



The landscapes of livestock diversity: grazing local breeds as a proxy for domesticated species adaptation to the environment

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Abstract

Context Domesticated animals play a central role in agricultural landscapes. However, livestock has been scarcely studied from a spatial perspective. Mapping of livestock diversity has been limited by the lack of distribution and demography data. This shortfall limits both the reach of actions aimed to conserve threatened breeds and their consideration as a tool for improving sustainability in livestock landscapes.

Objectives To analyse environmental drivers of local grazing livestock breed—those autochthonous to a specific region—distributions and delineate livestock ecoregions, i.e. areas where certain groups of breeds exhibit similar response to environmental factors in their distribution.

Methods We used non-metric multidimensional scaling and hierarchical clustering to explore the distribution of the areas of origin of 119 local livestock breeds of the bovine, ovine, caprine, equine and asinine species. In addition, we performed randomisations and preference index to establish livestock ecoregions.

Results Our results show contrasting spatial distributions of grazing local breeds across the studied species, explained by environmental factors. The distribution of cattle breeds is determined by the temperate influence of Atlantic Ocean, while sheep breeds are related to more continental climates, especially to those of the central Iberian plateau. Goat breeds are associated with limiting factors in the context of the Mediterranean climate, such as the seasonality of precipitation, and equine breeds are adapted to particular regions, reaching areas at the environmental extremes. The partitioning of the geographic and environmental space is reflected in the livestock ecoregions.

Conclusions Livestock intraspecific diversity has acted as an adaptive response of domesticated grazing animals to specific environmental conditions. Our delineation of livestock ecoregions could aid

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to move towards more sustainable agricultural and livestock landscapes and help in the conservation of agrobiodiversity.

Keywords Agrobiodiversity · Domesticated animal · Livestock ecoregion · Livestock landscapes · Spanish local breed

Introduction

Agrobiodiversity is an essential component of agricultural landscapes that underpins agricultural production and contributes to their sustainability. Domesticated herbivores contribute to determine plant structure and composition, to canalize energy flows and nutrient cycles, and strongly influence community dynamics, affecting interactions and fostering landscape complexity (Gliessman 2014). In general, livestock diversity is a key element of food security and rural development (FAO 2015a, 2018). Livestock breeds are considered the genetic management and conservation units of livestock diversity (FAO 2007a; Feliu et al. 2015). However, livestock breed diversity is largely threatened. For example, the 27% of the catalogued local livestock breeds worldwide are endangered and 65% have an unknown status (FAO 2020).

Although the value of the local breeds is largely recognised and there is global concern for their conservation (Interlaken Declaration 2007; World Bank 2009), local breeds have been less studied than those highly productive overall (Hoffmann 2013). Furthermore, the mechanisms involved in their adaptation remain scarcely known (Boettcher et al. 2014), despite the efforts done during recent decades in that direction (Ajmone-Marsan et al. 2011; Blackburn et al. 2017a; Mdladla et al. 2017). Most research on this topic focuses on genetics and productivity perspectives, neglecting ecological and geographical perspectives. Nevertheless, environmental factors and spatial heterogeneity have underpinned and mediated breed adaptation (Larson and Fuller 2014; Bertolini et al. 2018). Furthermore, environmental factors are also decisive to generate diversity in livestock systems, and to structure livestock production (Hoffmann 2011) and landscapes, especially in the case of extensively-managed domesticated herbivores. Studying grazing livestock

breed distributions could help to improve knowledge in adaptation mechanisms, focus conservation efforts, improve sustainability of livestock landscapes or enhance climate change mitigation strategies (Hoffmann 2010, 2011; Pelletier and Tyedmers 2010; Robinson et al. 2011; Velado-Alonso et al. 2020).

Besides that, understanding the distribution of livestock diversity is essential for the sustainable management of agricultural landscapes and the conservation of livestock breeds (FAO 2007a). Nevertheless, mapping of livestock systems worldwide has been very limited as information is generally unavailable (FAO 2007b; Robinson et al. 2011). Current mapping approaches are either aimed at modelling livestock species abundance (Robinson et al. 2014), or at quantifying suitability of foreign breeds in new agro-climatic areas (Lozano-Jaramillo et al. 2018). However, these studies do not include an extensive analysis of livestock agrobiodiversity and its significance. Lack of spatially explicit information on extensive livestock uses limits (i) the sustainable management of agricultural systems, i.e. boosting rational use of local resources benefitting from livestock adaptive ability, (ii) the correct assessment of their global change impacts, and (iii) the definition of conservation priority areas (FAO 2015b), and strategies for both wild and domesticated biodiversity.

The present work analyses distributional patterns of a selected group of grazing livestock species in a structurally diverse territory (Peninsular Spain). The objective is twofold. First, to explore the spatial patterns of grazing breeds, as a proxy for their adaptive ability. This analysis is based on the areas of origin of 119 local (those autochthonous of a specific region) livestock breeds, of bovine, ovine, caprine, asinine and equine species, in relation to different environmental factors. We expect marked, non-random, contrasting distribution patterns across studied species related to environmental heterogeneity (Leroy et al. 2016) and species adaptive ability and requirements. Second, we aim to map the key ecological regions based on the relationship among local breeds and environmental factors within a territorial sector. This proposal could serve as a basis for the identification of livestock ecoregions and the sustainable management of livestock landscapes.

