allelic richness, as a measure of genetic diversity), the geographic variables showed a measurable effect. The distance to the nearest settlement had an impact on both inbreeding (F_{IS}) and genetic diversity (A_r ; Table 1), as had the interaction with population position (either in the livestock corridor or in the agricultural matrix) – although it was only marginally significant in the case of genetic diversity.

Genetic descriptors		Coefficient estimate	<i>p</i>	model's AICc
F_{IS}	$\chi^2_5 = 20.82$, $R^2 = 26\%$, Gaussian spatial covariance structure.		0.001	-37.1
	Intercept	0.139 (0.028)		
	Distance to settlement	0.015 (0.032)	<0.0001	
	Position (drove road)	-0.015 (0.025)	0.280	
	Grassland cover	0.037 (0.009)	<0.0001	
	Distance x Position	-0.106 (0.037)	0.005	
A_r	$\chi^2_4 = 10.51$, $R^2 = 72\%$, Gaussian spatial covariance structure.		0.033	47.7
	Intercept	8.056 (0.459)		
	Distance to settlement	-1.724 (0.548)	0.006	
	Position (drove road)	1.254 (0.666)	0.076	

	Distance x Position	1.282 (0.705)	0.070	
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Table 1. Results of linear modeling of the inbreeding depression (F_{IS}), and rarefacted allelic richness (A_r) on landscape factors. Source: <https://doi.org/10.7717/peerj.7311/table-4>

Inbreeding (F_{IS}) increased with distance from human settlements in the agricultural matrix but followed the opposite trend in drove road populations (Fig. 1a). The presence of nearby grasslands also proved to be a significant factor, showing higher rates of inbreeding at higher grassland cover (Table 1).

Genetic diversity (A_r) was negatively related with the distance to settlements, A_r values between matrix and drove road positions showed a pattern of convergence at short distances and divergence at high distances from human settlements, with the agricultural matrix then showing less diversity (Figure 1b).

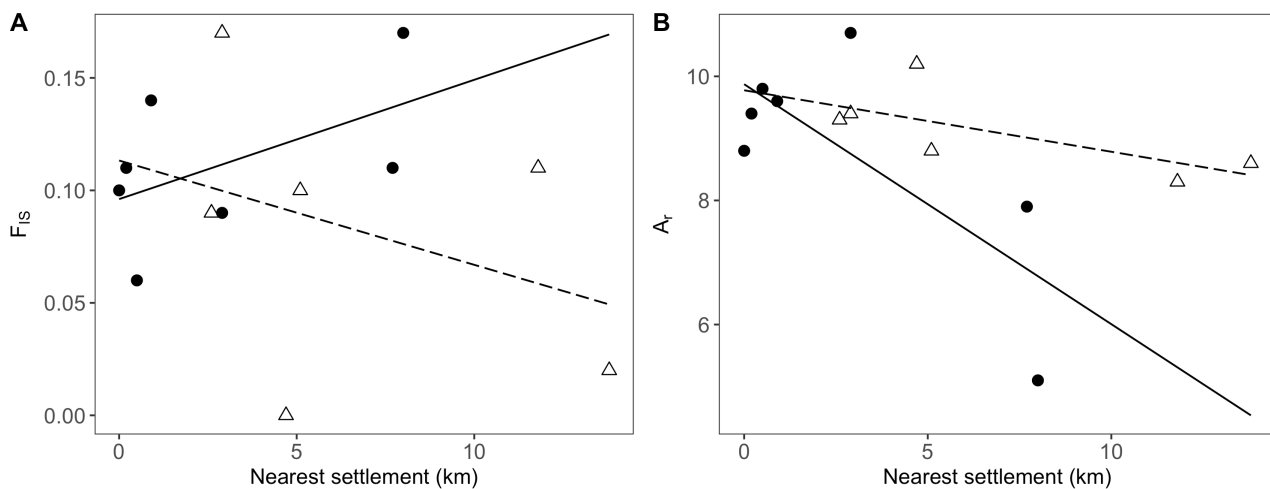


Figure 1. Linear regressions between distance to closest settlement for populations in the agricultural matrix (solid circles and solid line) and in the drove road (open triangles and dashed line), and genetic descriptors: (A) F_{IS} for inbreeding and (B) A_r for genetic diversity. Source: <https://doi.org/10.7717/peerj.7311/fig-4>

Interpretation of genetic results

Proximity to human settlements drives the hotspots for genetic diversity (A_r) in this landscape (Fig. 1b). The loss in genetic diversity with increasing distance to human settlements is weaker at drove roads (statistically marginally significant), mediated by the intense seed dispersal processes taking place. Drove roads seem therefore to function as linear structures that facilitate long-distance dispersal across the agricultural matrix, while the local *P. lagopus* populations situated in the agricultural matrix depend rather on short-distance seed dispersal for the recruitment of new individuals.

Drove roads were able to invert the inbreeding (F_{IS}) that otherwise appears in distant populations from the agricultural matrix (Fig. 1a). The smaller selfing coefficient and the reduced influence over F_{IS} observed along the drove road indicates a relevant role played by them in providing pollination services. This relationship is even clearer after controlling for landscape effects, namely the presence of grassland patches in the vicinity of the studied plant populations that could harbor further pollinators. The negative relationship observed between the presence of such patches and the pollinators, mirrors the results of Rico et al (2014b). The explanation could rely on the flowering plants on such patches being continuously grazed during the whole spring by resident sheep flocks. Meanwhile, the transhumant herds graze on the drove road only at the end of the spring, following a “green wave” when the plants have already grained, relatively untouched during the flowering phase. While a greater coefficient of inbreeding is a genetic indicator that can be related to pollinator limitation (Turner et al 1982, Van Etten et al. 2015), the structural role of drove roads as grassland corridors crossing agricultural landscapes has been proved to be determinant in supporting pollinator services (Hevia et al. 2016), which our study confirms. This result goes along other studies that have observed provision of heterogeneity at the landscape level because of the drove road’s structural role, translated in higher biodiversity levels (Azcarate et al. 2013, Hevia et al. 2013).

Implications

The consistent effect of human settlements on genetic diversity and inbreeding results in a functional landscape of settled, high human density areas being hotspots of dispersal that modulate the genetic patterns of diversity, probably mediated by commercial livestock exchanges but also by other dispersal types, mainly

human-mediated (Wichmann et al. 2009). The *P. lagopus* populations on the drove road don't show to be affected by these types of dispersal, likely because their human use is much diluted and human activities are comparatively simplified and less dense, consisting just in accompanying or herding livestock. This confirms the role of human activities in the spread of invasive species, while moderate seed dispersal processes as the ones mediated by mobile livestock would modulate the necessary spread to avoid genetic depauperation.

The positive role of mobile pastoralism for pollinators, with movements that are coupled with the phenology of both plants and pollinators, highlights possible causes of pollinator decline in Europe. Even measures designed to comply with agri-environmental schemes are damaging to pollinators because of the lack of adaptation to such rhythms (Tanis et al 2020). This could be a further outcome of the co-evolution of the European flora among now disappeared migratory megaherbivores (Vera 2000). A derived disruption of dispersal processes and the structural role for pollinators played by corridors themselves may further contribute to a generalized grassland biodiversity crisis motivated by land use intensification (Gossner et al. 2016) and climate change – and on the latter, a potential decoupling of herbivore “green wave” movements from the phenology and seed availability brings also concerns (Berg et al. 2010). Mobile pastoralism can be a powerful, adaptive tool to prevent such crises.

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