

# Relationships between the distribution of wildlife and livestock diversity

Elena Velado-Alonso<sup>1,2</sup>  | Ignacio Morales-Castilla<sup>2,3</sup>  | Salvador Rebollo<sup>1</sup>  | Antonio Gómez-Sal<sup>1,2</sup> 

<sup>1</sup>FORECO – Forest Ecology and Restoration Group, Department of Life Sciences, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain

<sup>2</sup>GloCEE – Global Change Ecology and Evolution Group, Department of Life Sciences, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain

<sup>3</sup>Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA

## Correspondence

Elena Velado-Alonso, FORECO – Forest Ecology and Restoration Group, Department of Life Sciences, Universidad de Alcalá, Ctra. Madrid-Barcelona Km 33,600, 28805, Alcalá de Henares, Madrid, Spain.  
Emails: elena.velado@uah.es; velado.elena@gmail.com

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## Abstract

**Aim:** Wild biodiversity and agrobiodiversity are affected by challenges such as agricultural intensification. However, it is unknown whether or not both components of biodiversity respond similarly to environmental factors and to these challenges. Here, we examine the spatial relationships between the distributions of wild biodiversity and agrobiodiversity, to quantify how and where they covary across the geography.

**Location:** Mainland Spain, a European region that harbours high values of both wild and agro- biodiversity.

**Methods:** We used geographically weighted regression models to analyse the spatial variation in the relationships between the distribution of wild vertebrates and environmental and agrobiodiversity variables. We modelled the spatial gradients in species richness of native terrestrial vertebrates—that is, specific groups of amphibians, reptiles, birds and mammals—as a function of local livestock breed richness—that is, bovine, ovine, caprine, asinine, equine and porcine—climate variables and human footprint.

**Results:** We found significant covariation between the distribution of native vertebrate species richness and climate, human footprint and livestock diversity. Overall, the association between species richness of the four wild terrestrial vertebrate groups and local livestock breed richness is positive across most of the studied area. However, local breed richness of cattle and sheep breed displays contrasting patterns, where cattle breeds associate positively to most wildlife vertebrates and sheep breeds show negative associations.

**Main conclusion:** Wildlife diversity distributions are significantly associated with livestock agrobiodiversity. These spatial relationships are mediated by large-scale environmental gradients. Since both, wildlife and livestock agrobiodiversity, tend to co-occur spatially, future strategies for conservation in agricultural landscapes could benefit from integrated approaches.

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## KEYWORDS

agrobiodiversity, biodiversity conservation, cattle, geographical distributions, local livestock breeds, sheep, Spain, terrestrial vertebrates

## 1 | Introduction

In recent decades, the conservation of agrobiodiversity—that is, the diversity of agricultural and livestock species, varieties and practices—has emerged as a major concern for biodiversity conservation (COP 5, 2000), as it supports food security and because of the growing impact of industrial agriculture and livestock on biodiversity. Little is still known about the distributional patterns of agrobiodiversity and its relationship with other wild components of biodiversity. There are few examples of integrated approaches, where the conservation of wild and agrobiodiversity is considered together, either in research or in policy making (Attwood, Park, Marshall, & Fanshawe, 2017). Yet, doing so could favour a more balanced management and thus, the nature conservation in regions of the world that have endured intense anthropic pressures over long periods of time (Jackson, Pascual, & Hodgkin, 2007).

Changes towards intensification in agriculture over the last decades are compromising the conservation of wild species and their habitats (Foley et al., 2011), but also challenge the conservation of agrobiodiversity (FAO, 2015). These threats have fostered a lively debate regarding land use and its effects on nature conservation, as managing land for food production while integrating the conservation of biodiversity is rather complex (see e.g. Chaplin-Kramer et al., 2015; Chappell & LaValle, 2011; Green, Cornell, Scharlemann, & Balmford, 2005; Law et al., 2015; Machovina, Feeley, & Ripple, 2015; Smith, Kirk, Jones, & Williams, 2019). Conventional intensification ignores the benefits for agroecosystem functioning derived from agrobiodiversity and does not guarantee that greater areas of land are geared towards natural zones (Rudel et al., 2009; Tschamtkke et al., 2012).

Protected areas and large landscapes with *wildlife friendly* management are necessary to promote biodiversity conservation (Kremen, 2015). In fact, highest values of biodiversity areas are not exclusively in protected areas, but also relatively high biodiversity can be found on surrounding agricultural landscapes (López-López, Maiorano, Falcucci, Barba, & Luigi, 2011; Rey Benayas & de la Montaña, 2003). A number of ecological theories—for example, intermediate disturbance hypothesis (Hutchinson, 1953) and the metacommunity theory (Leibold et al., 2004)—have been proposed to explain what drives biodiversity on agricultural landscapes (Kleijn, Rundlöf, Scheper, Smith, & Tschamtkke, 2011). In Europe, 50% of all species depend on agricultural habitats and the European Red List of Habitats shows that 53% out of all endangered habitats are grasslands threatened by the heavy use of fertilizers, shift into intensive crop cultivation or loss of traditional management (Janssen et al., 2016; Stoate et al., 2009).