Material and methods

Distribution data: local livestock breeds in Peninsular Spain

The studied area is Peninsular Spain, a territory that hosts a significant agrobiodiversity associated with the heterogeneity of cultures and landscapes, especially influenced by the historical importance of livestock uses (Gómez-Sal 2017). In the study, we included all local breeds, i.e. autochthonous, from the bovine, ovine, caprine, asinine and equine species in mainland Spain. We have selected those livestock species that are grazers and browser herbivores, and have been traditionally bred in extensive livestock systems, given their particular importance in the functioning of agroecosystems. This has led us to exclude swine breeds, despite their importance in some extensive silvopastoral systems in Spain (such as Dehesa landscapes), as these breeds mostly take advantage of acorn production in their specific season. To identify these local breeds, we used two different sources of information. First, we used the Official Catalogue of Livestock Breeds (MAPA 2019), including all currently recognised local breeds of peninsular Spain. Second, to identify those currently extinct, as the Spanish Official Catalogue does not account for breed extinctions, we selected those breeds detailed as extinct in the FAO Domesticated Animal Diversity-Information System (2017), also mentioned in the Spanish breed literature (supplementary material (SM) Appendix 1, Table S1). They represent a total of 119 breeds: 44 bovine, 38 ovine, 19 caprine and 18 equines (SM Appendix 1, Table S2).

To determine the geographic distribution of each breed, we identified their area of origin through a literature review of the main Spanish breed catalogues (SM Appendix 1, Table S1 for more detail). We considered as area of origin those zones where the breed was first described—claimed as original areas, and when that was not clear, we assigned the oldest region of distribution (Marsoner et al. 2018). We assume that breeds' areas of origin represent the historical and natural domain of the local breeds, and approximately represent the areas where each breed was located before the agricultural industrialization—i.e. when livestock systems, and thus local breeds, were mostly based on local resources and related to local environments. In this definition neither production

objectives nor traditional practices have been taken into consideration since they were not explicitly mentioned in the historical catalogues regarding areas of origin. Although transhumance practices have shown to be rather important in determining the adaptation of Mediterranean breeds (Serranito et al. 2021), our areas of origin cannot explicitly incorporate these practices due to data inexistence. Nevertheless, based on the distribution of the areas of origin we use, it is safe to assume that they encompass: the wintering areas of latitudinal transhumance systems, i.e. those areas where livestock breeds stayed the longest—generally periods of approximately 8 months—or the whole range in the case of altitudinal transhumance systems. Areas of origin were then digitally mapped (Fig. 1) using QGIS 2.18.26 “Las Palmas” software (QGIS Development Team 2017), employing as reference basis: digital land model, rivers and river basins layer, agricultural provinces, and administrative divisions of municipalities and provinces map.

Environmental variables

To analyse the relationships between breed diversity and landscapes, a set of environmental factors which represent climate, topography, lithology, vegetation type and primary production were selected. A total of 24 variables were chosen (Table 1), extracted at a resolution of circa 10 × 10 km.

The climate variables were obtained from the 30 s layer of WorldClim version 2 (Fick and Hijmans 2017). The coefficients of variation in precipitation were calculated using the database Spanish PRECipitation At Daily Scale (SPREAD) (Serrano-Notivol et al. 2017). The topographic variables were obtained based on the GTOPO30 digital model of the land (LP DAAC 2004). The lithology was based on the 1995 Geological Map of Spain at a scale of 1:1,000,000 (Alvaro et al. 2010). The potential net primary production was calculated based on the Enhanced Vegetation Index (satellite-derived Ecosystem Functional Attributes) (Alcaraz-Segura et al. 2006, 2009) on the basis of the Global MOD13Q1 for 2001–2017 and the type of vegetation was derived from the Spanish Forestry Map at a scale of 1:50,000 (MFE50 2013). Lastly, the bioclimatic types were obtained from Rivas-Martínez (1987).

All continuous variables were discretised into types according to the probability range of each

