Ganadería y Biodiversidad

Determinantes ecológicos y funciones de la diversidad de razas ganaderas autóctonas en la España peninsular

Elena Velado Alonso
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Ganadería y Biodiversidad. Determinantes ecológicos y funciones de la diversidad de razas ganaderas autóctonas en la España peninsular.

Tesis doctoral
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A mis abuelas, Dominga y Tomasa,
a quienes se les negó el derecho a la educación,
y sin embargo, nos inculcaron el amor al conocimiento.
A mi madre Severiana y a mi padre Máximo,
quienes siempre me han dado todo su cariño y apoyo,
base inequívoca para la perseverancia.
A mi hermana Ana,
que siempre planta cara en el aquí y en el ahora.
A mi sobrina Gimena, que es el futuro,
y a quien le hubiese gustado que esta tesis
fuese una prima con quien jugar.
A las personas que cuidan de otras personas,
a las que no olvidan los privilegios
y mantienen la dignidad.

Los que no sientan el entusiasmo de esta nueva empresa, los que en su corazón se mantengan bien avenidos con la tradicional modorra, los que más busquen adquirir títulos que levantar su espíritu y afilar su inteligencia, fuera mejor que abandonaran el propósito y giraran la vista a otras partes.

Manuel García Morente, decano de la Facultad de
Filosofía y Letras de la Universidad Central de Madrid, en
«La mujer, primera pobladora de la Ciudad Universitaria»,
22 de enero de 1933.

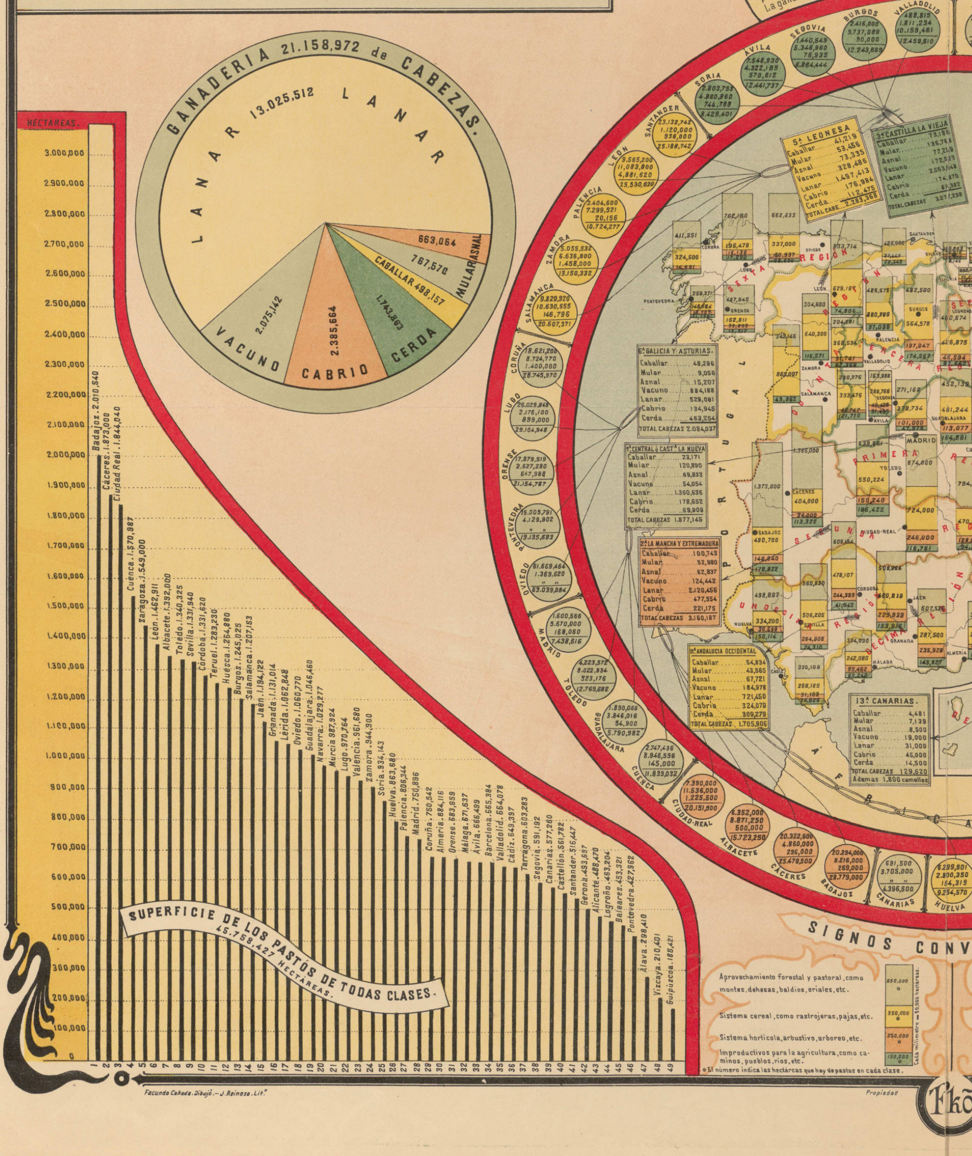
INFORME TÉCNICO

Hay un sello en relieve que dice: «Ministerio de Fomento».=Dirección general de Agricultura, Industria y Comercio.=Agricultura.

La Junta Consultiva agronómica, con fecha 20 del corriente mes, me dice lo siguiente:=Ilmo. Señor.=Examinados por la Junta los Mapas ó cuadros gráficos relativos al «Cultivo agrícola» (dos hojas) «Regadio», «Ganaderia», la «Producción de mosto y la Olivarera», de los que es autor D. Facundo Cañada López, que V. S. se sirvió remitir á informe, cumple manifestarle: Que las obras de referencia, consideradas en conjunto y bajo el punto de vista estético, revelan un buen gusto artístico en su Autor; condición de gran estima en todos aquellos estudios que tienen por norte y fin ilustrar y convencer intuitivamente.=Es incuestionable, que esta clase de trabajos estadísticos, son más fáciles de consultar y dan una idea más rápida y perfecta de lo examinado, que esos áridos estados de monótona y amanerada estructura que fatigan la imaginación, y á veces, hasta confunden el criterio de quien los estudia, perdiéndose pronto con el olvido de los guarismos el conocimiento de lo examinado.=Además, en España, desgraciadamente, hay poca afición á los estudios analíticos y estadísticos de naturaleza económica, quizás porque aún no nos hemos convencido de su decisiva influencia en el desarrollo del comercio, base primordial é insustituible de la prosperidad nacional, y que da la verdadera ventaja al negociar los tratados internacionales de comercio, sirviendo al propio tiempo de exacto indicador para regularizar y armonizar la tributación de las primeras materias y la de sus productos derivados.=Por consiguiente, toda manifestación que tienda más ó menos directamente á este fin, debe recibirse con aplauso, para que sirva de estímulo y contribuya á que la feliz iniciativa del Sr. Cañada se mejore, complete y generalice con sucesivos trabajos, análogos á los que son objeto de esta crítica.= Notoria injusticia sería tachar de inexactos los gráficos resúmenes de estadísticas del Sr. Cañada, puesto que en ellos se han vertido fielmente los únicos elementos disponibles representativos de la verdad legal, que son los datos que los Ingenieros agrónomos han aportado, no sin vencer grandes dificultades, à las estadísticas que anualmente publica esta Junta.=Con ellos à la vista, se aprecia bien la minuciosidad y exactitud con que ha sabido el Autor presentar, de un modo verdaderamente persuasivo, la producción española en sus diversas manifestaciones agrícola y pecuaria, tan ingeniosa y artísticamente agrupada y clasificada, que sin el menor esfuerzo de imaginación y al primer golpe de vista, se aprecia en detalle y en conjunto la importancia absoluta y relativa de dichas riquezas.=Por todo lo expuesto, la Junta, en sesión de ayer, acordó significar á V. S. I. que los gráficos antes citados, confeccionados por D. Facundo Cañada López, son de verdadera importancia y honran á su autor.=Lo que traslado á V. para su conocimiento y efectos consiguientes.=Dios guarde á V. muchos años.=Madrid, 27 de Diciembre de 1905.=El Director general.=Daniel López.=Hay una rúbrica.=Sr. D. Facundo Cañada López.=Es copia literal.

ESPA
LA GANADERIA, PR
EN 1º DE ENER
por
Facundo Cañad
Jefe Militar retirado, de la Real Socie
según datos
JUNTA CONSULTIV

Comprende la división de la Nación por Region
pitalidad, hectáreas que de cada clase de pastos exis
La ganaderia se detalla por Regiones con sus clases



Facundo Cañada. Dibujó. – J. Reinoso. Litº

Propiedad

PAÑA
…A. PRADOS Y PASTOS
ENERO DE 1905
por
Cañada López.
Real Sociedad Geográfica de Madrid.
gún datos de la
…LTIVA AGRONÓMICA.
…or Regiones Agronómicas, su número, nombre y ca-
…pastos existe en cada Prov.ª y valor de estos.
…sus clases y número de cabezas de cada clase.

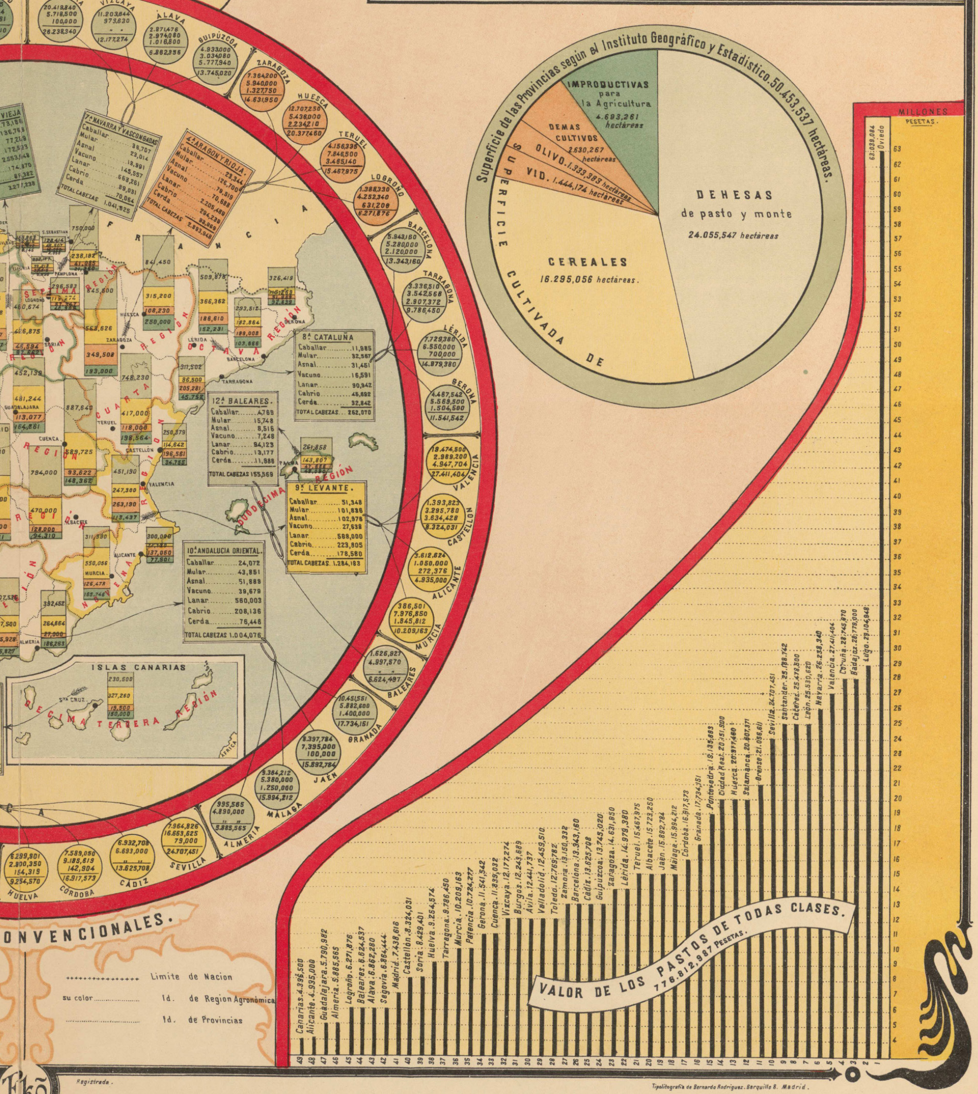
EXPLICACIÓN

La **Ganadería** se detalla en las cartelas, que con el número, nombre y color correspondientes á los límites de Región, se hallan alrededor del Mapa de la Nación que figura en el centro, con la división por **Regiones Agronómicas** y con las que se encuentran unidas éstas por medio de una flecha.

De estas cartelas arrancan las líneas que se dirigen á los círculos que representan las Provincias, con el color del límite de la Región Agronómica, en cada uno de los cuales se hallan cuatro cantidades, que son: la 1.ª el valor de los pastos adehesados; la 2.ª el valor de los pastos del sistema cereal; la 3.ª el valor de los pastos del sistema hortícola, arbustivo y arbóreo, y la 4.ª ó última, la suma de los tres anteriores, que es el valor total de todos los pastos de la Provincia.

En cada Provincia figura un rectángulo más ó menos prolongado, según la extensión de ella. Cada uno de estos se halla seccionado en cuatro departamentos con los colores verde, amarillo, oro y azul, con el tamaño proporcionado á su extensión de hectáreas y en el centro aparece la cantidad de estas que hay de pastos de las diferentes clases, como se indica en los signos convencionales.

Los diagramas del valor y superficie de los pastos de cada Provincia, así como los de cultivos diversos, pastos y tierras improductivas del total de la Nación, además de el de Ganadería con su diversidad de clases y cantidades, prueban claramente la situación actual aproximada de estos importantes ramos de la producción Nacional.



Registrada.

Tipolitografía de Bernardo Rodriguez. Barquillo 8. Madrid.