Humans have expanded the geographic distributions of domesticated animals outside their areas of origin for the last

9,000 years, reaching the Iberian Peninsula as early as 7,500 years ago (Zeder, 2017b). The intraspecific diversification of these domesticated animals has been triggered along with their geographic expansion, and in close association with human domestication of plants and environments (Zeder, 2017a). In human-modified ecosystems, herbivory has largely been driven by the locally adapted diversity of domesticated animals. Because of this, livestock diversity has helped shaping plan structure and composition, which in turn influences the diversity of animals in a bottom-up process (Arcoverde, Andersen, & Setterfield, 2017; Gómez-Sal, 2017; Ren et al., 2018; Török et al., 2016). In addition, livestock diversity acts as a driver and provider of ecosystem services—for example, food and resource provision, shelter and habitat maintenance for wild species—which depend on different productive systems and practices (Leroy et al., 2018).

The Mediterranean basin is considered a major “hotspot” of biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), characterized by an ancient history of anthropic uses (Shi, Singh, Kant, Zhu, & Waller, 2005). The Iberian Peninsula has been dominated by agricultural practices for at least the last millennium and current biodiversity is largely determined by this fact (López-López et al., 2011). Livestock activities in peninsular Spain have historical economic, social and cultural importance (Gómez-Sal, 2001) and have driven the differentiation and recognition of more than 150 local livestock breeds, most of which are endemic and currently endangered (MAPA, 2019). These local livestock breeds evolved long before industrialization, are unique autochthonous of certain regions and have been regarded to as *eco-cultural entities* (see e.g. Sponenberg, Martin, Couch, & Beranger, 2019), the product of adaptation to local environmental and human conditions (Colino-Rabanal, Rodríguez-Díaz, Blanco-Villegas, Peris, & Lizana, 2018). Despite the long history of interactions and potential influences of livestock on wildlife across this region, little is known about how and if, both wildlife diversity and livestock diversity are related.

At large geographic scales, the distribution of wild species on the Iberian Peninsula is strongly mediated by climate and human activities, influenced by highly spatially heterogeneous productivity gradients (Moreno-Rueda & Pizarro, 2009). This distribution is also influenced by the historical interplay between ecological and evolutionary processes, such as extinction and colonization events in response to climatic changes within the biogeographic constrains of the Iberian topography (Blondel & Murer-Chauviré, 1998). Much less is known about the distribution of local livestock breeds, but previous studies suggest that they would be positively correlated with terrestrial vertebrate diversity (Colino-Rabanal et al., 2018). The question arises as to whether this would be true for the geographic distributions of wildlife and domesticated livestock diversity in Spain.

Here, we analyse the relationships between both diversity components in mainland Spain, using native vertebrate species richness and local livestock breed richness as indicators. We hypothesize the existence of a significant association between their distribution patterns at coarse scales. This association could be explained by two, non-exclusive mechanisms. First, the distributions of wild species and livestock breeds could be responding similarly to environmental and human factors and thus covary positively across the geography (Leroy, Boettcher, et al., 2016; Moreno-Rueda & Pizarro, 2009). Second, breed diversity would modify the structure and composition of primary producers in agroecosystems (e.g. increasing habitat complexity and heterogeneity), with subsequent upscaling effects on wild biodiversity (e.g. Hendershot et al., 2020). Further, we expect these relationships to be spatially non-stationary, due to the marked non-monotonic gradients of environmental factors and the differentiated history of agrarian uses over the studied area (Gómez-Sal, 2017; Moreno-Rueda & Pizarro, 2009). Hence, we can ask whether the links of livestock breeds-wild species diversity might differ between domestic species. Ultimately, documenting the spatial variation in the relationships among distributional patterns of wild and domesticated diversity will aid in identifying areas where integrated conservation strategies could have positive for both types of biodiversity.

## 2 | Methods

### 2.1 | Distributional and environmental data

We calculated wildlife and livestock diversity indices for each of the 10 × 10 km UTM grid cells within mainland Spain, after removing island territories to avoid insularity effects, and coastal grid cells to avoid size effects. A total of 5,033 grid cells were used for analyses. To quantify diversity, we used species richness of terrestrial vertebrate groups—that is, mammals, birds, amphibians and reptiles—and richness of local livestock breeds, calculated by either summing the species or summing the breeds present in each UTM grid cell.