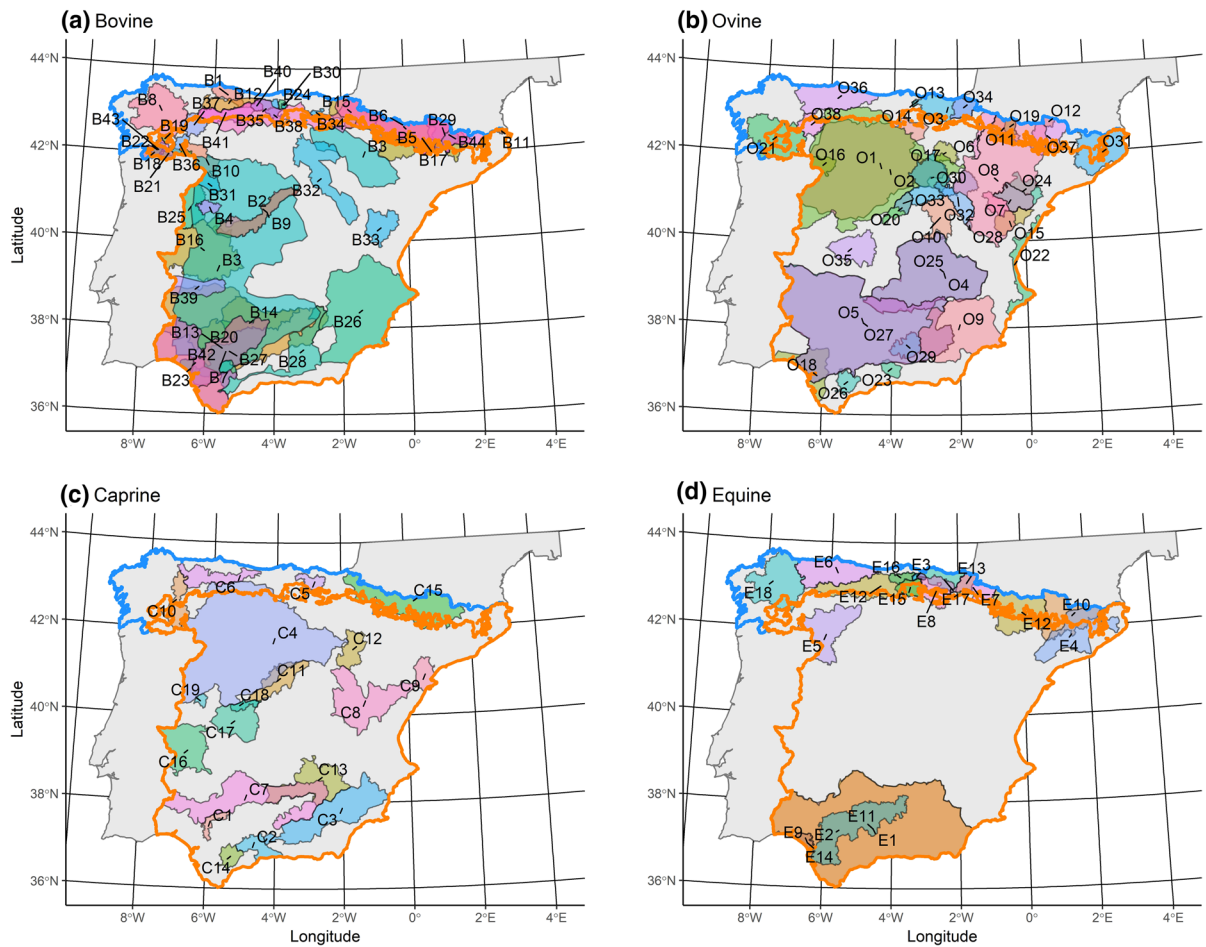


Fig. 1 Areas of origin of the 119 local livestock breeds for the domesticated species: bovine (a), ovine (b) caprine (c) and equine -including both horses and donkeys (d). Codes identifying each breed are shown using the capital letters B (bovine),

O (ovine), C (caprine) and E (equine) followed by a number (see Supplementary Materials, Appendix 1, Table S2 for details). The Atlantic and Mediterranean regions are delineated by a coloured line (Atlantic in blue, Mediterranean in orange)

variable (Morales-Castilla et al. 2013). The first and last type quantile range was determined to differentiate the most extreme values, and the rest of types were divided proportionally (SM, Appendix 1, Table S3). For the variables of a qualitative nature, simplified types were established grouping the categories described by the reference layer (SM, Tables S4, S5 and S6). Lastly, a contingency table was drawn up with the surface area occupied by each environmental variable type for each area of origin of the 119 analysed local breeds. We assume that these variables generally represent long-lasting environmental gradients along the studied territory at the broad scale adopted. Specifically, the assumption is that while we

acknowledge that some variables may have undergone shifts since livestock breed's areas of origin were defined, major temperature, moisture, and productivity gradients across Iberian Peninsula would hold.

Statistical analysis and mapping of the livestock ecoregions

Initially, hierarchical analyses were conducted to identify the main groups of local breeds, based on their response to environmental variation using the Kulczynski distances index, which ignores double absence, and Ward's grouping criteria (1963). To identify the main patterns linked to the distribution

Table 1 List of environmental variables

Environmental variable	Description	Unit
Annual mean temperature	Year average of monthly temperatures for the 1970–2000 period; indicator of energy received by the ecosystem annually	°C
Isothermality	Oscillation of annual temperature; indicator of oceanity-continentality. Quotient between the average of the monthly and the annual temperature ranges for the 1970–2000 period	%
Temperature seasonality	Temperature oscillation throughout year. Ratio of standard deviation of monthly mean temperature for the 1970–2000 period	°C
Temperature annual range	Temperature range throughout year. Subtraction of minimum temperature of coldest month from maximum temperature of warmest month for the 1970–2000 period	°C
Mean temperature of warmest quarter	Warm seasonal effect. Average temperatures for the 13 consecutive warmer weeks for the 1970–2000 period	°C
Mean temperature of coldest quarter	Cold seasonal effect. Average temperatures for the 13 consecutive cooler weeks for the 1970–2000 period	°C
Annual mean precipitation	Water input in the ecosystem. Sum of the monthly average rainfall for the 1970–2000 period	mm
Precipitation seasonality	Variation of precipitation throughout year. Coefficient of variation of precipitation for the 1970–2000 period	%
Precipitation of the wettest quarter	Precipitation that prevails during the wettest quarter. Precipitation average of the 13 consecutive wettest weeks for the 1970–2000 period	mm
Precipitation of the driest quarter	Precipitation that prevails during the driest quarter. Precipitation average for the 13 consecutive driest weeks for the 1970–2000 period	mm
Altitude	Vertical distance from sea level	masl
Slope	Inclination, with respect to the horizontal, of a slope. Calculated according to the Fleming and Hoffer algorithm, which works best for smoothed surfaces	°
Interannual precipitation variation	Interannual precipitation randomness. Precipitation coefficient of variation for the 1950–2012 period	
Inter-winter precipitation variation	Inter-winter precipitation randomness. Coefficient of precipitation variation for the months of January, February and March for the 1950–2012 period	
Inter-spring precipitation variation	Inter-spring precipitation randomness. Coefficient of precipitation variation for the months of April, May and June for the 1950–2012 period	
Inter-summer precipitation variation	Inter-summer precipitation randomness. Coefficient of precipitation variation for the months of July, August and September for the 1950–2012 period	
Inter-autumn precipitation variation	Inter-autumn precipitation randomness. Coefficient of precipitation variation for the months of October, November and December for the 1950–2012 period	
Mean vegetation productivity	Average of Enhanced Vegetation Index—optimized index of plant productivity for large areas with large biomass differences—for the 2001–2017 period	
Seasonal vegetation productivity	Standard deviation of Enhanced Vegetation Index—optimized index of plant productivity for large areas with large biomass differences—for the 2001–2017 period	
Maximum vegetation productivity	Maximum deviation of Enhanced Vegetation Index -optimized index of plant productivity for large areas with large biomass differences- for the 2001–2017 period	
Minimum vegetation productivity	Minimum of Enhanced Vegetation Index—optimized index of plant productivity for large areas with large biomass differences—for the 2001–2017 period	