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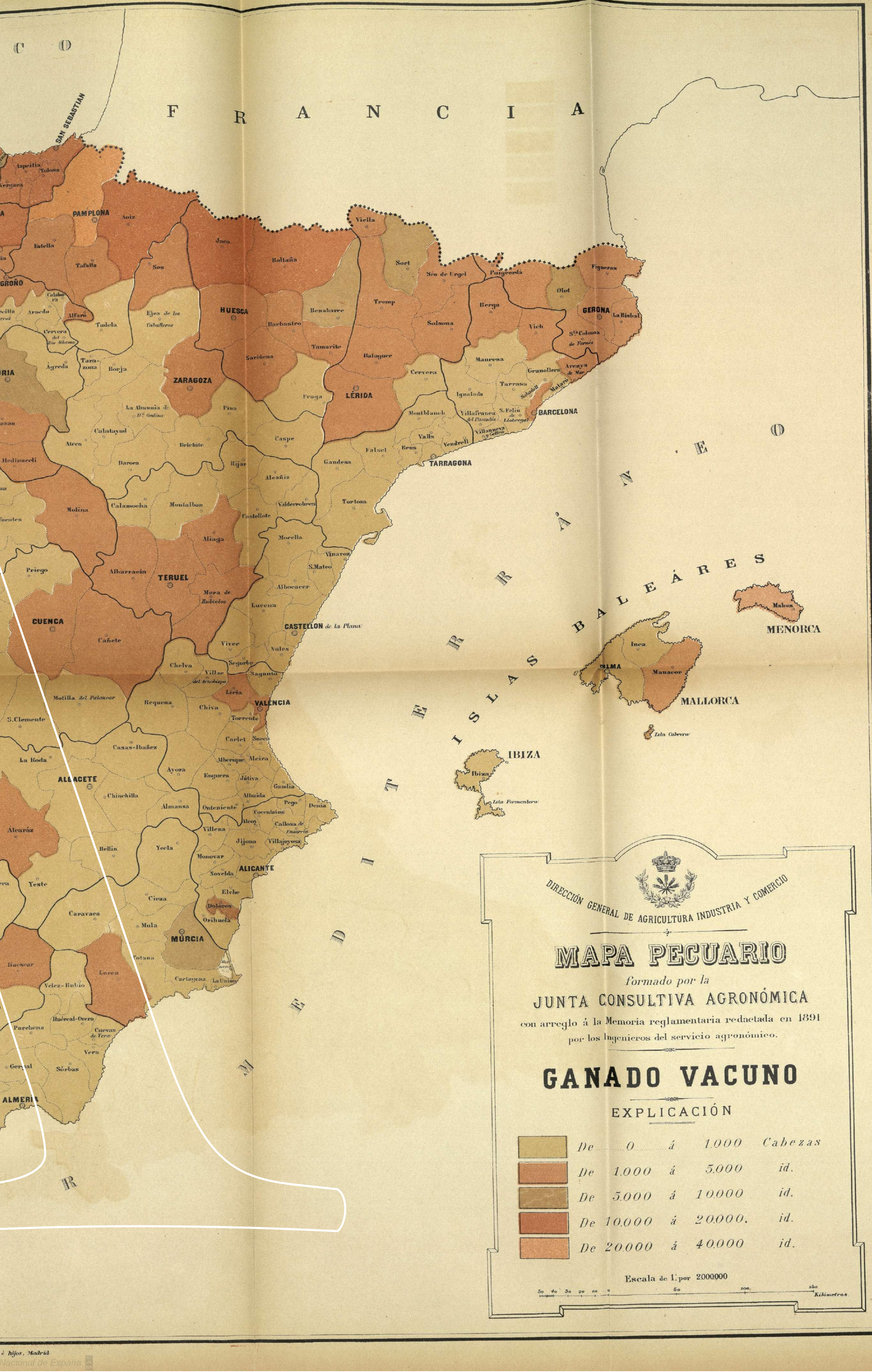

DIRECCIÓN GENERAL DE AGRICULTURA INDUSTRIA Y COMERCIO

MAPA PECUARIO

formado por la

JUNTA CONSULTIVA AGRONÓMICA

con arreglo á la Memoria reglamentaria redactada en 1891
por los Ingenieros del servicio agronómico.

GANADO VACUNO

EXPLICACIÓN

🟨	De	0	á	1.000	Cabezas
🟧	De	1.000	á	5.000	id.
🟫	De	5.000	á	10.000	id.
🟥	De	10.000	á	20.000.	id.
🟧	De	20.000	á	40.000	id.

Escala de 1: por 2000000

50 40 30 20 10 0 50 100 150 Kilómetros

é hijos, Madrid

A

SECCIÓN A

RESUMEN GENERAL

A.1. INTRODUCCIÓN GENERAL: ANTECEDENTES Y MARCO TEÓRICO

1.1 La Agrobiodiversidad

Según la conferencia sobre diversidad biológica celebrada en Nairobi en el año 2000 (COP 5, 2000), el concepto de agrobiodiversidad integraría todos los componentes de la diversidad biológica relevantes para la alimentación, la agricultura y los agroecosistemas, comprendiendo la variedad y variabilidad de plantas, animales y resto de organismos —considerados a nivel genético, de especie y ecosistémico—, necesarios para sostener las funciones, estructuras y procesos de los agroecosistemas. Esta sería la primera vez que este organismo de Naciones Unidas plantease una aproximación conceptual a la biodiversidad procedente de la actividad humana. La agrobiodiversidad se entiende por tanto como el resultado de la acción conjunta durante milenios de la selección natural y la intervención humana (Smith, 2011; Zeder, 2012), esencial para satisfacer las necesidades de alimentación humanas, contribuir de forma fundamental a su bienestar y proveer al mismo tiempo otros servicios de los ecosistemas (Jackson, Bawa, Pascual, & Perrings, 2005).

La agrobiodiversidad ha sido —y sigue siendo— desarrollada por las actividades y prácticas humanas y está íntimamente ligada a estas. Su mantenimiento depende entonces de las interacciones entre el ambiente, los recursos genéticos y las prácticas de manejo. Por ello, su conservación está ligada a usos sostenibles y racionales (COP 5, 2000). De hecho, la agrobiodiversidad está siendo considerada como un elemento central en las dimensiones sociales y ambientales de la sostenibilidad (Díaz et al., 2015; Zimmerer & de Haan, 2017) y es a menudo sugerida como clave en la mitigación y adaptación al cambio climático (Altieri, Nicholls, Henao, & Lana, 2015; Hoffmann, 2013; Wood et al., 2015). A pesar de ello, los planteamientos actuales en la agricultura y la ganadería se ven enfrentados a un doble problema: por un lado, mantener la agrobiodiversidad (COP 5, 2000) y por otro, mitigar los impactos negativos de los sistemas y prácticas agrícolas sobre el resto de los componentes de la diversidad biológica (Foley et al., 2011).

1.2. IMPORTANCIA DE LA AGROBIODIVERSIDAD GANADERA

Los alimentos de origen animal proveen un 33% de las proteínas y un 17% de las calorías consumidas por el ser humano globalmente (FAO, 2018). La variedad de fuentes de estos alimentos depende directamente de esta agrobiodiversidad ganadera, por lo que puede considerarse como elemento destacado de la seguridad alimentaria. La ganadería constituye de hecho el medio de vida de numerosas comunidades rurales —hasta en un 70%—, incluidas las de los países más pobres (FAO, 2015a). En muchas ocasiones estas comunidades son las responsables de mantener las razas ganaderas locales en dichos territorios. Por otra parte, la ganadería en general, incluyendo en este caso planteamientos industriales, sigue siendo un sector en alza. Se estima que la producción ganadera aumentará en las próximas décadas, pudiendo llegar en 2050 a duplicarse la producción del año 2000 (Alexandratos & Bruinsma, 2012).

La agrobiodiversidad ganadera es provisora de numerosos servicios para el bienestar humano, gracias a las complejas interacciones que mantiene con el ambiente, mediadas por los sistemas y prácticas de producción (Leroy et al., 2018). Por ejemplo, en el plano de los servicios de aprovisionamiento, no solo abastece de alimentos, sino que también es una importante fuente de fibras y otros subproductos, de combustibles, así como transporte y trabajo, especialmente en países en vías de desarrollo (FAO, 2006). Además, los recursos genéticos animales son utilizados para la tecnología y la innovación en diferentes campos como la medicina o la biotecnología (FAO, 2015b).

Los animales domésticos desempeñan un importante papel en el funcionamiento de los agroecosistemas (Gliessman, 2014), influyendo en los servicios de regulación. Por un lado, determinan la estructura de la vegetación, así como la diversidad animal que depende de esta (Arcoverde, Andersen, & Setterfield, 2017; Ren et al., 2018; Török et al., 2016). También canalizan los flujos de energía entre niveles tróficos y contribuyen a los ciclos de nutrientes (Belsky & Blumenthal, 1997; Parfitt et al., 2010; Reeder & Schuman, 2002). Por otro lado, influyen en las dinámicas de las comunidades, afectando a las interacciones, y en general, contribuyen a mantener un cierto nivel de complejidad en los agroecosistemas (Altieri et al., 2015).

Por todo ello, la agrobiodiversidad ganadera influye en servicios como la provisión de hábitat, la polinización, la regulación local del clima o incluso sobre las consecuencias de los eventos extremos (Leroy et al., 2018). Es evidente, sin embargo, que el pastoreo mostrará efectos distintos según la intensidad y modalidad con la que se practique, afectando a la composición y estructura de la vegetación (Cingolani, Noy-Meir, & Díaz, 2005; Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016), a la disponibilidad de nutrientes (Crain et al., 2009; Vuorio, Muchiru, Reid, & Ogutu, 2014) o la configuración del paisaje (Catorci, Gatti, & Cesaretti, 2012; Milchunas, Lauenroth, & Burke, 1998). Debido a ello, la actividad del pastoreo puede afectar positiva o negativamente a este tipo de servicios dependiendo de las prácticas que se implementen.

En relación a los servicios culturales, diversos beneficios no-materiales han sido reconocidos a la agrobiodiversidad ganadera, como su contribución al patrimonio cultural, la identidad y los valores espirituales, así como importantes funciones en la educación, la recreación y la estética del paisaje (Marsoner et al., 2018). La conservación de las razas ganaderas autóctonas se ha considerado como un bien público global (World Bank, 2009), dado que representa un legado histórico y cultural. Las razas ganaderas están de hecho ligadas al conocimiento tradicional sobre manejo de los sistemas de producción (Leroy et al., 2018).

1.3. El origen de la diversidad ganadera

1.3.1. Los caminos de la domesticación

La domesticación puede interpretarse como un largo y complejo proceso coevolutivo, en el que, junto a las interacciones entre animales, platas y seres humanos, han mediado factores ecológicos, biológicos y culturales (Larson & Fuller, 2014; Zeder, 2017a). Persisten todavía numerosos interrogantes sobre el proceso de domesticación y la diversificación de las especies domésticas. No obstante, se reconoce que la domesticación parece estar definida por la dependencia entre domesticadores y domesticados, consecuencia de una progresiva interacción, de la que ambas partes resultan beneficiadas. Un proceso determinado por el aumento paulatino de la actividad trasformadora y creativa de los seres humanos (Zeder, 2015). Resultado de ello es la gran diversidad intraespecífica existente en las especies domesticadas, que se refleja en el alto número de razas ganaderas existente (FAO, 2015b).

Zeder (2012) propone tres vías principales de domesticación, que se han ido solapando en el tiempo. En la primera de ellas, la vía comensalista, los animales entrarían en contacto con los seres humanos atraídos por los desperdicios o la posibilidad de cazar otros animales presentes en el entorno de los asentamientos humanos. De este modo se originaría un proceso de habituación a la presencia humana, que conduciría al establecimiento de las relaciones de domesticación. Se considera que este fue el caso de por ejemplo perros y pollos, y tal vez del cerdo. La segunda vía, seguida por la mayoría de las especies domesticadas, en particular por los rumiantes, es la vía de la caza. Estos animales eran habitualmente cazados por los grupos humanos, de acuerdo con una creciente organización y planificación, cuyos efectos favorecieron la mayor disponibilidad de presas. Medidas como el control en la disposición de las fuentes de alimento o la promoción de hembras frente a machos, debieron dar lugar a un pastoreo primitivo, que con el tiempo se fue intensificando, ejerciendo una presión cada vez mayor en la reproducción de estos animales. Esta es la vía de domesticación que siguieron vacas, ovejas y cabras.

Consecutivamente a la segunda vía, muchas de las especies domesticadas sufrieron procesos orientados a la obtención de otros productos y servicios distintos de la carne, como la leche, la lana o la tracción (Larson & Fuller, 2014). Este proceso es conocido como la revolución de productos secundarios (Sherratt, 1983). Por último, la tercera vía, más reciente en el tiempo, fue guiada en gran medida por el conocimiento desarrollado a través de esta diversificación de los productos secundarios. Se trata de la vía directa, donde ciertos animales con características deseables se vieron sometidos a la selección y manejo directo por parte de los humanos, como fue el caso de los caballos y los burros.

1.3.2. La diversificación de los animales domésticos

La dispersión de los animales domesticados desde sus centros de origen, tuvo lugar a través de las rutas migratorias de las poblaciones humanas (Zeder, 2017b), a menudo obligados a superar la capacidad adaptativa de sus parientes silvestres (Ethier et al., 2017). Esta dispersión geográfica del ganado tuvo efectos diversos que influyeron en la aparición de una mayor variabilidad dentro de cada una de las especies domesticadas (Larson & Fuller, 2014). Por un lado, el alejamiento y aislamiento respecto a los lugares de origen y sus condiciones ambientales promovieron eventos de deriva genética (Mignon-Grasteau et al., 2005). Por otro lado, los procesos de cruzamiento con ejemplares silvestres en los nuevos territorios parecen haber sido habituales, teniendo una gran relevancia en el desarrollo de la variabilidad intraespecífica en las especies domésticas y marcando la introducción de nuevos genes (Larson & Fuller, 2014).

Asimismo, la adaptación a nuevos ambientes locales, sistemas productivos y la diversificación de productos, ha fomentado la adquisición y heredabilidad de nuevos rasgos en los animales domésticos, como respuesta a la presión selectiva por parte de los seres humanos y los ambientes antropizados (Zeder, 2017a). Este proceso se ha ido repitiendo en fases subsecuentes de la historia humana (Felius et al., 2014). Asimismo la relajación de la selección natural, como por ejemplo la menor presión de depredadores en los ambientes antrópicos o la disminución de la competencia con otras especies de herbívoros, ha fomentado la aparición de nuevos fenotipos como colores en las capas animales sin significado adaptativo (Fang, Larson, Soares Ribeiro, Li, & Andersson, 2009). Por último, el traslado entre áreas y el cruzamiento con los animales ya establecidos en las nuevas zonas de acogida, incluyendo tanto silvestres como domésticos, ha sido común a lo largo de toda la historia, determinando el devenir de las poblaciones locales (Felius et al., 2014).

Producto de todo ello, se han ido formando y manteniendo diversas subpoblaciones intraespecíficas de animales domésticos, genética y fenotípicamente diferenciadas entre sí. Del mismo modo, debido a que los sistemas ganaderos hasta tiempos muy recientes han sido mayoritariamente extensivos, dependientes de los recursos cercanos y ligados a la tierra, la selección natural mantuvo un papel significativo en las dinámicas de adaptación y diversificación (Kim et al., 2016), a pesar de los procesos ya comentados, mediados por la selección cultural.