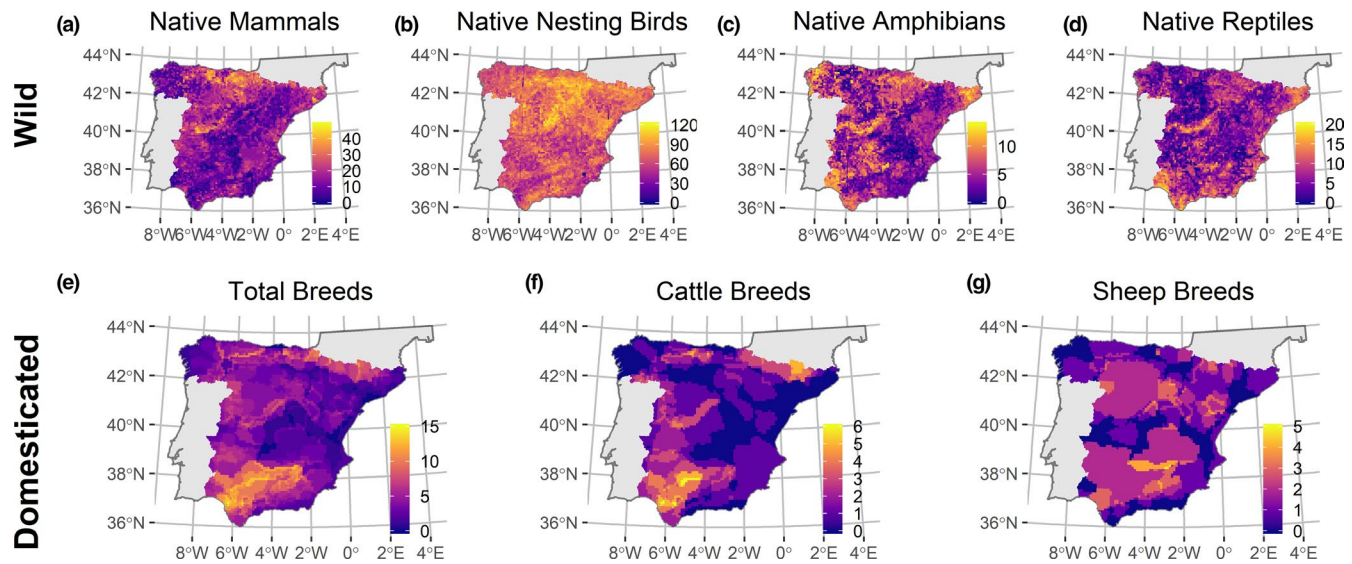
We calculated livestock breed richness using all local breeds of bovine, ovine, caprine, asinine, equine and porcine species managed by extensive traditional livestock systems. Note that in the particular case of Spain, local porcine breeds are currently (and have been traditionally) bred in extensive systems. To identify local breeds, we consulted two sources of information. First, we used the Official Catalogue of Livestock Breeds of Spain (MAPA, 2019), in order to determine currently recognized breeds, either increasing in number or under threat of extinction. Second, we reviewed the FAO DAD-IS (FAO, 2019) to identify breeds of mainland Spain that were not in the Official Spanish Catalogue but did appear in alternative breed catalogues (Appendix S1, Table S1). These breeds were considered extinct by the FAO as Spanish Ministry does not account for breed extinction. Extinct breeds have only recently undergone population declines, especially during the last decades of the 20th century. Thus, our data set encompasses all extant and recently extinct

breeds, based on their historical distributions, prior to being exposed to the effects of agricultural intensification over the last decades (Tisdell, 2003). Therefore, our measure of livestock diversity should be interpreted as the capacity of each grid cell to harbour long-term breed diversity or as the historical diversity of land-based livestock systems, reliant on local natural resources (Colino-Rabanal et al., 2018; Gómez-Sal, 2001), avoiding potential biases due to recent erosion of agrobiodiversity.

We documented a total of 128 local breeds: 44 bovine, 38 ovine, 19 caprine, 9 porcine and 18 equine, including horses and donkeys (Appendix S1, Table S2). With these breeds, we computed the following three different indicators of livestock agrobiodiversity: total breed richness, cattle breed richness and sheep breed richness. The focus on bovine and ovine breeds separately is due to their largest number of local breeds and, to their markedly different distributional patterns (see Figure 1e–g). The distribution of each breed, corresponds to its area of origin—that is, the region where the breed was first recorded—and was delimited and digitized after a comprehensive review, comparison and integration of the distributional descriptions in all catalogues of Spanish breeds (for a complete list of data sources see Appendix S1, Table S1). When a clear description of the area of origin was unavailable, we assigned the oldest area where the breed was distributed before the agrarian industrialization. We assume that these areas represent the historical *eco-cultural* domains of each local livestock breed (Colino-Rabanal et al., 2018). Within these areas, wildlife has interacted with livestock for extended periods of time.

Vertebrates species richness—that is, amphibians, reptiles, birds, mammals—was extracted from the Spanish Inventory of Terrestrial Vertebrate Species (MITECO, 2019b) and additional sources for completion (López & Martín, 2019; MITECO, 2019a). We grouped the vertebrate taxa according to the following criteria. First, as general metrics of wildlife diversity, we calculated each group total richness using native species and excluding exotic, littoral and marine species for all groups. We additionally excluded species from aquatic environments for mammals, birds and reptiles (Figure 1a–d). Our vertebrate data set included a total of 76 mammal species, 177 nesting bird, 41 reptile species and 28 amphibians (for more detail Appendix S1, Table S3–S6). Second, to deepen our understanding of wildlife–livestock relationship, we further subsetted each vertebrate group based on specific habitat preferences related to agricultural landscapes and livestock uses. For mammals, we considered lagomorphs, and artiodactyls as small and large herbivores, respectively. For birds, we used steppe birds, related to extensive agricultural landscapes and scavengers, feeds on livestock carcasses. Reptiles were divided into rocky habitats and shrubby habitats. Amphibians were separated into aquatic and land-based, according to whether their adult phase is developed in water bodies (for more detail Appendix S1, Tables S7–S13).