Table 1 (continued)

Environmental variable	Description	Unit
Lithology	Specific name of the lithology class in the centroid of the mesh from the Geological Map of the Iberian Peninsula, Balearic and Canary Islands at scale 1: 1.000.000, year 1.994	Lithology type
Vegetation type	Tree formation type, obtained for the centroid of the grid and the type of land use (TIPESTR) in the absence of forest mass from the Forestry Map of Spain at scale 1: 50,000 (MFE50), updated to 2013	Tree formation type
Bioclimatology	Bioclimatic type at the centroid of the grid from Rivas Martínez, 1987	Bioclimatic type

of local breeds in the peninsula, multivariate ordinations were compiled separately for the different domesticated species analysed, using Non-Metric Multidimensional Scaling (NMDS) (Kruskal 1964) as a statistical tool. Stress value was considered to measure the validity of NMDS configuration (Clarke 1993). This technique facilitates visualization of data with broad spatial heterogeneity in the distribution of abundance (Clarke 1993)—in this case represented by the number of cells occupied by a type of a given variable within the area of origin of each breed. Hellinger’s standardisation was used due to its versatility regarding the species abundance paradox and maximisation in relation to distances in geographic gradients (Legendre and Gallagher 2001).

Lastly, the relationships between each group of local breeds and the environmental variable types most represented in the territory that each group occupies were examined. To establish the presence of a specific variable type beyond randomly expected, a randomisation procedure was implemented. One thousand randomisations were performed for all groups of breeds and environmental variable types, which can be considered as a distribution of null models from which to determine those types that are preferred. Types that showed a $P=0.99$ probability of being chosen were selected. Additionally, a preference index was used with the quotient between the observed variable—rate of the area occupied by a variable type compared to the set of types for the same variable by a specific group of breeds, compared to that expected—rate of the area occupied by a variable type for a specific group compared to the set of types of said variable for the whole species. Lastly, the livestock ecoregions were established in territories in which at least 50% of the preferred types by each group of local breeds co-occur.

All of the analyses were completed in R software (R Core Team 2018), using the “vegan” (Oksanen et al. 2017) package to process data, the “raster” (Hijmans 2018) and “letsR” (Vilela and Villalobos 2015) packages to map livestock distributions and ecoregions and “ggplot2” (Wickham 2016) and “tmap” (Tennekes 2018) for graphic representation.

Results

The studied domesticated species showed markedly different spatial distributions and associations with ecological factors. Intraspecific diversity of livestock did not vary along the same environmental clines for all species (Fig. 2). Instead, breed diversity for each species differentially responded to specific environmental axes.

Bovine breeds were more diverse in the western half of peninsular Spain (Fig. 1a). Six groups were identified according to the results of the cluster analysis (SM, Appendix 2, Figure S5), with three differentiated groups in the Atlantic area (a subregion of the Eurosiberian bioclimatic region) and other three groups in the Mediterranean bioclimatic region. This is also reflected in the NMDS ordination (stress=0.12) with Atlantic bovine breed groups mainly located along the positive abscises and Mediterranean groups along the negative abscises (Fig. 2a). Annual precipitation and temperature seasonality marked bovine breed distribution over space (Fig. 2a), with an observed greater richness of breeds increasing with the Atlantic Ocean influence (Fig. 1a). Differences were found between those breeds that are typical of more regulated climates, with the variation in temperature buffered by humidity (e. g. Fig. 2a, green and blue polygons), compared to those that admit greater seasonal thermal variation