1.3.3. La aparición del concepto de raza ganadera y la erosión actual de la agrobiodiversidad

A partir del s. XVIII aparece una nueva etapa en el desarrollo de la agrobiodiversidad ganadera, al empezar a aplicarse una selección controlada y sistematizada sobre ciertas subpoblaciones de animales domésticos, orientada a la selección de determinados caracteres de interés (Felius et al., 2014). Es en este periodo cuando aparece el concepto de raza ganadera (Hall, 2004), que irá ligado a grupos de animales con fenotipos homogéneos, sometidos a selección intencionada, decidida y controlada por grupos de criadores, generalmente ligada a lograr una mayor eficiencia en las funciones para las que la raza fue seleccionada.

Durante los últimos dos siglos, pero especialmente a partir de la segunda mitad del s. XX, los procesos de industrialización y mejora de las técnicas productivas y reproductivas de la ganadería han fomentado la proliferación y dominancia a escala global de un grupo reducido de razas altamente especializadas y con ello la homogeneización de los sistemas de producción, bajo condiciones de manejo controladas (FAO, 2015a). Todo ello ha llevado a una gran erosión de la diversidad ganadera global, debido fundamentalmente al reemplazo de razas locales, su cruzamiento con las razas industriales o el abandono de aquellas razas menos rentables en la economía globalizada (FAO, 2015b). En la actualidad, el sistema de información sobre animales domésticos de la FAO (DAD-IS) considera que solo un 8% de las razas ganaderas locales (autóctonas de determinados territorios) no está amenazada (FAO, 2019). En la Figura 1 se presenta un esquema conceptual resumen de los procesos que han intervenido en la conformación de las razas ganaderas actuales.

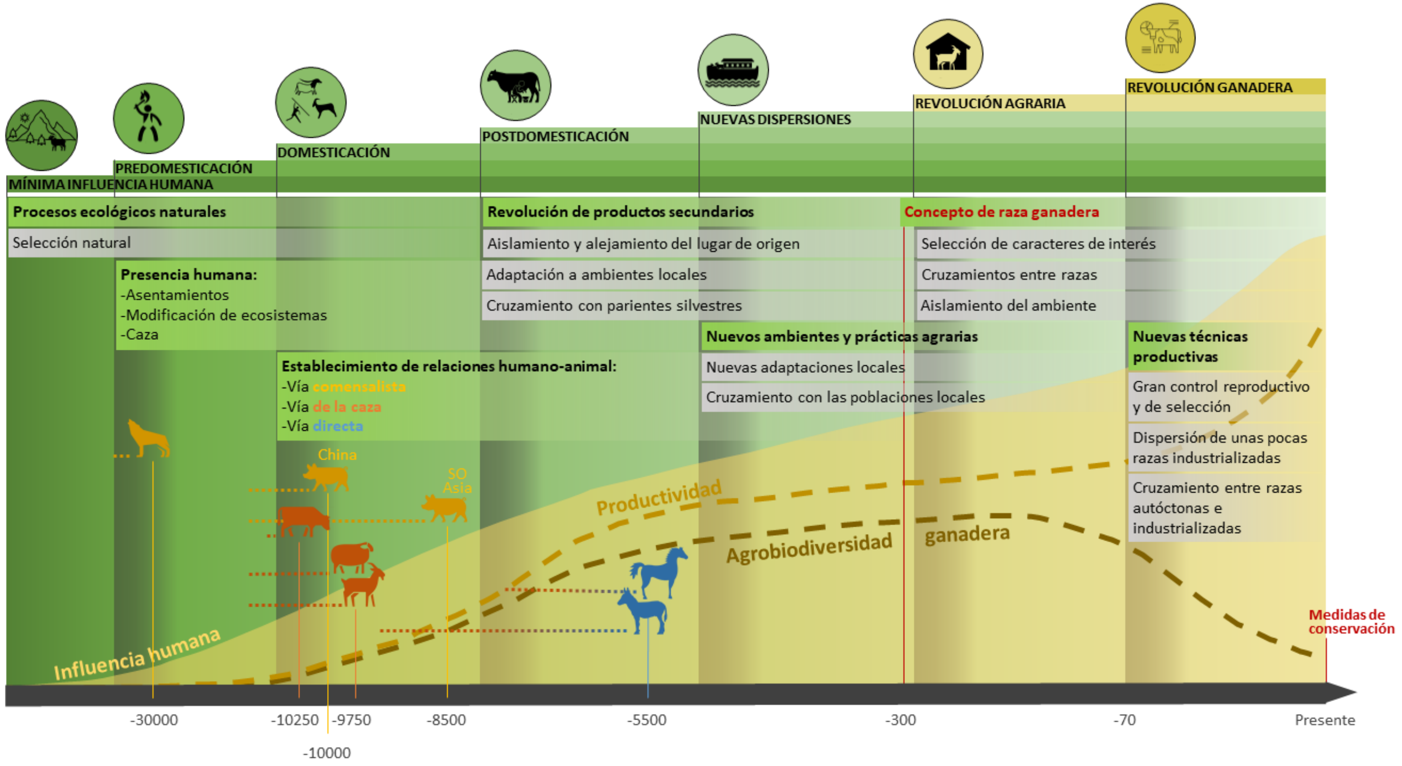

Figura 1: Esquema conceptual del origen de la diversidad ganadera incluyendo la dinámica de factores ambientales y humanos a lo largo de la historia. Elaboración propia.

1.4. Las razas ganaderas autóctonas, grandes desconocidas

Debido a la gran amenaza sobre la diversidad ganadera, existe un acuerdo internacional para su conservación, esencialmente centrado en los recursos genéticos (Interlaken Declaration, 2007). El mencionado concepto de raza ganadera presenta limitaciones para la aplicación de políticas efectivas. Se trata de una noción más cultural que técnica, que difiere entre países y regiones, haciendo difícil la caracterización de estas entidades mediante una aproximación meramente genética (Boettcher et al., 2010). La FAO (2000), por ejemplo, considera válidos para ser incluidos en el concepto de raza, tanto los grupos homogéneos subespecíficos de animales domésticos con características externas que les diferencian de otros grupos, como aquellos grupos homogéneos que, aunque semejantes a otros, su área de distribución claramente disyunta ha llevado a una aceptación general de su distinta identidad.

En general, aunque el concepto de raza tenga algunas ambigüedades, que requerirían ser precisadas, se suele aceptar que son grupos de animales domésticos con características físicas y productivas semejantes y heredables. Diferenciados, ya sea por características fenotípicas o por el área geográfica y sometidos a manejo por parte de grupos humanos (Hall, 2004). Pese a su relativa indefinición el concepto de raza, está ampliamente admitido como unidad de manejo genético (Felius, Theunissen, & Lenstra, 2015) y es aceptado por la FAO como la unidad de conservación de los recursos genéticos animales y la agrobiodiversidad ganadera (FAO, 2007).

Asimismo, existe una especial preocupación por intentar preservar las razas locales debido a su mayor grado de amenaza. El interés reside en que estas razas suponen una importante reserva de variabilidad genética, presentan un mayor grado de adaptación a condiciones extremas, están ligadas al conocimiento ecológico local y proporcionan alimentos de alta calidad. Destacarían así, por su valor estratégico, como apoyo para afrontar retos futuros (Sponenberg, Beranger, Martin, & Couch, 2018).

Sin embargo, las razas ganaderas autóctonas son grandes desconocidas. Están peor descritas y caracterizadas que las razas especializadas (Hoffmann, 2010), y están siendo ignoradas en la literatura científica sobre agrobiodiversidad. A modo de ejemplo, una búsqueda bibliográfica rápida en las bases de datos Web of Knowledge y Scopus, utilizando las palabras clave "Agrobiodiversity" & "Livestock" & "Breed" da como resultado un total de 8 y 10 artículos respectivamente, incluyendo artículos de investigación en revistas especializadas, revisiones, capítulos y libros científicos (Figura 2).

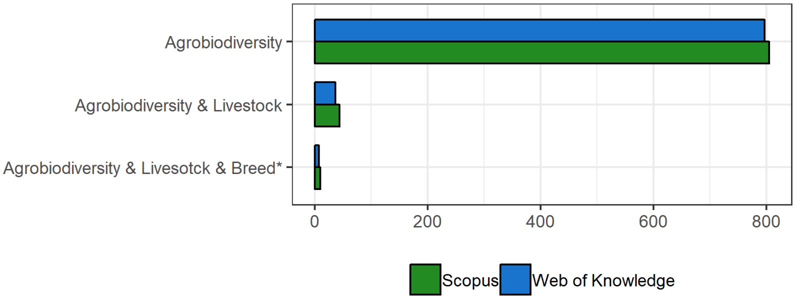

Figura 2. Resultados de la búsqueda de palabras clave "Agrobiodiversity", "Livestock" y "Breed" en las bases de datos *Scopus* y *Web of Knowledge*, consultado el 17 de febrero de 2020. Elaboración propia.

Como síntesis de lo anterior, podemos afirmar que, a pesar de que las razas autóctonas son valoradas y reconocidas por su adaptación a condiciones locales (Hoffmann, 2011), aún no se conocen en profundidad los mecanismos y procesos que facilitan dicha adaptación (Boettcher et al., 2014). Por otra parte, a pesar de que la conservación *in situ* es el método de conservación recomendado (FAO, 2007), la literatura científica se centra mayoritariamente en cuestiones productivas y genéticas (Hoffmann, 2011), ignorando la perspectiva ecológica. De hecho, aunque ciertas razas son reconocidas por su adaptación a condiciones extremas, no están siendo utilizadas por ejemplo en las estrategias de adaptación al cambio climático (Hoffmann, 2010), ni incluidas en los estudios que consideran la biodiversidad como medida y herramienta para la adaptación (como por ejemplo en: Campbell et al., 2009; Kazemi, Klug, & Kamkar, 2018).

En general, la investigación en ecología sobre la diversidad ganadera se ha centrado en los efectos del pastoreo y usos ganaderos sobre otros componentes de los ecosistemas, como por ejemplo la vegetación —composición de los pastos o la estructura del paisaje—, el suelo o las especies silvestres, mientras que la literatura específica de las razas ganaderas autóctonas se centra en aspectos productivos y genéticos (ver a modo de ejemplo las Figuras 3, 4 y 5). De modo que, a pesar de algunos antecedentes —por ejemplo, en nuestro país los trabajos sobre comportamiento en pastoreo de algunas razas y su interacción con los recursos (Castro, Castro, & Gómez Sal, 2004; De Miguel, Rodríguez, & Gómez Sal, 1997; Gómez Sal, Rodríguez, & De Miguel, 1992)— el estudio de la autoecología de las razas ganaderas autóctonas ha quedado relegado.

Figura 3. Nube de palabras formada con los títulos de los artículos, revisiones y libros del área de ecología encontrados en la búsqueda de palabras clave "diversity" & "livestock" en la base *Web of Knowledge*, consultada el 17 de febrero de 2020. Elaboración propia.

Figura 4. Nube de palabras formada con los títulos de los artículos, revisiones y libros del área de ecología encontrados en la búsqueda de palabras clave "diversity" & "livestock" & "breed" en la base *Web of Knowledge*, consultada el 17 de febrero de 2020. Elaboración propia.

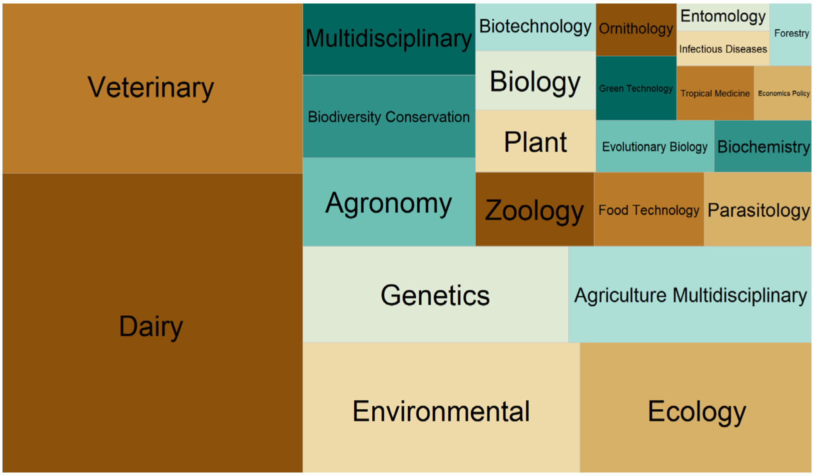

Figura 5. Proporción de artículos, revisiones y libros (878 en total) por área temática encontrados en la búsqueda bibliográfica en la base *Web of Knowledge* con las palabras clave "livestock" & "local breed" OR "authochthonous breed" OR "native breed" OR "heritage breed" OR "landrace breed" OR "endangered breed", consultada el 17 de febrero de 2020. Elaboración propia.

1.5. LA DISTRIBUCIÓN DE LA AGROBIODIVERSIDAD GANADERA

Para fomentar el uso racional y la conservación de la agrobiodiversidad ganadera es fundamental conocer su distribución (FAO, 2007). Por un lado, como se ha ido explicando, la heterogeneidad espacial ha jugado y aún juega un papel importante en los procesos evolutivos de los animales domésticos (Larson & Fuller, 2014). Por ello, las aproximaciones geográficas resultan imprescindibles para investigar los mecanismos de la adaptación (Boettcher et al., 2014; Mdladla, Dzomba, & Muchadeyi, 2017). Por otro lado, conocer la distribución de las razas es necesario para mejorar su gestión, entre otras razones para poder centrar los esfuerzos de conservación en áreas geográficas prioritarias (FAO, 2007) o para conocer en profundidad los riesgos y amenazas derivados del cambio global (Hoffmann, 2010), tanto para las razas como sobre los sistemas de producción. Asimismo, resultaría también de gran utilidad para mejorar la estimación de la producción ganadera, evaluar su impacto ambiental, mejorar la sanidad animal, controlar las enfermedades emergentes y entender mejor los aspectos sociales y culturales vinculados a la ganadería (Robinson et al., 2011).

No obstante, pese a su importancia, los aspectos geográficos y el mapeo de sistemas ganaderos a nivel mundial apenas se ha iniciado. La FAO identifica esta falta de información sobre la distribución de los sistemas de producción de las diferentes especies ganaderas, como el principal problema para su cartografía (Robinson et al., 2011). Las propuestas actuales se basan en la modelización por especie de la densidad de animales en el territorio (Neumann et al. 2009; Robinson et al., 2014) o en la adecuación de razas foráneas para ser introducidas en nuevas zonas agroclimáticas (Lozano-Jaramillo et al., 2018). Sin embargo, estos trabajos no incluyen el estudio de la distribución de diversidad ganadera local.