To examine whether the relationships between wild and domesticated biodiversity are mediated by either environmental factors or human impacts, we calculated average values of a suite of variables for each grid cell. We extracted climate from the WorldClim database,



**FIGURE 1** Diversity maps for wild and domesticated animals in Peninsular Spain. The panels are for species richness of wild native vertebrates including mammals (a), nesting birds (b), amphibians (c) and reptiles (d) and for breed richness of domesticated livestock species, including total richness of cattle, sheep, goats, pigs, horses and donkeys (e), cattle breeds only (f) and sheep breeds only (g). Note that upper panels show diversity of species while lower panels show intraspecific breed (i.e. genetic) diversity

used annual mean temperature (BIO1), annual precipitation (BIO12) and precipitation seasonality (BIO15) variables (Fick & Hijmans, 2017). These descriptors were chosen as they have been previously used to characterize the major large-scale environmental gradients in the Iberian Peninsula (Maiorano et al., 2013). To characterize human disturbance of natural systems, we used the terrestrial Human Footprint for 2009 (Venter et al., 2018). This source of data has often been used to analyse the influence of human activities on biodiversity (Garnett et al., 2018; Sebastián-González et al., 2019). We z-scored all variables to facilitate the comparison across models (Schielzeth, 2010).

## 2.2 | Statistical analyses

To analyse the relationship between wild species richness and livestock breed richness and environmental variables while accounting for the spatial non-stationarity of these relationships, we performed geographically weighted regression models (GWR) (Fotheringham, 2002). This technique fits a regression for each spatial unit that is, each  $10 \times 10$  km UTM grid cell—and its neighbouring units up to a given radius or bandwidth, weighted by a distance function. To allow for result comparison, we used an adaptive bandwidth of 5% or the spatial units in our data set (ca. 100 km bandwidth), which is an adequate scale to capture the spatial heterogeneity and non-stationarity of the environmental gradients (see e.g. Bickford & Laffan, 2006). GWR models identify spatial shifts in the direction of the associations among variables while overcoming issues related to spatial non-stationarity and spatial autocorrelation (Bini et al., 2009; Legendre, 1993).

We fitted suites of GWR models for each wildlife richness grouping, including an increasing number of predictors, in order to understand the joint and independent contributions of each

predictor to explain variation in species richness of wild vertebrates. The goal is analogous to that of variation partitioning (see e.g. Borcard, Legendre, & Drapeau, 1992; Legendre et al., 2009), but its application in a GWR setting is not straightforward. Thus, we apply a forward stepwise fitting of GWR models and compare model accuracy between simplified versions of the models and full models including all predictors. The full models used climate predictors (annual mean temperature, annual precipitation and precipitation seasonality), human footprint and one of the livestock breed richness indices, that is total breed, cattle breed or sheep breed richness. Reduced models included pairwise combinations or unique predictors. To account for global multicollinearity of predictors, we calculated the Variance Inflation Factor of generalized linear models (see e.g. Morales-Castilla, Olalla-Tárraga, Purvis, Hawkins, & Rodríguez, 2012), ensuring an acceptable level of collinearity ( $VIF < 4.0$  in all predictors of our models).