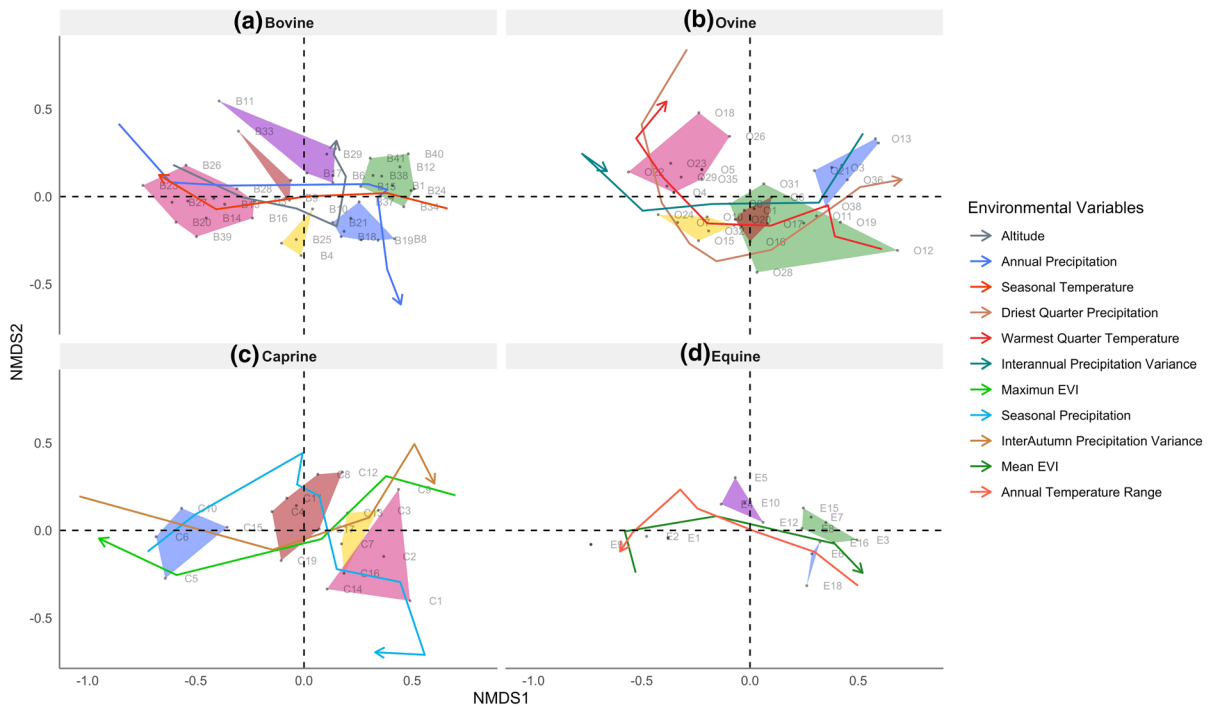


Fig. 2 NMDS Ordination of peninsular Spain local livestock breeds of four domesticated species: bovine (a), ovine (b) caprine (c) and equine (d)-including both horses and donkeys-; stress: a=0.12, b=0.12, c=0.09, d=0.05. Arrows represent a summary of the gradients of environmental variables (see legend) from lower to higher values (Supplementary Material, Appendix 2 Figures S1–S4 for more detail about environmen-

tal gradients). Codes identifying each breed are shown using the capital letters B (bovine), O (ovine), C (caprine) and E (equine) followed by a number (see Supplementary Materials, Appendix 1, Table S1 for details). The coloured polygons represent the breed groups obtained through hierarchical cluster (see also Supplementary Material, Appendix 2 Figures S5–S8)

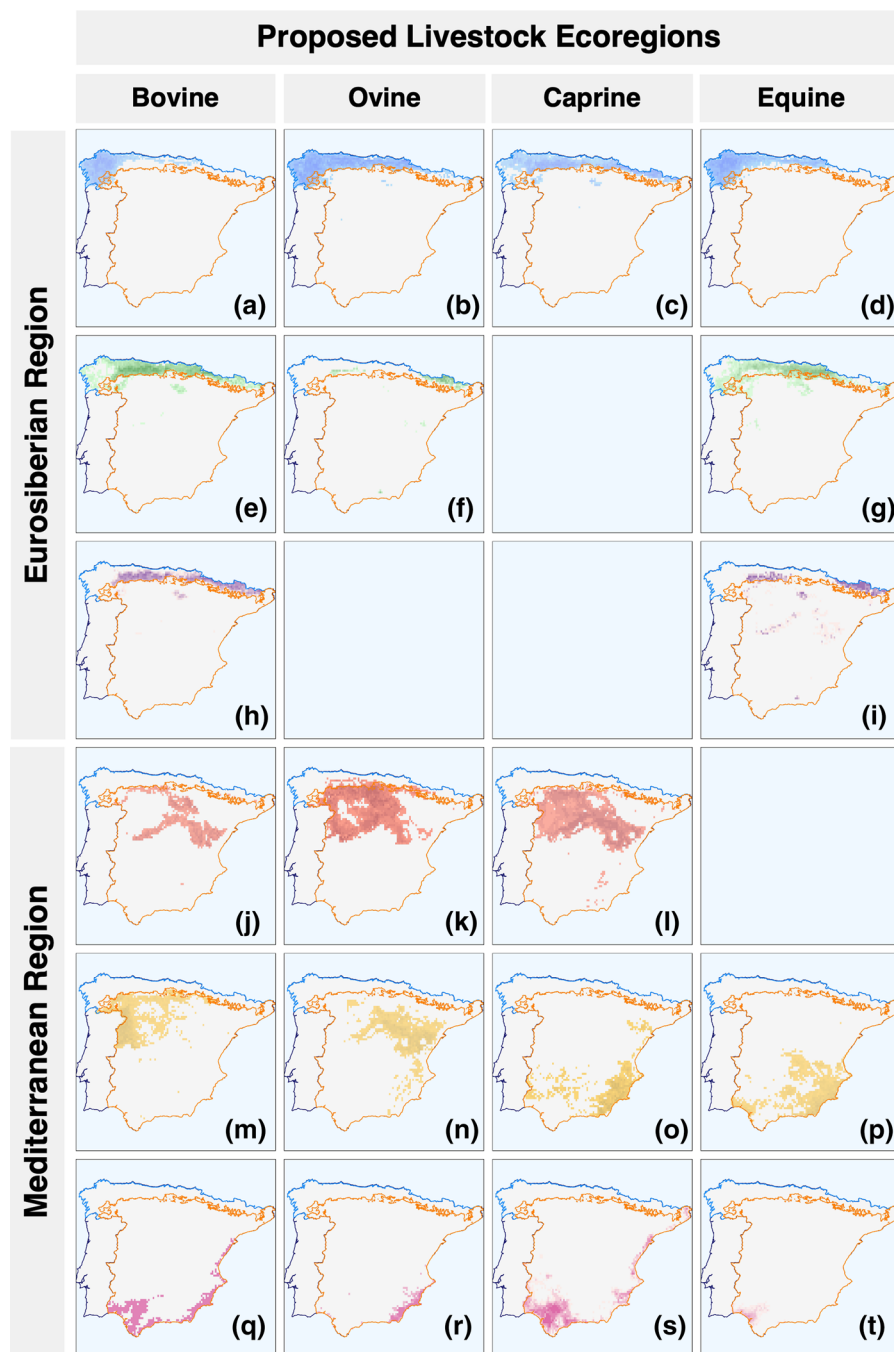
(e.g. Figure 2a, pink polygon). Altitude also constrained bovine diversity by separating breeds associated with mountain areas in the mid-north peninsula (Fig. 2a, polygon blue from green), or those typical of South-western low plains from those of the central plateau (Fig. 2a, polygon pink from yellow) (consult SM Appendix 2, Figures S1 for more details about environmental gradients).