A pesar de las carencias de información y enfoque apuntadas, existen otras limitaciones, que podemos denominar intrínsecas al problema, para un estudio biogeográfico de la diversidad ganadera. En primer lugar, la ganadería se ha basado mayoritariamente en un número reducido de especies (Diamond, 2002), y si nos referimos a ungulados, las especies dominantes a escala mundial han sido en general domesticadas en ambientes cercanos dentro de un área geográfica específica (Zeder, 2015). Hoffmann (2013) alega que ello representa una dificultad, dado que no existirían diferencias biogeográficas marcadas entre las especies domésticas dominantes. No obstante, estas especies tienen una biología diferenciada, y han seguido diferentes procesos de diversificación y especialización a medida que se alejaban de los centros de origen (Ethier et al., 2017; Larson & Fuller, 2014). A pesar de ello la pregunta sigue abierta, ¿qué clase de presiones selectivas fomentaron la aparición de constelaciones de rasgos semejantes en especies diferentes? (Zeder, 2017a).

En segundo lugar, como ya hemos indicado, unas pocas razas, las especializadas para la ganadería industrial, se encuentran ampliamente distribuidas a nivel global (p. ej. Robinson et al. 2014), por lo que su distribución se superpone con sistemas de producción muy diferenciados y solapa con la de numerosas razas locales, que a su vez se encuentran ligadas a una gran diversidad de ambientes y variados sistemas de manejo en extensivo (Hoffmann, 2010). Por último, las importantes carencias de información georreferenciada, ya mencionadas, sobre las razas autóctonas, los sistemas de producción asociados a ellas o sobre aquellos rasgos morfológicos, productivos o reproductivos de posible interés en estas razas (Hoffmann, 2011; Robinson et al., 2011).

Como síntesis derivada de lo anterior podemos indicar que, aunque la dispersión del ganado en el mundo ha estado asociada a las migraciones humanas (Hall, 2004; Zeder, 2017b), los factores ambientales han debido ser también determinantes en la diversidad de razas. Por ejemplo, existen evidencias de la influencia de factores climáticos en la selección del genoma de distintas especies domésticas y razas ganaderas, en relación con procesos fisiológicos (Bertolini et al., 2018; Lv et al., 2014; Xu et al., 2015). Del mismo modo, la dispersión de las especies domésticas estuvo ligada a la disponibilidad de recursos en las nuevas zonas (Ethier et al., 2017) y a la plasticidad adaptativa de estos animales (Zeder, 2017a).

1.6. La agrobiodiversidad ganadera en España

La ganadería ha sido una actividad preeminente en España a lo largo de su historia, con una gran importancia económica, social y cultural (Gómez-Sal, 2001). El territorio peninsular de España, donde se sitúa el trabajo de esta tesis, se caracteriza por una larga historia de usos agrícolas y heterogeneidad de paisajes, que han determinado la distribución de la biodiversidad (Gómez-Sal, 2017). También ha fomentado la creación de un elevado número de razas ganaderas autóctonas (Tabla 1) que han conseguido llegar hasta nuestros días, aunque la mayor parte en un estado de gran amenaza (MAPA, 2019).

No tenemos constancia exacta de cuándo se formaron las distintas razas autóctonas españolas, aunque ya desde la Edad Media existe información sobre la importancia económica de alguna de ellas, como en el caso de la oveja Merina. Según distintas fuentes, la ganadería en

Tabla 1. Número de razas ganaderas autóctonas españolas, clasificadas según su grado de amenaza (MAPA, 2019; 129FAO 2017) y comparativa con los datos globales (obtenido de Leroy et al., 2016). Elaboración propia.

Especie	Razas de Fomento	Razas en Peligro de Extinción	Extintas	Total	Media de razas por país	País con el número máximo de razas (nº)
Bovino	8	32	9	49	12	Reino Unido (107)
Ovino	10	34	1	45	6	Italia (57)
Caprino	6	16	2	24	9	Reino Unido (109)
Porcino	3	9	5	17	6	China (142)
Asnal	0	6	0	6	-	-
Caballar	1	15	0	16	-	-

España y su distribución territorial mantuvo una estructura bastante estable durante toda la Edad Moderna tras la expansión de esta actividad con la Reconquista (García Sanz, 1994). Durante la Edad Moderna y en general hasta el predominio de la agricultura y la ganadería industriales, los sistemas agrícolas seguían un modelo tradicional, de integración de la producción para mejorar el aprovechamiento de los distintos recursos. De este modo la gestión de los aprovechamientos agrícolas, ganaderos y forestales era interdependiente y se manejaba de manera cohesionada, aprovechándose en los distintos sistemas los subproductos provenientes del resto de sistemas (Valle Buenestado, 2011).

El Censo Ganadero de 1865 y el Avance sobre la Riqueza Pecuaria de España de 1891 ponen de relieve la importancia histórica de las razas ganaderas españolas, señalando su gran variedad en los sistemas extensivos de aquel momento (Junta Consultiva Agronómica, 1891; Junta General Estadística, 1868). También fuentes internacionales valoran la gran diversidad ganadera existente en España a principios de siglo XX (Faelli, 1932). Por todo ello, podemos considerar que las razas ganaderas autóctonas que aún podemos apreciar como recursos valiosos han estado asociadas a sistemas extensivos y tradicionales. Muy probablemente una gran mayoría de estas razas sean anteriores al siglo XIX, por lo que ya estaban presentes al inicio de la industrialización del campo español, y han persistido a pesar de la dinámica transformadora del sector ganadero a lo largo del siglo XX (Figura 6). Este hecho puede también entenderse como un respaldo a la racionalidad y coherencia de los agroecosistemas tradicionales, dentro de los cuales las distintas razas desempeñaban un papel esencial (Gómez-Sal, 2001; Montserrat, 2009).

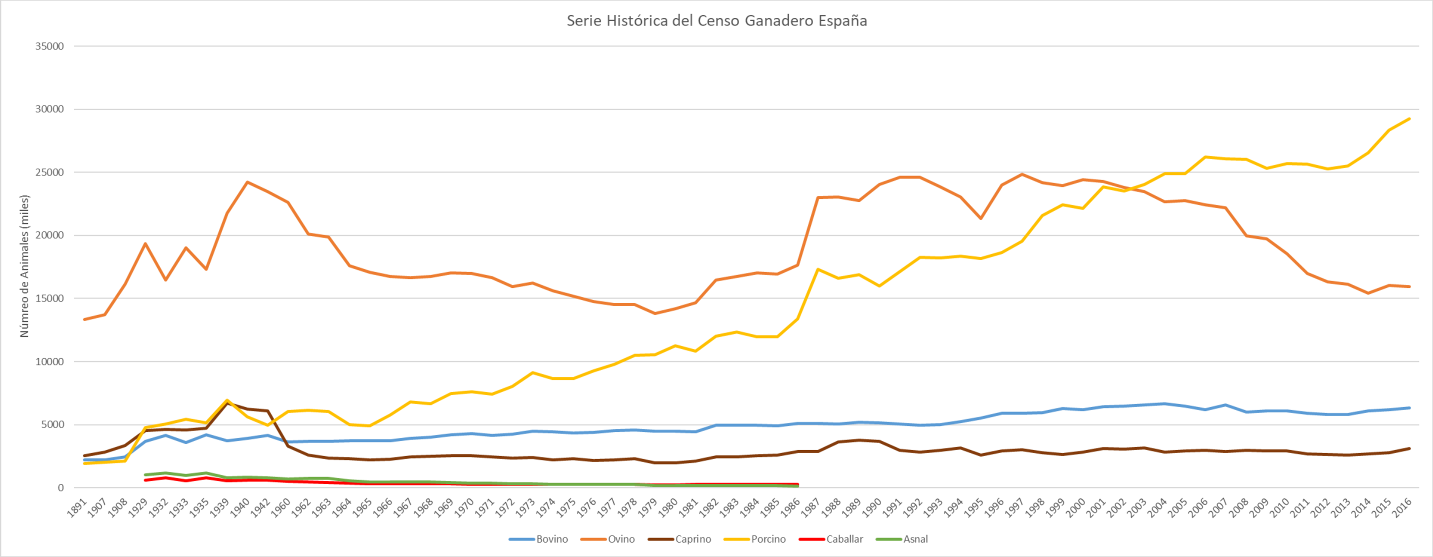

Figura 6. Serie histórica del número de animales en España desde 1891 hasta 2016 para las distintas especies ganaderas. Se han quitado aquellos años cuya metodología no respondía con la general, para minimizar sesgos. Fuente: Censos Ganaderos-Anuarios de Estadística Agraria. Elaboración propia.

A.2. OBJETIVOS DE LA TESIS DOCTORAL

Esta tesis pretende contribuir al conocimiento de las razas ganaderas autóctonas. Su objetivo principal es analizar los patrones de distribución de la agrobiodiversidad ganadera en la España peninsular para facilitar el desarrollo de una gestión productiva integrada y sostenible, compatible con la conservación de la biodiversidad. Se considera que la distribución de las razas estaría marcada por factores ambientales y humanos, debido a la importancia que estos han tenido en el desarrollo de la agrobiodiversidad ganadera. En concreto se estudiará la distribución de las razas de las diferentes especies ganaderas, relacionándolas con factores ambientales que se expresan en escalas amplias, tanto abióticos como bióticos, su concordancia con la distribución de la diversidad silvestre y el efecto que la huella humana, a través de los cambios en los usos agrarios ocurridos en las últimas décadas.

Los objetivos específicos son:

- Analizar los patrones de distribución de las diferentes especies de ungulados domésticos, considerando la diversidad de razas autóctonas, para explorar su capacidad adaptativa en relación con las condiciones ambientales del territorio estudiado. A partir de ello, establecer un conjunto de ecorregiones pecuarias en la España peninsular.

- Investigar la relación entre los patrones de distribución de la diversidad de razas ganaderas y distintos componentes de la diversidad silvestre.

- Cuantificar la influencia de los determinantes ambientales sobre la distribución original de las razas locales y el efecto de los cambios recientes de los usos del suelo sobre su distribución actual.

A.3. ORGANIZACIÓN DE LA TESIS DOCTORAL

Esta memoria de tesis doctoral está dividida en cuatro secciones. La primera sección A, contiene un resumen general del conjunto de la tesis. Incluye los antecedentes y el marco teórico, los objetivos generales y específicos, la metodología general, así como un resumen de cada uno de los trabajos de investigación que constituyen los capítulos y de las principales conclusiones.

La sección B, reúne los tres capítulos (Chapter 1-3) en los que se recogen los trabajos de investigación presentados (ver Tabla 2). Estos capítulos están estructurados como manuscritos científicos en: resumen, introducción, métodos, resultados, discusión, referencias y material suplementario. La presentación de estos capítulos se realiza en inglés, idioma en que están redactados, encontrándose en proceso de publicación. En ellos se incluye información detallada de los objetivos específicos, las hipótesis, así como los métodos y resultados pormenorizados, discusión y conclusiones.

La sección C, presenta en primer lugar la discusión general, donde se diserta sobre la contribución de los tres trabajos al conocimiento de las razas ganaderas autóctonas y la conservación de la biodiversidad, tanto doméstica como silvestre. En segundo lugar, se presentan las conclusiones que sintetizan los principales resultados de la tesis. Por último, la sección D, presenta una guía visual de las razas autóctonas actuales estudiadas (se trata de una información complementaria que se presenta a modo de anexo, aunque elaborada con motivo de esta tesis), el currículo vitae de la autora y los agradecimientos.

A.4. METODOLOGÍA GENERAL

4.1. Los datos sobre las razas ganaderas autóctonas

Para alcanzar los objetivos de esta tesis, uno de los principales desafíos era la obtención de una base de datos con información detallada sobre la distribución de las razas ganaderas autóctonas españolas. Debido a que las bases públicas del Sistema Nacional de Información de las Razas Ganaderas de España solo disponen de información desglosada a nivel de provincia como menor resolución, para el desarrollo de esta tesis se siguió un largo proceso de recopilación de datos.

En primer lugar, se realizó una revisión de: i) las principales antologías

Tabla 2. Resumen de los trabajos de investigación presentados en esta tesis y publicaciones relacionadas.

	Título	Objetivo	Hipótesis	Métodos		Publicación
				Variables	Estadística	
Capítulo 1	Patrones espaciales de la biodiversidad pecuaria. Determinantes ecológicos y regionalización de las razas ganaderas autóctonas españolas.	Analizar los patrones de distribución de las razas ganaderas de las diferentes especies domesticadas y establecer ecorregiones pecuarias en la España peninsular.	La diversidad de razas en cada territorio responderá a gradientes contrastados, relacionados con la heterogeneidad ambiental y la capacidad adaptativa de las especies domesticadas a los ambientes locales.	-Áreas de origen de 119 razas autóctonas españolas. -24 variables ambientales, basadas en la orografía, el clima, la litología, la producción y el tipo de vegetación.	-Clasificaciones jerárquicas y ordenaciones multivariantes. -Randomizaciones e índices de preferencia.	Velado-Alonso, Morales-Castilla & Gómez-Sal (en revisión). Agriculture, Ecosystem & Environment.
Capítulo 2	Sobre las relaciones entre la distribución de la vida silvestre y la diversidad del ganado en la España peninsular.	Evaluar la relación entre los patrones de distribución de la diversidad silvestre y domesticada en la España peninsular.	La distribución de la biodiversidad silvestre y domesticada está relacionada en la España peninsular debido al efecto indirecto del ambiente y la gran influencia humana en dicho territorio.	-Riqueza total, de vacas y de ovejas de las razas autóctonas españolas. -Riqueza de mamíferos, aves, anfibios y reptiles nativos españoles, y riqueza de ciertos grupos específicos. -3 variables climáticas. -1 factor humano.	-Modelos de regresión geográficamente ponderados.	Velado-Alonso, Morales-Castilla, Rebollo & Gómez-Sal (en revisión). Diversity & Distribution.
Capítulo 3	Los seres humanos distorsionan la adaptación de la agrobiodiversidad. Cambios recientes en la distribución de las razas ganaderas autóctonas españolas.	Cuantificar el efecto de los factores ambientales en la distribución de las razas locales a través del tiempo y explorar cómo los cambios de uso del suelo han determinado la ubicación actual las razas.	Los factores ambientales determinan la distribución de la agrobiodiversidad ganadera debido a la importancia que el ambiente ha tenido en los procesos de diversificación de los animales domesticados	-Riqueza total y de las especies bovina, ovina, caprina, porcina, asina y equina, de razas ganaderas autóctonas españolas. -4 factores ambientales. -Clasificación de los cambios de uso del suelo en los municipios españoles.	-Modelos de regresión geográficamente ponderados. -Regresiones logísticas ordinales	Velado-Alonso, Morales-Castilla & Gómez-Sal (en revisión). Scientific Reports.

sobre razas ganaderas autóctonas españolas, ii) la legislación sobre ganadería extensiva y razas y iii) los anuarios de estadística agraria, publicados a lo largo del s. XX. Se comprobó con ello que no existe información disponible pormenorizada o estandarizada sobre las dinámicas de la distribución de las razas ganaderas autóctonas a lo largo del tiempo. Por ello, se estableció una doble estrategia de recopilación de la información geográfica de las razas.