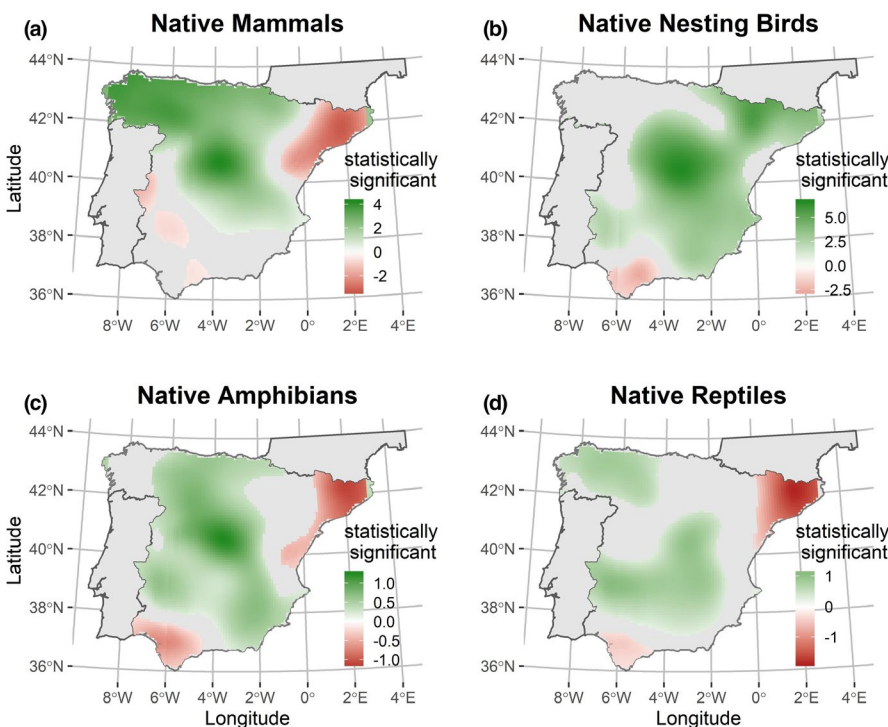
We evaluated model accuracy using global quasi- $R^2$  to assess the global explained variance and the Akaike information criterion (AIC) (Burnham, Anderson, & Huyvaert, 2011) to determine whether including livestock diversity as a predictor improves model performance. The global quasi- $R^2$  is calculated from the coefficients in the local models, not by aggregating the local  $R^2$  (Fotheringham, 2002). Finally, for GWR models assessing the relationships between wild species richness and livestock breed richness, we documented the spatial variation in regression coefficients and their statistical significance (at  $[p = 0] \leq .05$ ) to map only significant results and quantify their ratio. All data processing and analyses were performed in R v3.6.0 software (R Core Team, 2019) using the “raster” package (Hijmans, 2019) to process the environmental data, the “spgwr” package (Bivand & Yu, 2017) to perform the geographically weighted models, and “sf” (Pebesma, 2018) and “ggplot2” (Wickham, 2016) for result visualization.

### 3 | Results

Overall, the results show moderate to strong relationships between the species richness of the four native terrestrial vertebrates and climate, human disturbance and livestock agrobiodiversity richness predictors. When considering the full GWR model, we found a significant positive association between total livestock breed richness and the four native terrestrial vertebrate groups concentrated on the central part of Spain (Figure 2). Model's standardized global coefficients inform that across over two thirds of the territory, an increase of 10 local breeds associates with an average increase of wildlife diversity of, 14.6 mammal species, 15.4 bird species, 3.6 amphibian species and 4.6 reptile species ( $p < .05$ ; see Appendix S2, Tables S1–S4 for details). These positive associations shift to negative ones in South-western lowlands—that is, the Guadalquivir Basin with less vertebrate species richness (Figure 1a–d) and high breed richness (Figure 1e)—and north-eastern of the Spain—that is, the Ebro Basin with scarcity of livestock breeds (Figure 1e) and high vertebrate species (Figure 1a–d)—for all groups, except birds in the north-east (Figure 2b).

Single predictor GWR models explain between a quarter and a third of the variation in wild biodiversity of the four groups of vertebrates (global quasi- $R^2$  ranging from .19 to .39; Table 1). However, sequentially adding predictors does not increase the explained variation with respect to the climate-only model, indicating a major association of climate with wild biodiversity, but also with agrobiodiversity predictors (Table 1). In all cases, the full models outperformed simplified versions in terms of both global explained variation in species richness and AIC, more so for mammals and birds than for amphibians and reptiles (see Table 1).

Full models using each of the three indicators for livestock diversity—that is, total breed, cattle breed and sheep breed richness—display similar ability to explain variation in the diversity of each vertebrate group in terms of quasi- $R^2$  (Table 2). Yet, cattle and sheep breed richness show markedly different distributions (Figure 1f,g). Because of this, contrasting patterns are found between local cattle and local sheep breed richness slopes for the full GWR models when considering specific groups of vertebrates (Figure 3, for more details see Appendix S2, Tables S5–S19). On the one hand, cattle breed richness shows positive significant associations with artiodactyls ( $\beta = 0.17 \pm 0.16$ , across 67% of the territory), land-based amphibians ( $\beta = 0.27 \pm 0.38$ , across 65% of the territory) and rocky habitat reptiles ( $\beta = 0.35 \pm 0.29$ , across 69% of the territory) and negative associations with steppe birds ( $\beta = -0.48 \pm 0.74$ , across 60% of the territory) (see Figure 3b,e,h,k). On the other hand, the sheep breed richness is negatively associated to artiodactyls ( $\beta = -0.08 \pm 0.16$ ; across 45% of the territory), land-based amphibians ( $\beta = -0.27 \pm 0.2$ , across 60% of the territory) and rocky habitat reptiles ( $\beta = -0.32 \pm 0.21$ , across 56% of the territory), but positively related with steppe birds ( $\beta = 0.84 \pm 0.39$ , in 72% of the territory) (Figure 3c,f,i,l). These links are also significant but less intense for the rest of wild fauna groups analysed—lagomorphs, scavengers, water-based amphibians and shrubby habitat reptiles—for more details see Appendix S2, Tables S5–S19). The strongest associations between wild vertebrate species and livestock breeds occur in different areas of the studied region. For example, positive relationships of artiodactyls with cattle breeds are stronger in the north part of mainland Spain (Figure 3b), whereas in the case of steppe birds and sheep richness happen across central Iberian plateaus. In the case of native land-based amphibians and cattle breeds, we observe a