Ovine breeds showed preference for the Continental-Mediterranean climates found in the central Iberian plateau (Fig. 1b). The classification identified five main ovine breed groups (SM Appendix 2, Figure S6), of which only one was strictly associated with the Atlantic area (Fig. 2b, blue polygon) and another with mountain areas of both Euro-Siberian and Mediterranean climates (Fig. 2b, green polygon). The general distribution of ovine livestock would reflect the species adaptation to continental environments, as precipitation of the driest quarter, temperature of

the warmest quarter and the randomness of precipitation between years reflected the main environmental drivers (Fig. 2b, NMDS stress=0.12). Ovine breeds benefited from the heterogeneity of Mediterranean ecosystems in the peninsula, especially the continental portion, although being distributed from the rigorous central mountain ranges, to thermal coastal areas or mountain areas of the mid Southern-eastern peninsula (Figs. 1b, 3k, n, r), (consult SM Appendix 2, Figures S2 for more details).

Caprine livestock comprised fewer breeds (n=19) than ovine and bovine species (n=44 and n=38, respectively). Even so, we identified four groups (SM Appendix 2, Figure S7), three of which were Mediterranean (Fig. 2c, red, yellow and pink polygons) and one Eurosiberian (Fig. 2c blue polygon). Caprine breed distribution was more dispersed (Fig. 1c), constrained by the seasonal limitations in resource availability characteristic of Mediterranean ecosystems

Fig. 3 Livestock ecoregions maps representing those geographic regions where the environmental conditions correspond to the variable types associated to each grouping of local breeds—at least 50% of the preferred types (see Supplementary Materials, Appendix 2, Figures S9–S12). Livestock ecoregions are distributed in three Eurosiberian sub-regions: blue (a–d), green (e–g) and purple (h, i); and three Mediterranean sub-regions: red (j–l), yellow (m–p) and pink (q–t) for domestic bovine (a, e, h, j, m, q), ovine (b, f, k, n, r) caprine (c, l, o, s), equine and asinine species, both included in equine (d, g, i, p, t). The overall colour scheme used for each group mirrors that of the hierarchical cluster groupings in Fig. 2, with darker shades of each colour indicating a higher proportion of environmental variables types selected in each pixel. The Atlantic and Mediterranean regions are delineated by a coloured line (Atlantic in blue, Mediterranean in orange)



and the adaptive ability of goats to benefit from woody species in heterogeneous environments as the Mediterranean mountains. Gradients marked by environmental variables such as the seasonality of precipitation, the maximum potential productivity of vegetation and the randomness of interannual precipitation in the autumn months stand out (Fig. 2c,

NMDS stress=0.09, consult SM Appendix 2, Figures S3 for more details).

Since there were low numbers of equine breeds, horses (14) and donkeys (4) were analysed together. Most of the local equines were distributed in the Atlantic (Eurosiberian) bioclimatic region (Fig. 1d). Five groups were identified (SM Appendix 2, Figure

S8), though some of them are integrated by a small number of local breeds. Some environmental drivers related to the distribution of these local breeds were annual temperature range and vegetation productivity (Fig. 2d, NMDS stress=0.05). They led to a marked differentiated distribution at the extremes of both Atlantic and Mediterranean zones (Fig. 1d), and a selective utilization of the contrasted environments of the northern and southern slopes of the Cantabrian Mountain Range, which marks the separation between both biogeographic regions (Fig. 2d, difference between blue, green and purple polygons gradient), consult SM Appendix 2, Figures S4 for more details).

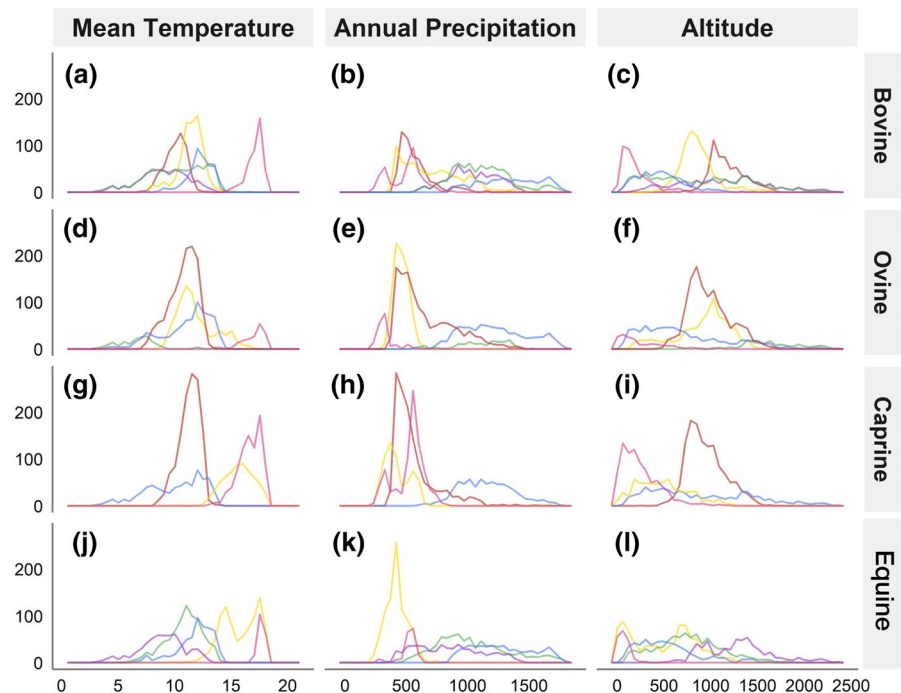
The livestock ecoregions of peninsular Spain (Fig. 3) also showed how the analysed species differ in their patterns of land occupation (Fig. 1). Cattle and sheep had the most continuous distribution areas, reflecting adaptations to a wide variety of environmental possibilities (Fig. 3 Bovine, Ovine). On the contrary goats and equine (horses and donkeys) breeds had more disperse and specialised distributions, but still included a wide range of environmental heterogeneity, reaching areas at the environmental extremes (Fig. 3 Caprine, Equines). Overall, livestock ecoregions were robust to spatial projections using

either 25% or 75% of the types preferred by each group of breeds co-occur (see Supporting Materials Appendix 2, Figures S9–S12).