Por un lado, se determinaron las áreas de origen de cada una de las razas actuales y extintas a través de una revisión de las principales antologías sobre razas españolas (Tabla 3). Para ello, primero, se utilizó el Catálogo Oficial de Razas Ganaderas para identificar todas las razas ganaderas autóctonas de la España peninsular actualmente reconocidas (MAPA, 2019). Segundo, dado que el Catálogo Oficial no reconoce aquellas razas extintas, se utilizó la información facilitada en el DAD-IS sobre razas ganaderas autóctonas consultada en 2017 (FAO DAD-IS, 2017) y se incluyeron como extintas aquellas razas así reconocidas en este sistema que también aparecen mencionadas en las antologías consultadas.

Se identificaron como áreas de origen aquellas zonas consideradas por los autores como tales, donde cada raza fue descrita por primera vez, y cuando esto no establa claro, se asignó la región de distribución más antigua, excepto para aquellas razas porcinas del cerdo Ibérico que en el pasado eran consideradas variedades (Torbiscal, Entrepelado, Retinto, Lampiño, y Manchado de Jabugo). Para estas últimas razas no se encontró información específica diferenciada para la distribución en el pasado.

Asumimos que estas áreas de origen de las razas autóctonas representarían en cierto modo los dominios históricos y naturales de las razas ganaderas (Colino-Rabanal, Rodríguez-Díaz, Blanco-Villegas, Peris, & Lizana, 2018). Consideramos, que estas áreas representan la distribución aproximada en dónde las razas estaban localizadas previamente a la industrialización de la agricultura, es decir, cuando los sistemas estaban mayoritariamente basados en los recursos locales y determinados por factores ambientales. Asimismo, se corresponderían con las áreas donde las razas han pervivido durante más tiempo, basándonos en la información disponible, considerando diversas fuentes desde mediados del s. XIX (Junta Consultiva Agronómica, 1891; Junta General Estadística, 1868).

Las áreas fueron digitalmente mapeadas utilizado el sofware QGIS 2.18.26 “Las Palmas” (QGIS Development Team, 2017). Se utilizaron como referencia base para la delimitación: el modelo digital del terreno, las capas de ríos y cuencas de España, las provincias agrarias y los mapas de

Tabla 3. Listado de las fuentes bibliográficas consultadas para la identificación de las áreas de origen de las razas ganaderas autóctonas españolas.

Autor	Año	Edición	Título
Faelli, F.	1932	Edición Española- Revista Veterinaria de España (1ªEdición 1902)	Razas Bovinas, Equinas, Porcinas, Ovinas y Caprinas. Traducción anotada por Tomás de la Fuente Muñoz.
Aparicio, G.	1947	Segunda Edición (1ª Edición 1944)	Zootecnia Especial. Etnología compendiada.
Esteban Muñoz, C. & Tejón Tejón, D.	1980	Primera Edición	Catálogo de Razas Autóctonas Españolas. I-Especies Ovina y Caprina
Sánchez Belda, A.,	1984	Primera Edición	Razas Bovinas Españolas
Sámchez Belda, A. & Sánchez Trujillano, M.C.	1986	Segunda Edición (Primera Edición 1974).	Razas Ovinas Españolas
García Dory, M.A., Martínez Vicente, S. & Orozco Piñán, F.	1990	Primera Edición	Guía de Campo de las Razas Autóctonas de España
Sánchez Belda, A.	2002	Primera Edición	Razas Ganaderas Españolas Bovinas
Esteban Muñoz, C.	2003	Primera Edición	Razas Ganaderas Españolas Ovinas
Yanes García, J.E.	2005	Primera Edición	Razas Asnales Autóctonas Españolas
Esteban Muñoz, C.	2008	Primera Edición	Razas Ganaderas Españolas Caprinas
Sánchez Belda, A.	2012	Primera Edición	Razas Ganaderas Españolas Caballares

Información disponible en el ARCA (Sistema Nacional de Información de las Razas Ganaderas) website del MAPA (Ministerio de Agricultura, Pesca y Alimentación) también ha sido consultada: http://www.mapama.gob.es/es/ganaderia/temas/zootecnia/razas-ganaderas/razas/catalogo/ consultada entre marzo y julio de 2017.

las divisiones administrativas de municipios, provincias y comunidades autónomas.

En segundo lugar, para obtener la información detallada de la distribución actual de las razas, utilizamos la información referida en el Programa Nacional de Conservación, Mejora y Fomento de las Razas Ganaderas Españolas. Se realizó una recopilación de todos los números de identificación de las explotaciones ganaderas colaboradoras con dicho programa referidas a algún momento del periodo 2017-2019. Esta información fue obtenida de diversas fuentes. La mayor parte de la información fue facilitada por la Administración, ya sea a través del servicio ARCA del Ministerio de Agricultura o a través de los servicios autonómicos. Sin embargo, para aquellas razas cuya información no estaba disponible a través de esta vía (un total de 29 razas), se contactó directamente con las diversas Asociaciones de Criadores (FEAGAS, FEDERAPES, y asociaciones de razas concretas) y para aquellas razas en las que fue imposible recopilar la información a través de su asociación, utilizamos el listado de explotaciones colaboradoras especificado en el programa de conservación, publicado posteriormente al año 2015. De este modo se recopiló información de 117 razas, una única raza fue imposible de recopilar, el cerdo Euskal Txerria.

Con dicha información se determinó el municipio en el que se encuentran las explotaciones con razas ganaderas autóctonas en la actualidad. Para aquellas razas consideradas por el Catálogo como "en peligro de extinción" (en torno a un 80% de las incluidas en esta tesis) el 100% de las explotaciones con la raza son colaboradoras en los programas de conservación, y por tanto se puede asumir que el total de explotaciones donde se cría la raza ha sido incluido. Sin embargo, para aquellas catalogadas como "de fomento" (aproximadamente un 20% de las razas), no ocurre lo mismo. Para estas últimas solo en 10 razas fue posible recopilar más del 80% de los datos, para 7 de ellas entre un 50-80% de las explotaciones han sido integradas y para 4 de ellas, menos de la mitad de la información pudo ser recopilada a través del método seguido (son estos los casos de: oveja Carranzana, oveja Ojinegra de Teruel, vaca Morucha y vaca Pirenaica). Por último, en el caso de las razas de fomento del cerdo Ibérico —Ibérico, Entrepelado y Retinto— y el caballo Español (4 razas en total), no podemos estar seguros de dicho porcentaje, pero consideramos que es probable que sea menos de la mitad. De modo que solo para un 8% de las razas reconocidas en la actualidad incluidas en el trabajo, la información disponible es incompleta. Toda esta información fue digitalizada y cartografiada utilizando el software R (R Core Team, 2019).

Creemos necesario resaltar que la información recopilada mediante este proceso es la más completa disponible en la actualidad, ya que integra datos de distribución en dos momentos históricos del conjunto de todas las razas autóctonas de fomento y en peligro de extinción para la España peninsular. Esta información reflejaría los cambios acontecidos a lo largo de las últimas décadas en la ganadería española, siendo indicadora de los procesos de expansión, reducción o modificación en la distribución de las razas asociados a la industrialización agraria y a la pérdida de población en una amplia zona del espacio agrario de nuestro país.

4.2. Los factores ambientales y humanos y la distribución de las especies silvestres

Para evaluar la influencia ambiental se han utilizado diversos factores provenientes de distintas fuentes. Las variables climáticas proceden de la capa de 30s WorldClim version 2 y la base de datos SPREAD. Las variables topográficas han sido obtenidas del modelo digital del terreno GTOPO30. La litología fue extraída del Mapa Geológico Español a escala 1: 1000000 de 1995. La productividad de la vegetación fue derivada de la información del Global MOD13Q1 para el periodo 2001-2017. El tipo de vegetación se obtuvo del Mapa Forestal Español a escala 1:50000. Por último, los pisos bioclimáticos fueron obtenidos del Mapa de Series de Vegetación de 1987 de Rivas-Martínez.

En cuanto a los factores humanos, se ha utilizado la Huella Humana en el 2009, como indicador de la perturbación de los sistemas naturales por parte de los seres humanos. También, se ha utilizado el mapa propuesto por Fernández-Nogueria y Corbelle-Rico de transiciones de uso del suelo basadas en la información del Corine Land Cover para el periodo 1990, 2000 y 2012, a nivel de municipio en España (Fernández-Nogueira & Corbelle-Rico, 2018). Ambos tipos de factores han sido utilizados para analizar la influencia de las actividades humanas en gradientes de biodiversidad.

La información referente a las especies silvestres fue obtenida a partir del Inventario Español de Especies Terrestres (MITECO, 2019). Los cuatro grupos de tetrápodos (mamíferos, aves, anfibios y reptiles) fueron clasificados para identificar todas las especies nativas, excluyendo las exóticas o típicas de ambientes acuáticos y marinos para mamíferos, aves y reptiles. Además, se realizó una segunda clasificación de los anteriores basada en las preferencias de hábitat de cada grupo con relación a los usos ganaderos y los paisajes agrarios. Con todo ello se calcularon distintos índices de riqueza que sirvieran como indicadores de la biodiversidad silvestre.

4.3. La escala y los análisis estadísticos

Los distintos capítulos de investigación estudian la agrobiodiversidad pecuaria en la España peninsular de manera amplia. La unidad base de muestreo elegida para el desarrollo de la tesis ha sido de aproximadamente 10 × 10 km, dado que es una escala con suficiente resolución para capturar la complejidad de la heterogeneidad espacial existente en la Península Ibérica, al mismo tiempo que facilita la exploración de los patrones espaciales de distribución considerando el conjunto del territorio peninsular de España.

En el caso del primer capítulo, el estudio geográfico se basa en la superficie ocupada por las distintas razas dentro de los rangos de las variables ambientales analizadas. De este modo, utilizando métodos de estadística multivariante se establecieron grupos de razas dentro de cada especie y se analizaron los gradientes espaciales que estos grupos forman basados en la heterogeneidad territorial. Posteriormente, se analizaron las variables ambientales asociadas por encima del azar a las áreas de ocupación de cada grupo mediante procesos de randomización e índices de preferencia. Con esta información se establecieron como Ecoregiones Pecuarias aquellas áreas donde coocurren más de un 50% de las variables asociadas estadísticamente con cada uno de los grupos de razas.

En el segundo y tercer capítulo se utilizaron modelos de regresión geográficamente ponderados. Esta técnica estadística no asume que un subconjunto de los datos represente al total del conjunto de los datos analizados, de manera que permite recoger estadísticamente la variación espacial. Dado que los procesos ecológicos que determinan la distribución de las especies tienen distintos efectos a distintas escalas espaciales (McGill, 2010), la escala a la que se realizan estos análisis determina los resultados. En el caso del segundo capítulo esta tiene una extensión de aproximadamente 100 km de radio. Dicha escala es adecuada para observar cambios en los gradientes ambientales y ha sido utilizada previamente para analizar la biodiversidad ibérica. En el tercer capítulo en cambio, se realizan los análisis a distintas escalas de análisis de manera que se puede comparar la variación espacial de las tendencias de los predictores.

La metodología seguida en el segundo capítulo se basa en un ajuste progresivo del modelo. Para ello compara los resultados entre versiones simplificadas, que únicamente incluyen subgrupos de predictores —un único predictor o combinaciones por pares—, y el modelo completo, que incluye todos los predictores. Los predictores utilizados en el modelo completo son; factores climáticos, la huella humana y alguno de los índices de riqueza de la agrobiodiversidad ganadera. De esta manera se analizan las relaciones en los patrones de distribución entre los distintos grupos de especies silvestres y la diversidad ganadera.

Por último, el tercer capítulo realiza dichos modelos geográficos utilizando los predictores ambientales para cuantificar su efecto en la distribución en el pasado y en el presente sobre las razas. Dado que ambas series de datos tienen una naturaleza diferente, se realizaron distintos modelos utilizando también distintas escalas de muestreo, para evaluar posibles sesgos. Finalmente, se realizaron regresiones logísticas ordinales para calcular la probabilidad de que ocurran procesos de intensificación o abandono en aquellas áreas que ocupan actualmente las razas ganaderas autóctonas.

En la Tabla 2 se puntualiza las distintas variables utilizadas en cada uno de los capítulos de investigación. Los detalles sobre la metodología seguida, así como para la extracción y utilización de cada una de las variables ambientales y humanas, así como las fuentes utilizadas y el significado biológico pueden ser encontrados en el desarrollo de los distintos capítulos de investigación.

A.5. RESUMEN DE LOS CAPÍTULOS DE INVESTIGACIÓN

Capítulo 1. Patrones espaciales de la biodiversidad pecuaria. Determinantes ecológicos y regionalización de las razas ganaderas autóctonas españolas.