**FIGURE 2** Maps of regression coefficients resulting from geographically weighted regression models fitting the relationships between species richness of mammals (a), nesting birds (b), amphibians (c) and reptiles (d), using as predictors annual mean temperature, annual precipitation, precipitation seasonality, human footprint and total breed richness. Depicted coefficients are for total breed richness and are only coloured when statistically significant at  $[p = 0] \leq .05$ . Green colour represents positive coefficients and thus, increasing species richness with increasing breed richness and red colour represents negative associations between diversity of vertebrates and of livestock

TABLE 1 Global quasi- $R^2$  for the different performed models—Climate: annual mean temperature, annual precipitation and precipitation seasonality

Vertebrate group	Climate	Human footprint	Total breed richness	Climate + human footprint	Climate + total breed richness	Climate + human footprint + total breed richness
Global quasi- $R^2$						
Native Mammals	.40	.32	.35	.42	.41	.44
Native Nesting Birds	.35	.28	.29	.37	.37	.38
Native Amphibians	.24	.20	.21	.26	.26	.28
Native Reptiles	.26	.19	.20	.28	.27	.29
AIC	33,217.22	33,856.62	33,602.50	33,049.47	33,103.75	32,914.34
Native Nesting Birds	41,298.93	41,877.56	41,804.06	41,228.43	41,195.56	41,119.08
Native Amphibians	24,319.40	24,626.79	24,537.26	24,192.35	24,197.08	24,068.07
Native Reptiles	26,812.89	27,241.97	27,206.95	26,689.95	26,719.83	26,594.65

TABLE 2 Global quasi- $R^2$  for the full model interchanging the three different agrobiodiversity indicators

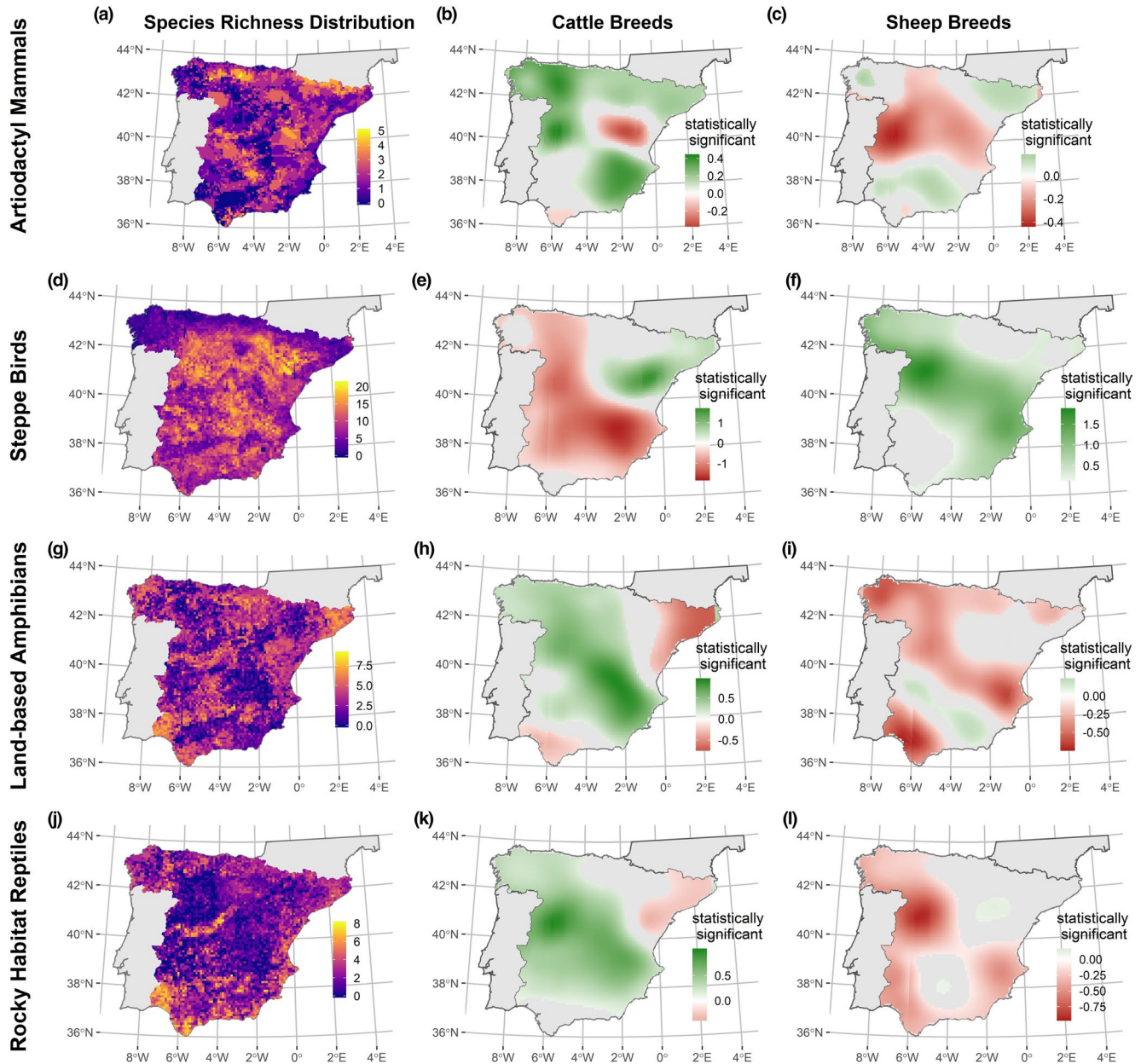
Global quasi- $R^2$	Total breed richness	Cattle breed richness	Sheep breed richness
Native mammals	.35	.35	.32
Native nesting birds	.28	.28	.27
Native amphibians	.21	.21	.20
Native reptiles	.20	.22	.20