Bovine livestock ecoregions predominated in the Atlantic area, characterised by vegetation of temperate and humid areas, with average annual precipitation greater than 1000 mm for 3 of the livestock ecoregions detected, encompassing the heterogeneity of the Atlantic bioclimatic types (Figs 3, a, e, h, 4a–c). In the Mediterranean bioclimatic area, bovine ecoregions differentiated the contrast between the higher areas of the inland plateaus and the warm plains of the Guadalquivir basin at the southwestern (Fig. 3j, m, q). The ovine local breeds showed a great capacity to occupy the different productive options present in the territory, although they displayed a preference for the Mediterranean climate and within this the continental variants, steppe plains and medium mountain areas (Fig. 3k, n). Ovine ecoregions showed greater distribution in dry and elevated areas, having fluctuating climatic conditions (Fig. 4d–f), however Atlantic zones are also represented (Fig. 3b), including mountainous areas (Fig. 3f) in a smaller extension.

Caprine livestock was associated more with areas that have lower precipitation and altitude; three out of four ecoregions (Figs. 3l, o, s), were in areas with

Fig. 4 Distribution range of each group of local breeds (see Supporting Materials, Appendix 2, Figures S9–S12), by domesticated species: bovine (a–c), ovine (d–f), caprine (g–i), equine (both horse and donkey), j–l represented by the frequency of pixels for the variables: annual mean temperature (°C), annual mean precipitation (mm) and altitude (masl). The colour lines used for each group mirrors that of the hierarchical cluster groupings showed in Figs. 2 and 3



annual mean precipitation of less than 500 mm and an altitude of less than 500 masl (Fig. 4g–i). The dispersed distribution of goat breeds (Fig. 1) indicates their adaptive flexibility to make the most of low nutritional quality resources in specific areas that are very different within their climatic environment, preferably warm and dry in the Iberian Peninsula (Fig. 3l, o, s), but also in transition to low altitude and mountainous Atlantic areas (Fig. 3c). Lastly, the groups obtained for equines showed a very wide adaptive range of adaptation and ability to occupy extreme areas, both in the northern, Atlantic mountain areas and the inland high moorlands (Fig. 3d, g, i) and in the southern, hot and humid low plains (Fig. 3p, t). For more details on the physical characteristics of the different livestock ecoregions, see Fig. 4.

Discussion

Livestock distributional patterns of analysed species suggest that historical livestock activity, combining the artificial selection of local breeds with their original adaptive ability to different environmental conditions, has partitioned the geographic space and enhanced intraspecific diversity. This reflects the differentiated adaptive ability of these livestock species and their potential contribution to promote original agricultural landscapes. Moreover, the distribution of local breed diversity shows marked differences between species, coinciding with the different distribution ranges of wild progenitor species based on archaeological evidences (Larson and Fuller 2014). Despite the aforementioned, most of the selection indicators identified in livestock genetic studies are associated to productivity-related traits or morphological standards (Rothhammer et al. 2013), usually studied in modern intensive breeds, while environmental selection factors acting at the genetic level have been scarcely studied in local breeds (Lv et al. 2014; Xu et al. 2015; Bertolini et al. 2018), neither from an ecological perspective. Nor has them been studied from the perspective of improving agricultural landscapes' sustainability.

In general, the spatial distribution of local grazing livestock breeds shows a tendency to occupy landscapes that are ecologically limiting in terms of primary productivity. This is consistent with the results presented by Milla et al. (2018) who studied

phylogenetic patterns of domesticated species and showed that domestic mammals belong to clades adapted to moderately productive environments. It also concurs with results by Velado-Alonso et al. (2020) who discussed intraspecific diversification of domesticated animals due to adaptation to new and challenging environmental conditions experienced historically (but not currently). The distribution of livestock ecoregions is determined by in danger of extinction breeds, and can be interpreted based on the ability of domesticated species to maximise energy intake from seasonal productivity optima, which is also related to the manyfold transhumance modes found in peninsular Spain (Gomez Sal and Lorente 2004). These are associated either with ecosystems such as mountains, Atlantic grasslands, and Mediterranean pastures landscapes or, with resources of such as stubble, scrub, pruned trees, and pasture rich in fibre. Our results prompt livestock diversity, not only in terms of adaptation to a complex territory, but also in maximizing the use of available resources (Gómez-Sal 2001).

Our study explored the relationship between local breeds and environmental factors through the areas of origin. In the case of local breeds, originally linked to traditional agricultural landscapes, environmental factors should have been of greater importance than in those breeds selected for intensive and industrial rearing. Leroy et al. (2016) identified a positive correlation between environmental diversity and the diversity of breeds in non-OECD countries that support this idea. Our results point in the same direction, through areas of origin of local livestock breeds, representing the historical extensive livestock uses, especially before agricultural industrialization. Different historical sources underline the high number and variety of Spanish local breeds and state that the territorial distribution was maintained fairly stable throughout the last centuries (García Sanz 1994).

Approaches similar to ours could be extended to other regions of the world. Doing so would help to determine to what extent domestication and livestock diversity are mediated by intrinsic species traits, coevolutionary forces (Zeder 2012) or cultural processes (Smith and Zeder 2013; Zeder 2017), where competition with other species is diminished and the adequacy of habitat has been directed by humans, i.e. broaden our understanding of livestock niches (Colino-Rabanal et al. 2018) worldwide. Furthermore,

it would help to expand niche construction theory beyond domestication (Smith 2016), integrating post-domestication differentiation processes. Thus, helping to apply ecological theory to improve livestock sustainability through agrobiodiversity, by, for example, enhancing a more rational use of local resources, diminishing the impact of livestock activities and searching for co-benefits between wild and agro-biodiversity.