Elena Velado Alonso, Ignacio Morales Castilla y Antonio Gómez Sal

Los animales domésticos tienen un papel central en el funcionamiento de los agroecosistemas. Sin embargo, la agrobiodiversidad ganadera apenas ha sido estudiada desde una perspectiva espacial y poco se sabe sobre la biogeografía de las razas ganaderas locales —las autóctonas de una determinada área geográfica—. El mapeo de los sistemas de producción y la agrobiodiversidad ganadera han estado limitados por la falta de datos sobre distribución y demografía de las razas ganaderas. Ello limita tanto el alcance de las medidas destinadas a conservar las razas amenazadas, así como la consideración de estas como instrumento para mejorar la sostenibilidad de los sistemas de producción ganadera en el marco del cambio global. En este trabajo se documenta la distribución de la diversidad intraespecífica de las especies bovina, ovina, caprina, equina y asinina, basada en las áreas de origen de 119 razas ganaderas autóctonas de la España peninsular. Los resultados muestran una distribución espacial contrastada entre las razas locales en las distintas especies estudiadas, la cual está asociada a gradientes ambientales. La distribución de las razas de vacuno está determinada por la altitud y la influencia atemperante del océano atlántico, mientras que las de las ovejas están más relacionadas con los climas continentales dentro del ámbito mediterráneo, especialmente aquellos de la meseta ibérica. Las razas de cabras están asociadas con factores limitantes del clima mediterráneo, como la estacionalidad de la precipitación o el relieve abrupto. Por otro lado, las razas de équidos están adaptadas a zonas específicas, incluyendo áreas en los extremos ambientales. La agrobiodiversidad ganadera es un producto eco-cultural, resultado de procesos coevolutivos entre humanos y animales. Nuestros resultados muestran una partición del espacio geográfico, señalando que la diversidad intraespecífica ha actuado como respuesta adaptativa de las especies domesticadas, a condiciones ambientales determinadas, lo que permite proponer una sectorización. En función de ello se han definido ecorregiones pecuarias, que podrían servir de apoyo para entender y mejorar los sistemas de producción extensivos, adaptados a diferentes condiciones, así como a la conservación de las razas ganaderas autóctonas españolas.

CAPÍTULO 2: SOBRE LAS RELACIONES ENTRE LA DISTRIBUCIÓN DE LA BIODIVERSIDAD SILVESTRE Y LA DIVERSIDAD DEL GANADO EN LA ESPAÑA PENINSULAR.

Elena Velado Alonso, Ignacio Morales Castilla, Salvador Rebollo y Antonio Gómez Sal

La diversidad silvestre y domesticada rara vez se consideran conjuntamente bajo enfoques integrados para la conservación, a pesar de que ambos componentes de la biodiversidad afrontan algunos problemas comunes, como la intensificación agraria. Además, apenas existe conocimiento sobre las relaciones en la distribución de ambos tipos de diversidad, pese a los numerosos esfuerzos internacionales para mantener la biodiversidad y promover prácticas agrícolas sostenibles compatibles con la conservación. En este trabajo analizamos si la distribución actual de algunos componentes de la fauna silvestre en la España peninsular está mediada por la agrobiodiversidad ganadera. Este territorio se caracteriza por albergar altos valores de diversidad silvestre y domesticada, y el dominio de los usos agrícolas y ganaderos desde al menos el inicio del último milenio. Utilizamos modelos de regresión geográficamente ponderados para cuantificar la variación espacial de las relaciones entre la distribución de los vertebrados silvestres y variables ambientales y de agrobiodiversidad. Para ello, utilizamos la riqueza de los vertebrados nativos silvestres (grupos de mamíferos, aves, anfibios y reptiles) como variable respuesta, y la riqueza de razas ganaderas autóctonas (de las especies bovina, ovina, caprina, asinina, equina y porcina), variables ambientales (temperatura media anual, precipitación anual y estacionalidad de la precipitación) y la huella humana como variables predictoras, calculadas para las celdas UTM de 10 × 10 km. Los resultados muestran una marcada variación espacial en las relaciones entre las especies de vertebrados nativos, el clima, la huella humana y la agrobiodiversidad ganadera. En general, las asociaciones entre la riqueza de los 4 grupos de vertebrados nativos silvestres y la agrobiodiversidad ganadera son positiva para la mayor parte del área de estudio. Cuando se consideran grupos específicos de vertebrados nativos, la riqueza de razas de vacuno y ovino muestran patrones contrastados. De este modo, la distribución de la fauna silvestre está relacionada significativamente con la agrobiodiversidad ganadera en la España peninsular. Nuestros resultados señalan la importancia de la relación entre ambos tipos de diversidad, hasta ahora desconocida, con implicaciones para el diseño de medidas de conservación, especialmente en los paisajes agrarios.

Capítulo 3. Los seres humanos distorsionan la adaptación de la agrobiodiversidad. Cambios recientes en la distribución de las razas ganadera autóctonas españolas.

Elena V*elado Alonso, Ignacio Morales Castilla y Antonio Gómez Sal*

Las razas ganaderas autóctonas, las específicas de una determinada zona, están adaptadas localmente, ayudan a mantener la diversidad de recursos genéticos animales, garantizan la seguridad alimentaria y contribuyen a la provisión de diferentes servicios por parte de los agroecosistemas. Sin embargo, estas razas locales están muy amenazadas por distintos procesos de intensificación y abandono ligados a la industrialización agraria. A pesar de que la conservación *in situ* es la forma principal de conservación recomendada, hay una falta de conocimiento sobre la relación raza-ambiente. En este trabajo, adoptando una perspectiva de cambio temporal, se cuantifica la relación entre la riqueza de la agrobiodiversidad ganadera, basada en las razas autóctonas y un conjunto seleccionado de factores ambientales. Se analiza también la distribución de la diversidad de razas en la actualidad considerando las distintas tendencias de cambios en los usos del suelo en las últimas décadas. Los resultados muestran un efecto preponderante del ambiente en la distribución de la agrobiodiversidad ganadera antes de la intensificación de la agricultura. Sin embargo, este efecto disminuye claramente cuando se considera la distribución actual. Por otra parte, los cambios en la distribución de las razas reflejan una tendencia a situarse en zonas más productivas en el presente. Finalmente, aquellos lugares donde se encuentran las razas ganaderas autóctonas en la actualidad continúan estando afectados por procesos de abandono de los usos agrarios. Por todo ello, se propone que son necesarias nuevas medidas de conservación basadas, no solo en los aspectos genéticos y productivos, habituales para las razas, sino que también en criterios ecológicos y socioculturales, dado que diferentes procesos del cambio global son determinantes para la diversidad ganadera.

A.6. CONCLUSIONES

1. Existen muy pocos estudios centrados en la ecología de las razas ganaderas autóctonas. Apenas se conocen los determinantes de la distribución y funciones de la diversidad ganadera, lo que limita la gestión y conservación de esta. Existe, por tanto, un vacío en el conocimiento que abre una nueva línea de investigación.

2. La actividad ganadera, combinando factores naturales y humanos y adaptándose a la variedad de condiciones ambientales, ha favorecido la diversidad intraespecífica de las especies domésticas. El ambiente ha tenido un papel fundamental en el origen y distribución de la diversidad ganadera.

3. Las distintas especies estudiadas responden de manera diferente a los gradientes ambientales y a la heterogeneidad territorial. En la España peninsular, el ganado bovino se ve favorecido por la influencia atemperante del océano Atlántico y su diversidad responde a gradientes de altitud y precipitación, mientras que el ganado ovino está más relacionado con los climas continentales del ámbito mediterráneo. El ganado caprino en contraste se asocia a áreas más templadas del ámbito mediterráneo, montaña mediterránea y zonas con estacionalidad muy marcada. El ganado equino y asinino muestra una mayor diversidad en el ámbito atlántico, aunque su distribución ocupa asimismo zonas situadas en los extremos ambientales.

4. En general, aquellas zonas que han albergado una mayor diversidad de razas también han sostenido una mayor diversidad silvestre de vertebrados en la España peninsular. La distribución de las especies de vertebrados silvestres estudiadas en este trabajo se relaciona de manera positiva con la riqueza de razas en la mayor parte del territorio estudiado. La relación es mayor en el caso de los mamíferos y las aves que en el de los anfibios y los reptiles. No obstante, dichas relaciones varían cuando se consideran determinados grupos de vertebrados y especies ganaderas concretas. Estos resultados sugieren la posibilidad de plantear de forma conjunta la gestión de la biodiversidad natural y doméstica en el territorio estudiado.

5. El efecto de los factores ambientales en la distribución de la diversidad de razas ganaderas autóctonas ha disminuido con el paso del tiempo y su naturaleza ha cambiado. De este modo, la riqueza de razas autóctonas antes de la intensificación agrícola tendía a ocupar lugares de productividad limitada, mientras que en la actualidad ocupa áreas potencialmente más productivas.

6. La distribución contemporánea de las razas autóctonas está ligada a los procesos de transformación del sector ganadero en España y se relaciona con las extensas áreas afectadas por el abandono agrícola y rural en las últimas décadas.

7. La gestión y conservación de las razas ganaderas autóctonas se enfrenta por tanto a un doble reto en el mundo cambiante actual según los resultados obtenidos: el cambio climático y el cambio de usos del suelo. Es necesario por tanto adoptar una perspectiva más holística, que incluya dimensiones no solo técnicas, productivas y económicas, sino también ecológicas, sociales y culturales. Dicho enfoque tendría efectos positivos sobre los dos componentes de la biodiversidad (doméstica y silvestre) que han sido estudiados en este trabajo.

8. Las ecorregiones pecuarias propuestas sintetizan la variedad de posibilidades ecológicas y geográficas en las que se distribuye la diversidad ganadera. Pueden ser consideradas como una herramienta útil para avanzar hacia una gestión ganadera más racional, basada en la interpretación y aprovechamiento de la heterogeneidad ambiental.

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CHAPTER 1

Spatial patterns of livestock biodiversity: ecological determinants and regionalisation of Spanish local livestock breeds

Elena Velado-Alonso, Ignacio Morales-Castilla & Antonio Gómez-Sal

ABSTRACT

Domesticated animals play a central role in agroecosystem functioning. However, livestock biodiversity has rarely been studied from a spatial perspective and little is known about the biogeography of local livestock breeds —those autochthonous to a specific region. Mapping of livestock production systems and their 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 production systems under global change. Here we document the distribution of intraspecific diversity, based on the areas of origin of 119 local breeds, of the bovine, ovine, caprine, equine and asinine species in mainland Spain. We analyse environmental drivers of local breed diversity gradients, using non-metric multidimensional scaling and hierarchical clustering, and delineate livestock ecoregions –i.e. areas similarly utilized by subsets of local breeds. Our results show contrasting spatial distributions of the local breeds across the studied species, which are explained by environmental gradients. The distribution of cattle breeds is determined by altitude and the temperate influence of Atlantic Ocean, while sheep breeds are more related to continental Mediterranean climates, especially to those of the central Iberian plateau. Goat breeds are associated with limiting factors of the Mediterranean climate, such as the seasonality of precipitation. Equid breeds are adapted to particular regions, reaching areas at the environmental extremes. Livestock biodiversity is largely an eco-cultural product, resulting from a coevolutionary process between humans and animals. Our results show a partitioning of the geographic space, highlighting that livestock intraspecific biodiversity has acted as an adaptive response of domesticated species within local agroecosystems. Finally, our delineation of livestock ecoregions could aid to move towards more sustainable livestock management and the conservation of livestock biodiversity.

1.1. INTRODUCTION

Agrobiodiversity greatly contributes to sustain the agroecosystem structure and processes and underpins the agricultural production. The diversity of domesticated animals contributes to determining plant structure and composition, to channelling energy flows and nutrient cycles, and influences community dynamics, affecting interactions and fostering agroecosystems complexity (Gliessman, 2014). Additionally, it is a key element of food security and rural development, as animal-source foods provide 33% of the proteins and 17% of the calories of human consumption globally (FAO, 2018), and animal husbandry contributes to the livelihood of up to 70% of rural communities (FAO, 2015a). Local livestock breeds —i.e. those autochthonous to a specific region— act as a driver and provider of agroecosystem services, thanks to their complex interaction with the environment, moderated by livestock production systems and practices (Leroy et al., 2018). However, livestock breed diversity is greatly threatened. Currently, there are 7,136 catalogued local livestock breeds worldwide, of which 27% are endangered and 65% have an unknown status (FAO, 2019). Thus, it is urgent to obtain further information on local livestock breeds.

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 poorly studied overall. Moreover, they are disregarded in climate change mitigation strategies (Hoffmann, 2010), and are usually ignored by studies that consider biodiversity as an adaptive solution (e.g., Campbell et al., 2009; Kazemi, Klug, & Kamkar, 2018). Furthermore, the mechanisms involved in livestock breed adaptation remain unknown (Boettcher et al., 2014). Most research on this topic focuses on genetics from a productivity perspective, neglecting ecological or evolutionary perspectives. And yet, the interactions between adaptation and environmental factors are critical in generating diversity in agroecosystems, and structuring livestock production (Hoffmann, 2011).

The livestock sector is key for improving the sustainability of food systems and reducing their impact on the planet (FAO, 2018; Pelletier & Tyedmers, 2010). Local livestock breeds have been claimed as part of the solution because they are locally adapted (Hoffmann, 2013; Leroy et al., 2018). The protection of livestock breeds is relevant to current debates about alternative biosphere models and must be emphasized from perspectives such as Nature's Contribution to People (Díaz et al., 2018), al., 2018), due to coevolution with humans. However, land-based livestock systems and their associated local breeds, are experiencing rapid changes in the sector, as well as the effects of global change —e.g. emerging diseases, increasing mortality, production and fertility reduction, and the predicted reduction of quality and availability of forage (FAO, 2015b; Thornton, van de Steeg, Notenbaert, & Herrero, 2009).

Understanding livestock agrobiodiversity and its distribution is essential for its conservation and sustainable management (FAO, 2007). Nevertheless, mapping of livestock systems worldwide is very limited as information is generally unavailable (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, Bastiaansen, Dessie, & Komen, 2018). However, these studies do not include an extensive analysis of livestock agrobiodiversity. Lack of spatially explicit information on land-based livestock uses limits (i) the sustainable management of these agroecosystems, (ii) the correct assessment of their global change impacts, and (iii) the definition of conservation priority areas (FAO, 2015b), for both wild and domesticated biodiversity.

The evolution of animal domestication has been a complex coevolutionary process (Larson & Fuller, 2014; Zeder, 2012). The post-domestication diversification process has been influenced by numerous factors over time, in which human beings have acted as dispersers, selectors and environment modifiers (Hall, 2004; Zeder, 2015). Other evolutionary processes where spatial heterogeneity is key —e.g. synanthropic speciation, introgression, genetic isolation, founder effect, among others— have also played a central role in livestock diversification (Larson & Fuller, 2014). In addition, environmental factors underpin and mediate among these processes (Bertolini et al., 2018). As a result, local breeds could be regarded as proxies for domesticated species' potential to adapt to regional and local environments (Bertolini et al., 2018; Bowles, Carson, & Isaac, 2014; Colli et al., 2014, 2018; Lv et al., 2014; Stucki et al., 2017).

The present work analyses distributional patterns of domesticated species in Peninsular Spain, to explore the adaptative ability of livestock agrobiodiversity to land complexity. The analysis is based on the areas of origin of 119 local livestock breeds (both extant and extinct), of bovine, ovine, caprine, asinine and equine species, in relation to different environmental factors across a large territorial extent. Previous work has disregarded the influence of environment on the distribution of livestock agrobiodiversity. We hypothesise that breed diversity in each territory reflects the adaptative ability of domesticated species to local environments. We expect marked, non-random, contrasting gradients across studied species related to environmental heterogeneity (Leroy et al., 2016) and species requirements. Furthermore, we delineate livestock ecoregions based on local breed composition that could serve as a basis for the sustainable management of extensive livestock farming and its role in supporting biodiversity.