positive effect that increases in magnitude following the aridity gradient (Figure 3h), while rocky habitat reptile richness is found most strongly associated to cattle breed richness in the stony, shallow soil region in the western-central part of mainland Spain (Figure 3k).

#### 4 | Discussion

The distributions of both local livestock breed diversity and wildlife diversity are moderately to strongly associated across peninsular Spain. As hypothesized, this relationship is spatially non-stationary—that is, shifting in magnitude and direction across the geography, in response to environmental gradients—and differs when considering different livestock species. The relationship between wildlife and domesticated diversity also differs across groups of native vertebrate species with varying ecological requirements. The associations are positive across most of Spain for all vertebrates (see Figure 2), but stronger for nesting birds and mammals than for reptiles and amphibians (Table 1). Overall, our results indicate that the regions that have historically harboured a higher diversity of livestock breeds tend to sustain more wild species too. Thus, measurements aimed at conserving one component of biodiversity, that is, either wildlife or domesticated diversity—could have positive outcomes on the other, and *vice versa*, providing that the conservation of livestock breeds is *in situ*, based on local natural resources.

In general, our results agree with previous studies showing that historical factors and land use diversity are important to determine and maintain terrestrial vertebrate diversity in the Iberian Peninsula (Moreno-Rueda & Pizarro, 2007; Nogués-Bravo & Martínez-Rica, 2004). Thus, the general positive associations between wild and domesticated diversity at the coarse spatial scale considered here support the previous interpretations that livestock diversity can act as a proxy for land use or landscape diversity (Gómez-Sal, 2001). Moreover, the spatially non-stationary relationships between the distribution of native vertebrate groups and total breed, cattle breed and sheep breed richness (see Figure 3) confirm that wild species distributions are influenced by ecological processes operating over multiple spatial scales (George & Zack, 2001; Hooper et al., 2005; McGill, 2010; Pearson & Dawson, 2003; Willis, 2002). The meso-scale considered here captures how livestock systems and practices would have promoted environmental heterogeneity, which could



**FIGURE 3** Maps of regression coefficients resulting from geographically weighted regression models fitting the relationships between species richness of specific groups artiodactyl mammals (a), steppe birds (d), land-based amphibians (g) and rocky habitat reptiles (j), using as predictors annual mean temperature, annual precipitation, precipitation seasonality, human footprint and cattle (b, e, h, k) or sheep (c, f, i, l) breed richness. Depicted coefficients are for total breed richness and are only coloured when statistically significant at  $[p = 0] \leq .05$ . Green colour represents positive coefficients and thus, increasing species richness with increasing breed richness and red colour represents negative associations between diversity of vertebrates and of livestock

have promoted vertebrate species richness. Overall, birds and mammals would have probably been favoured by the direct effects of livestock grazing on the habitats shared by both domestic and wild species. In the case of amphibians and reptiles, the influences would have been indirect through the heterogeneity caused by livestock free-ranging activities for other species (as the case of water bodies) or refuge habitats (as rocky places, not frequented by livestock).

The positive associations between wild artiodactyls and cattle breed richness probably reflect similarities in their habitat requirements. Notably, the interaction between cattle and grasslands in

extensive traditional livestock systems influences the distribution and composition of vegetation and animals in rangelands by, for example, fostering compositional heterogeneity at fine and large scales (Derner, Lauenroth, Stapp, & Augustine, 2009) or increasing plant richness (Boavista, Trindade, Overbeck, & Müller, 2019). This is the case, for example, of African savannah grasslands where domestic grazing activities contribute to complex savanna nutrient cycles maintaining high productivity of vegetation, that decreases when livestock production is intensified and homogenizes the grazing activities (Du Toit & Cumming, 1999). If higher richness of cattle breeds

had an impact on increasing the heterogeneity, richness and availability of diverse grazing resources, then it could indirectly favour the diversity of wild artiodactyls. While our analyses do not allow establishing the causal direction of wild-domesticated associations, exploring it may be an interesting avenue for future investigations.