Studies of mammals introduced by humans outside their native geographic ranges (including the Bovidae family which shows the highest rate of species introduced by humans; (Blackburn et al. 2017a, b), identify a suite of traits that predispose these species to be more tolerant to new occupied areas. Areas of introduction may sometimes exceed species realized ecological niches, and thus, successful candidates would benefit from broad environmental breadths (Blackburn et al. 2017a, b; Capellini et al. 2015), supported by humans in the case of domesticated animals. This endorses the idea that adaptive plasticity in domesticated livestock species is intrinsic, or closely related, to the adaptive ability of wild relative species (Zeder 2017), not only an outcome of artificial selection. Therefore, expanding our ecological knowledge of livestock breeds would boost more sustainable use of livestock diversity, tailoring practices and breeds to current environmental conditions and future global change.

There are numerous limitations to the biogeographic study of livestock diversity. First, livestock is composed of a few species, most of them domesticated in nearby environments within the same geographical areas (Diamond 2002; Zeder 2015), which could lead to the expectation that there are no marked biogeographical differences between species distributed where humans decide to locate them. Second, a few breeds—i.e. used in intensive livestock systems—are widely distributed globally (e.g. Robinson et al. 2014), so their spatial distribution overlaps with highly differentiated production systems, limiting our knowledge of the variety of extensive systems linked to the local environments and the respective local breeds (Hoffmann 2010) and associated cultural landscapes. Third, there are significant gaps in georeferenced information on different production systems and local breeds (FAO 2007b; Hoffmann 2010; Robinson et al. 2011). Despite these limitations, our study pioneers in the application of Agriculture

Biogeography principles (Katinas and Crisci 2018) to livestock sector.

However, it must be pointed out that the breed concept is dynamic, with a fundamental human dimension. It is not only a biological or genetic conception, but also a socio-cultural entity, where geographical, historical, environmental, productive and social aspects should be considered, including current decisions that depend on the legislation of each country (Hall 2004; Hoffmann 2013). For that, local livestock breeds represent an opportunity to explore biophysical and sociocultural dynamics of livestock landscapes. Nevertheless, this definition complicates the comparison between countries with different livestock histories and cultures. Approaches such as the one proposed here—i.e. review of literature on areas of origin—make documenting the historical distribution and diversity of local breeds and livestock uses possible. Future release of broad-scale data on production factors—historical, sociological, or political—and traditional practices such as transhumance could aid improve the delineation of livestock ecoregions as this information would complement environmental variables to better capture the multidimensional nature of livestock breeds (Velado-Alonso et al. 2021).

The geographically explicit projection of groups of breeds with similar responses to environmental factors offers a novel and versatile research tool: the livestock ecoregions, i.e. an agroecological regionalisation proposal based on livestock breeds. These can be delineated at varying degrees of resolution, according to the environmental variables selected or the criteria for grouping the breeds, seeking in each case the most appropriate to enhance more sustainable agricultural landscapes.

Moreover, policy combining agricultural uses and nature conservation tends to ignore the spatial heterogeneity of biodiversity, including agrobiodiversity (Lankoski 2016). The livestock ecoregions proposed in this work make the relationships between local agrobiodiversity and spatial heterogeneity explicit and allow subsequent policies to plan livestock landscapes. In fact, the integration of adaptive measures at local or regional level has been considered as an essential point for improving the sustainability of agricultural landscapes within the new European Common Agricultural Policy (CAP) and its acceptance by practitioners (Navarro and López-Bao 2018).

Our livestock ecoregions proposal could help to determine target landscapes in which to set specific environmental objectives (McDonald et al. 2018; Harlio et al. 2019), such as CAP eco-schemes (the next CAP green-architecture initiative that promotes environmental subsidies tailored by national governments—against historical payments regulations), or by making the implementation of conservation measures more flexible and adapted to local ecological and socio-political needs, interests and determinants, e.g. in Natura 2000 areas (Sokos et al. 2013), or for specific groups of wildlife species (Velado-Alonso et al. 2020).

Despite the significant role that humans have played in the origin and distribution of local livestock breeds, the different livestock species show different responses to the environmental heterogeneity, indicating that the innate domesticated species adaptive ability is also expressed as a response to territorial conditions and not only modulated by human selection. This result calls for more attention to ecological aspects of livestock diversity. Thus, it must be taken into account in the conservation strategies of animal genetic resources, especially in the case of local livestock breeds, but also in the design of sustainable agricultural landscapes and adaptive measurements to ongoing global change.

This study quantifies the relationships between grazing livestock diversity and environmental factors, and pioneers in proposing a regionalisation based on original local breed diversity distributions. The results open up a new route for the study of livestock agrobiodiversity. This line of research raises relevant questions in the current context, such as to what extent is the diversity of breeds in a territory useful for adapting livestock to the effects of global change? How can local livestock breeds help to make livestock landscapes more sustainable? How can we improve the co-benefits of wild and domesticated biodiversity conservation? In a context where livestock farming is regarded to as a major component of global change, local livestock breeds should be further studied from the ecology and their potential to handle agricultural systems more sustainably should not be longer disregarded.

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Author contributions EV-A and AG-S conceived the main idea; EV-A collected the data; EV-A analysed the data with support from IM-C. The manuscript was written by EV-A, with input of AG-S and IM-C. All authors made substantial contributions to the interpretation of results and the editing of the manuscript.

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Data availability The data that support the findings of this study will be openly available in a public repository. We are working on the elaboration of a data paper related to the livestock distribution information.

Code availability Code will be available under demand to the main author.

Declarations

Conflict of interest Authors declare not conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication I give my consent for the publication of this work.

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