1.2. MATERIAL AND METHODS

1.2.1. Distribution data: local livestock breeds in Peninsular Spain

The studied area is Peninsular Spain, a territory that hosts 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 extant and extinct local breeds from the bovine, ovine, caprine, asinine and equine species in mainland Spain. 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. Secondly, to identify those currently extinct, as they are not included in the Spanish Official Catalogue, we selected those breeds detailed as extinct in the FAO Domesticated Animal Diversity-Information System (2017), also mentioned in the Spanish breed literature (Supporting Information –SI– Appendix I, Table S1). They represent a total of 119 breeds: 44 bovine, 38 ovine, 19 caprine and 18 equid –including horses and donkeys (SI Appendix I, Table S2).

To determine the geographic distribution of each breed, we identified the area of origin of each breed through a literature review of the main anthologies of Spanish breeds (SI Appendix I, 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. We assume that these areas of origin represent the historical and natural domain of breeds (Colino-Rabanal, Rodríguez-Díaz, Blanco-Villegas, Peris, & Lizana, 2018) —a sort of eco-cultural spatial niche- of the local breeds, and approximately represent the areas where each breed was located before the agricultural industrialization occurred —i.e. when the livestock systems, and thus the local breeds, were mostly based on local resources and related to local environments— and had existed since. Areas of origin were then digitally mapped (Figure 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, provinces and autonomous regions maps.

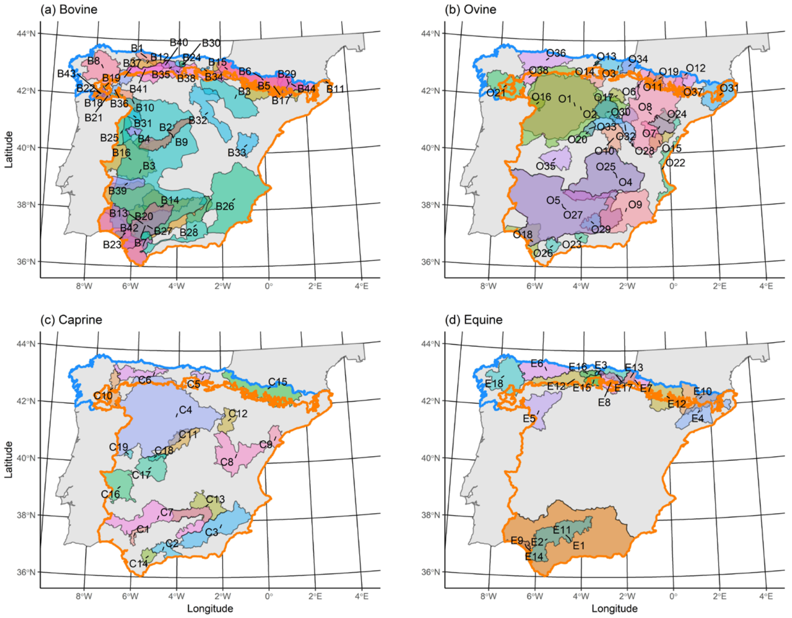


Figure 1. Areas of origin of the 119 local livestock breeds for the domesticated species: bovine (a), ovine (b), caprine (c) and equid —including both horses and donkeys— (d). Codes identifying each breed are shown using the capital letters B (bovine), O (ovine), C (caprine) and E (equid) followed by a number (see Supporting Information, Appendix I, Table S2 for details). The Atlantic and Mediterranean regions are delineated by a coloured line (Atlantic in blue, Mediterranean in orange).

1.2.2. ENVIRONMENTAL VARIABLES

To analyse the relationships between the original distribution of breed diversity and territory, a set of environmental factors that represent climate, orography, and vegetation of territorial heterogeneity were selected. A total of 24 variables were chosen (Table 1), extracted at a resolution of circa 10 x 10 Km.

The climate variables were obtained from the 30s layer of WorldClim version 2 (Fick & Hijmans, 2017). The coefficients of variation in precipitation were calculated using the database Spanish PREcipitation At Daily Scale (SPREAD) (Serrano-Notivoli, Beguería, Saz, Longares, & de Luis, 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-

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	ºC
Isotermality	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.	ºC
Temperature Anual Range	Temperature range throughout year. Subtraction of minimum temperature of coldest month from maximum temperature of warmest month for the 1970–2000 period.	ºC
Mean Temperature of Warmest Quarter	Warm seasonal effect. Average temperatures for the 13 consecutive warmer weeks for the 1970–2000 period.	ºC
Mean Temperature of Coldest Quarter	Cold seasonal effect. Average temperatures for the 13 consecutive cooler weeks for the 1970–2000 period.	ºC
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.	º

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.	
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 the Series of Vegetation Map of Spain, Rivas Martínez, 1987.	bioclimatic type

derived Ecosystem Functional Attributes) (Alcaraz-Segura, Cabello, & Paruelo, 2009; Alcaraz-Segura, Paruelo, & Cabello, 2006) 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 the Vegetation Map of Spain by Rivas-Martínez (1987).

All continuous variables were discretised into types according to the probability range of each variable (Morales-Castilla, Rodríguez, Kaur, & Hawkins, 2013). The first and last type quantile ranges were determined to differentiate the most extreme values, and the rest of types were divided proportionally (SI, Appendix I, Table S3). For the variables of a qualitative nature, simplified types were established grouping the categories described by the reference layer (SI, Appendix I, 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.

1.2.3. 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 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 & 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 specie. 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" package to process data, the "raster" and "LetsR" packages to map livestock distributions and ecoregions and "ggplot2" and "tmap" for graphic representation.

1.3. RESULTS

The domesticated species studied 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 (Figure 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 (Figure 1a). Six groups were identified according to the results of the cluster analysis (SI, Appendix II, Fig. S5), with three differentiated groups in the Atlantic (Eurosiberian) zones and another three groups in the Mediterranean bioclimatic region. This is also reflected in the NMDS ordination (stress = 0.12) with Atlantic groups mainly located along the positive abscises and Mediterranean along the negative abscises (Figure 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 (e.g. Fig. 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 plains from those of the central plateau (Fig. 2a, polygon pink from yellow) (consult SI Appendix II, Fig. S1 for more details about environmental gradients).

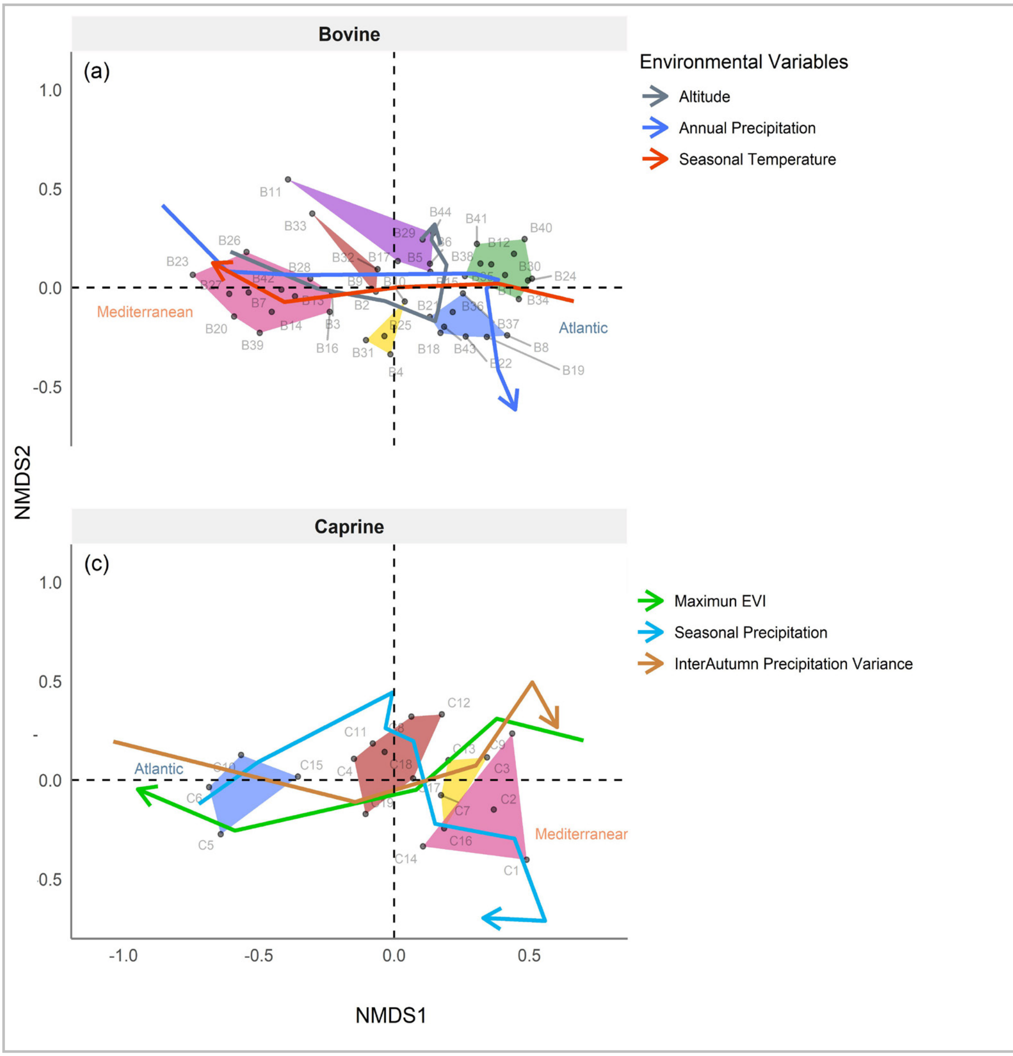
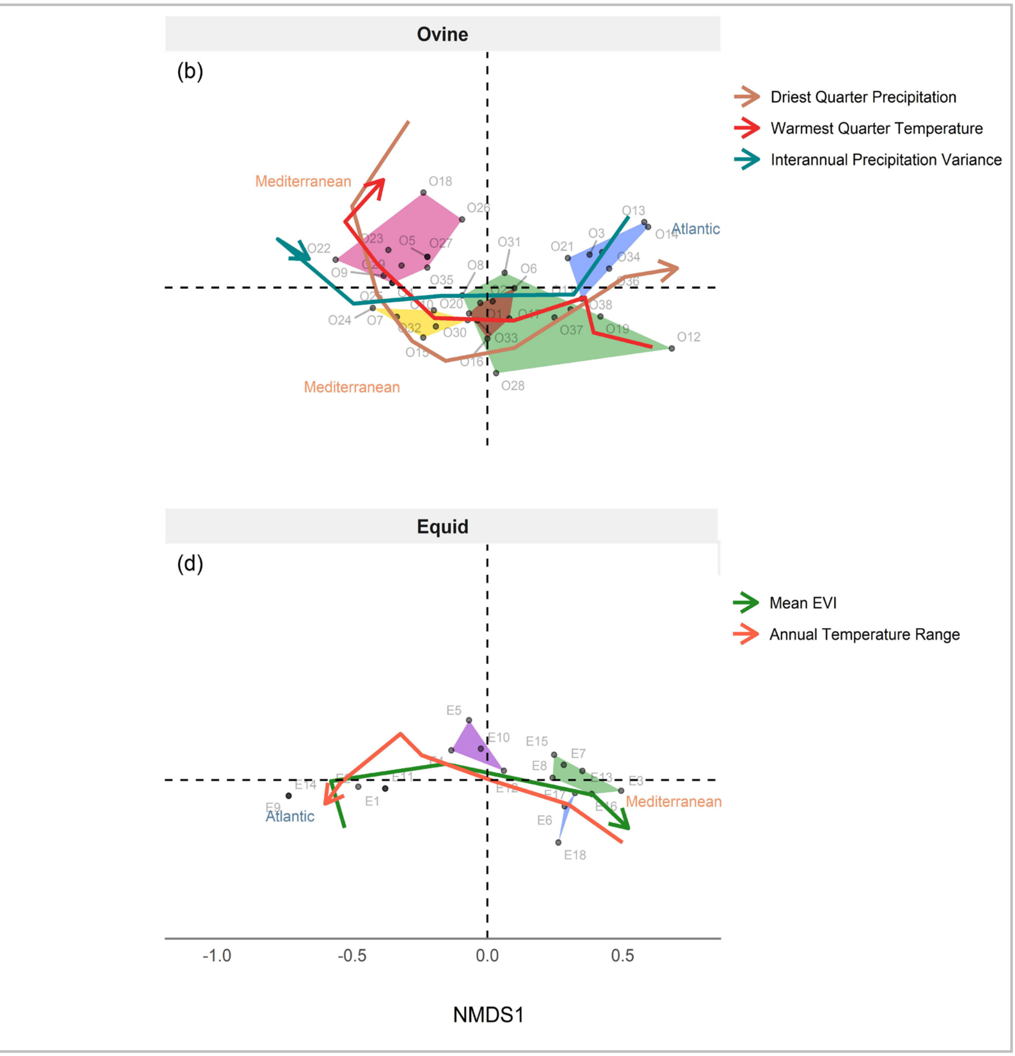


Figure 2. NMDS Ordination of peninsular Spain local livestock breeds of four domesticated species: bovine (a), ovine (b) caprine (c) and equid (d) —including both horses and donkeys—; stress: a = 0.12, b = 0.12, c = 0.09, d = 0.05. Arrows represent a summary of the gradients of environmental variables (see legend) from lower to higher values (Supporting Information, Appendix II Figures S1-S4 for more detail about environmental gradients). Codes identifying each breed are shown using the capital letters B (bovine), O (ovine), C (caprine) and E (equid) followed by a number (see Supporting Information, Appendix II, Table S1 for details). The coloured polygons represent the breed groups obtained through hierarchical cluster (see also Supporting Information, Appendix II Figures S5-S8).