Steppe birds and sheep breed diversity show positive associations in central Spain (see Figure 3), possibly due to sheep traditional grazing practices promoting steppe bird's preferred habitats. The maintenance of steppe birds depends on the conservation of extensive grazing practices involving the preservation of large open fields, pastureland areas, fallow rotations and adequate livestock densities (Milchunas et al., 1998; Santangeli & Cardillo, 2012; Silva, Palmeirim, & Moreira, 2010). Local sheep diversity in Spain is related to traditional extensive grazing practices on shrublands and grasslands of regions with cold Mediterranean climate (Gómez-Sal, 2001). Further, sheep diversity likely influences soil quality, plant composition and habitat structure, which seems to have a positive effect on steppe birds (Blanco, Tella, & Torre, 1998). Ongoing intensification of grazing practices for these local breeds of sheep may represent a threat for steppe species (Fonderflick, Caplat, Lovaty, Thévenot, & Prodon, 2010).

The positive relationship found between amphibians and cattle breeds follows a noticeable aridity gradient in the Iberian Peninsula (Figure 3). Historical extensive grazing systems may have created and maintained adequate habitats for amphibians by increasing the availability and spatial distribution of artificial ponds (Da Silva, Gibbs, & Rossa-Feres, 2011; Knutson et al., 2004; Rannap, Löhmus, & Briggs, 2009), especially in the driest areas. Furthermore, livestock activities could influence amphibian diversity through different factors such as water quality or predator occurrence and quality of the surrounding habitat, all of which promote amphibian diversity (Curado, Hartel, & Arntzen, 2011; Hartel, Schweiger, Öllerer, Cogălniceanu, & Arntzen, 2010; Hartel & von Wehrden, 2013; Lescano, Bellis, Hoyos, & Leynaud, 2015; Roche, Latimer, Eastburn, & Tate, 2012). In this sense, the loss of traditional agricultural landscapes and extensive grazing practices is linked to the decline of amphibian populations in southern Spain (Roche et al., 2012). Regarding reptiles, diversity is greater in agro-silvopastoral systems where a scattered tree layer with a well-preserved shrub mosaic and low livestock densities are maintained (Godinho, Santos, & Sá-Sousa, 2011). Our results support these habitat preferences, which coincide with habitats of increasing cattle diversity (Figure 3j,k).

Our study challenges views where the wild and domesticated components of biodiversity are largely disconnected, with the former related to ecological drivers (e.g. Aragón, Lobo, Olalla-Tárraga, & Rodríguez, 2010; Fraser, 1998 but see for example Moreno-Rueda & Pizarro, 2009) and the latter to human migrations and activities (Hall, 2004; Mason, 1973). Instead, in regions like the Mediterranean basin, long dominated by agricultural landscapes, both wild and livestock biodiversity may feedback and respond similarly to environmental drivers. It derives that the integration of agrobiodiversity into wildlife conservation schemes could be mutually beneficial. Examples of integrative conservation measures would include the following:

promoting local livestock breeds linked to environmental objectives in the post 2020 European Common Agricultural Policy (Navarro & López-Bao, 2019); protecting habitat heterogeneity and landscape connectivity (e.g. Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012); and accounting for land use dynamics surrounding protected areas (DeFries, Hansen, Newton, & Hansen, 2005; Ervin et al., 2010; Laurance et al., 2012; Rey Benayas & de la Montaña, 2003). More research is needed to fully understand the causal relationships between wild biodiversity and livestock agrobiodiversity at different geographic scales and across periods of time.

The associations between wildlife and agrobiodiversity revealed by our results have implications for conservation, especially in regions with ancient agricultural and livestock traditions. Land-based livestock systems, characterized by regions with higher local breed richness, represent an opportunity to aid wildlife conservation, as they can harbour more wild biodiversity than industrialized agricultural lands (Kleijn et al., 2011). This is supported by the positive covariation between wild species and livestock breeds (see Figure 2). Agricultural landscapes play a critical role for biodiversity conservation in protected areas of Spain (Maldonado, Ramos-López, & Aguilera, 2019), a country with a long history of agriculture and some examples of sustainable uses—for example, it is the country with the highest density of UNESCO's Biosphere Reserves, which are specifically designed to protect cases of sustainable development. Our pioneering work poses new scientific questions, for example, could results for Spain be easily extrapolated or, instead, they would only apply to world regions with a long history of domestication and diversification of local breeds? In any case, it opens a major conservation avenue for a very large part of the humanized biosphere. In this way, wild biodiversity and agrobiodiversity can be integrated to improve the sustainability of livestock farming systems and the conservation of wildlife.

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## DATA AVAILABILITY STATEMENT

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. A dataset has been upload to dryad with the <https://doi.org/10.5061/dryad.0gb5mkkzd>.

## ORCID

Elena Velado-Alonso  <https://orcid.org/0000-0003-4805-2929>

Ignacio Morales-Castilla  <https://orcid.org/>



org/0000-0002-8570-9312

Salvador Rebollo  <https://orcid.org/0000-0001-8797-1122>

Antonio Gómez-Sal  <https://orcid.org/0000-0003-1925-4580>

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**BIOSKETCH**

**Elena Velado-Alonso** is interested in the sustainability of extensive livestock system and human–environment interactions. She currently works on the biogeography of local livestock breeds. This paper is part of her PhD work at the University of Alcalá.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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