Ovine
(b)
Driest Quarter Precipitation
Warmest Quarter Temperature
Interannual Precipitation Variance
Mediterranean
Atlantic
Mediterranean
O18
O26
O13
O14
O23
O5
O27
O22
O31
O21
O3
O34
O29
O9
O8
O6
O35
O36
O25
O4
O2
O11
O10
O20
O38
O24
O7
O1
O17
O32
O30
O37
O19
O12
O33
O15
O16
O28
Equid
(d)
Mean EVI
Annual Temperature Range
E5
E10
E15
E7
E8
E13
E3
E14
E11
E12
E17
E1
E9
Atlantic
Mediterranean
E16
E6
E18
-1.0
-0.5
0.0
0.5
NMDS1

Ovine breeds showed preference for the Continental-Mediterranean climates found in the central Iberian plateau (Fig. 1b). The classification identified five main groups (SI Appendix II, Fig. S6), of which only one was strictly associated with the Atlantic sub-region (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, being distributed from the rigorous central mountain ranges, to thermal coastal areas or mountain areas of the mid Southern-eastern peninsula (Fig. 1b, Fig. 3k, n, r), (consult SI Appendix II, Fig. 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 (SI Appendix II, Fig. 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 systems and the adaptive ability of goats to benefit from woody species in heterogenous 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 SI Appendix II, Fig. S3 for more details).

Since there were low numbers of asinine breeds, horses and donkeys were analysed together. Most of the local equids were distributed in the Atlantic (Eurosiberian) bioclimatic region (Fig. 1d). Five groups were identified (SI Appendix II, Fig. 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 extreme differentiated distribution in both Atlantic and Mediterranean zones (Fig. 1d), and a special utilization of the gradient between 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 SI Appendix II, Fig. S4 for more details).

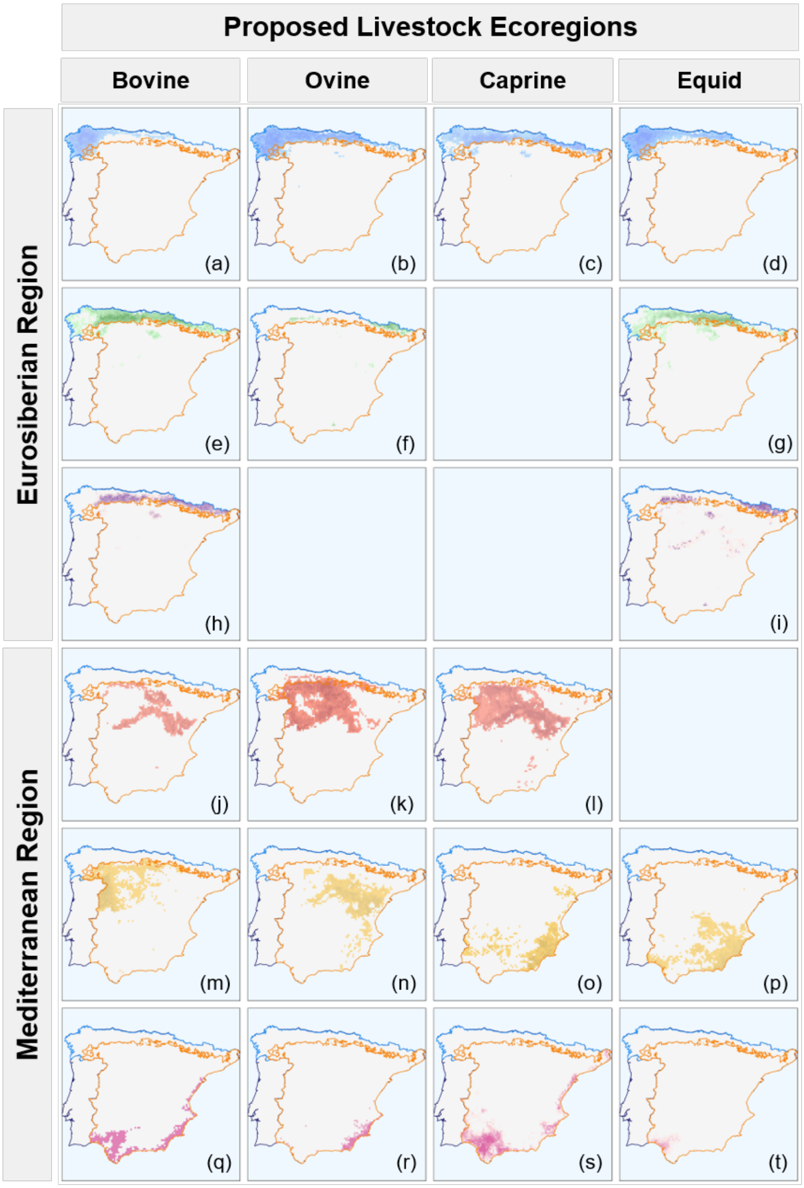


Figure 3. Livestock ecoregions maps representing those geographic regions where the environmental conditions correspond to the variable types associated to each grouping of local breeds —at least 50% of the preferred types— (see Supporting Information, Appendix II, Figures S9-S12). Livestock ecoregions 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 equid (d, g, i, p, t). The overall colour scheme used for each group mirrors that of the hierarchical cluster groupings in Figure 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).

The livestock ecoregions of peninsular Spain (Fig. 3) also showed how domesticated species differ in their patterns of land occupation (Fig. 1). Bovine and ovine species had the most continuous distribution areas, reflecting adaptation to a wide variety of ecogeographical possibilities, noted in the characteristics of the territory studied (Fig. 3 Bovine, Ovine). Caprine and equine breeds had more discontinuous distributions, but still included a wide range of environmental heterogeneity, reaching areas at the environmental extremes (Fig. 3 Caprine, Equid). 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 SI Appendix II, Fig. S9-S12).

Bovine livestock ecoregions predominated in the Atlantic area, characterised by vegetation of areas that are temperate and humid, with average annual precipitation greater than 1,000 mm, for three of the livestock ecoregions detected, encompassing the heterogeneity of the Atlantic bioclimatic types (Fig. 3a, e, h, and Fig. 4a-c). In the Mediterranean bioclimatic area, bovine ecoregions differentiated the contrast between the higher areas of the interior plateaus and the warm plains of the Guadalquivir basin (Fig. 3j, m, q). The ovine local breeds, on the other hand, 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 (Fig. 3l, o, s), were in areas with annual mean precipitation of less than 500mm 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 low altitude and mountainous Atlantic areas (Fig. 3c). Lastly, the groups obtained for equids showed a very wide adaptive range due to the occupation of 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 plains (Fig. 3p, t). For more details on the physical characteristics of the different livestock ecoregions, see Figure 4.

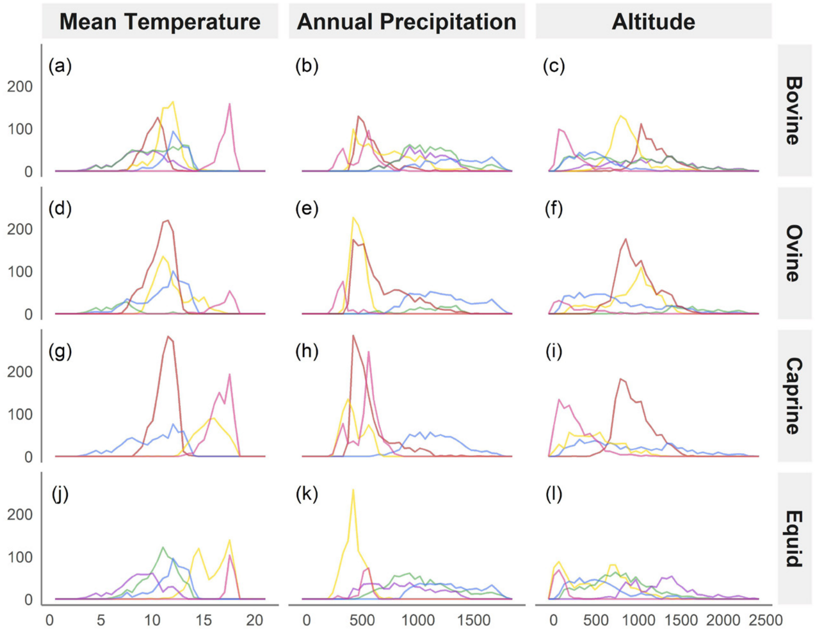


Figure 4. Distribution range of each group of local breeds (see Supporting Information, Appendix II, Figures S9-S12), by domesticated species: bovine (a-c), ovine (d-f), caprine (g-i), equid (both horse and donkey, j-l) represented by the frequency of pixels for the variables: annual mean temperature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

1.4. DISCUSSION

Livestock distributional patterns suggest that livestock activity, combining the artificial selection of local breeds with their adaptation to different environmental conditions (Colino-Rabanal et al., 2018), has partitioned geographic space and promoted intraspecific diversity. This indicates the adaptive ability of livestock species. Moreover, the distribution of local breed diversity shows marked differences between species, coinciding with the significant differences found in the distribution of livestock species globally (Robinson et al., 2014) and the different distribution ranges of wild progenitor species based on archaeological evidences (Larson & Fuller, 2014). Despite the aforementioned, most of the selection indicators identified in livestock genetic studies are associated to productivity-related traits or morphological standards (Rothammer, Seichter, Förster, & Medugorac, 2013), usually studied in modern intensive breeds. While environmental selection factors acting at the genetic level have scarcely been studied in domesticated livestock species (Bertolini et al., 2018; Lv et al., 2014; Xu et al., 2015), neither from an ecological or biogeographical perspective.

The spatial distribution of the different livestock ecoregions shows a tendency to occupy areas that are ecologically limiting in terms of primary productivity. This coincides 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. The distribution of livestock ecoregions can be interpreted based on the ability of domesticated species to maximise energy intake from seasonal productivity optima (Gómez-Sal & Lorente, 2004). These are associated either with ecosystems such as mountains, Atlantic grasslands and Mediterranean pastures or, with resources such as stubble, scrub, pruned trees, and pasture rich in fibre. Our results prompt livestock biodiversity, not only in terms of adaptation to the territory, but also in maximizing the use of available resources (Gómez-Sal, 2001).

Our study explored the relationship between the distribution of Spanish local breeds and environmental factors across broad spatial scales. In local breeds linked to land-based systems, environmental factors should have been of greater importance than in industrialised breeds or breeds selected for intensive or 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 land-based 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 (e.g. construction of livestock niches, Colino-Rabanal et al., 2018), where competition with other species is diminished and the adequacy of habitat has been directed by humans.

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., 2017), identify a suite of traits that predispose these species to be more tolerant to new occupied areas. Areas of introduction may sometimes exceed specie realized ecological niches, and thus, successful candidates would benefit from broad environmental breadths (Blackburn et al., 2017; Capellini, Baker, Allen, Street, & Venditti, 2015). This supports the idea that adaptive plasticity in domesticated livestock species is intrinsic to the adaptive ability of wild relative species, rather than an outcome of artificial selection. Therefore, the livestock biodiversity of a given species could show similar patterns in different biogeographical regions in the presence of a similar set of environmental conditions as shown in our study, e.g. bovine local breeds respond to altitude along Mediterranean and Atlantic bioclimatic zones.

There are numerous limitations to the biogeographic study of livestock diversity. First, livestock is composed of a few species, most of them domesticated in similar environments (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 models— are widely distributed globally (e.g. Robinson et al., 2014), so their spatial distribution overlaps with highly differentiated production systems, limiting knowledge of systems linked to the land and the respective local breeds (Hoffmann, 2010). Third, there are significant gaps in georeferenced information on different production systems and local breeds (Hoffmann, 2010; Robinson et al., 2011).

It must be pointed out that the breed concept is somewhat undefined. 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). This lack of definition complicates the comparison between countries with different livestock histories and cultures. However, 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. The geographically explicit projection of groups of breeds with similar responses to environmental factors offers a novel and versatile research tool: the livestock ecoregions. These can be delineated at varying degrees of resolution, according to the environmental variables selected or the criteria for grouping the breeds.

Moreover, policy combining the conservation of nature and agricultural uses 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 extensive livestock production systems. In fact, the integration of adaptive measures at local or regional level has been considered as an essential point for improving the sustainability of the new European Common Agricultural Policy (CAP) and its acceptance by practitioners (Navarro & López-Bao, 2018). Our livestock ecoregions proposal could help to determine target territories in which to set specific environmental objectives (Harlio, Kuussaari, Heikkinen, & Arponen, 2019; McDonald et al., 2018), 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, Mamolos, Kalburtji, & Birtsas, 2013).

1.5. CONCLUSIONS

Despite the significant role that humans and productive systems 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 domesticated species adaptive ability is also expressed according to territorial conditions and not only modulated by human selection. This result must be taken into account in the conservation strategies of animal genetic resources, especially in the case of local livestock breeds. Besides, documenting and understanding the geographic distribution of agrobiodiversity will be critical to design adaptive measurements to ongoing global change.

This study pioneers the quantification of the relationships between livestock biodiversity and environmental factors in detail, and in proposing a regionalisation based on local breed diversity distributions. The results open up a new route for the study of biogeographic patterns of domesticated species and, in particular, livestock biodiversity. 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 land-based livestock systems more sustainable? How can we improve the conservation of biodiversity, both wild and domesticated? In a context where livestock farming is regarded to as a major component of global change, local livestock breeds should be further studied and their potential to handle livestock production more sustainably should not be longer disregarded.

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1.7. SUPPORTING INFORMATION

Appendix 1

Table S1. List of bibliographic sources used to identify the areas of origin of Spanish local livestock breed distribution.

Authors	Year	Edition	Title
Faelli, F.	1932	Edición Española- Revista Veterinaria de España (1ªEdición 1902)	Razas Bovinas, Equinas, Porcinas, Ovinas y Caprinas. Traducción anotada por Tomás de la Fuente Muñoz.
Aparicio, G.	1947	Segunda Edición (1ª Edición 1944)	Zootecnia Especial. Etnología compendiada.
Esteban Muñoz, C. & Tejón Tejón, D.	1980	Primera Edición	Catálogo de Razas Autóctonas Españolas. I-Especies Ovina y Caprina
Sánchez Belda, A.,	1984	Primera Edición	Razas Bovinas Españolas
Sámchez Belda, A. & Sánchez Trujillano, M.C.	1986	Segunda Edición (Primera Edición 1974).	Razas Ovinas Españolas
García Dory, M.A., Martínez Vicente, S. & Orozco Piñán, F.	1990	Primera Edición	Guía de Campo de las Razas Autóctonas de España
Sánchez Belda, A.	2002	Primera Edición	Razas Ganaderas Españolas Bovinas
Esteban Muñoz, C.	2003	Primera Edición	Razas Ganaderas Españolas Ovinas
Yanes García, J.E.	2005	Primera Edición	Razas Asnales Autóctonas Españolas
Esteban Muñoz, C.	2008	Primera Edición	Razas Ganaderas Españolas Caprinas
Sánchez Belda, A.	2012	Primera Edición	Razas Ganaderas Españolas Caballares
Information available on the ARCA (Breed Information National System) website of the MAPA (Ministry of Agriculture, Fisheries and Food) has also been consulted: http://www.mapama.gob.es/es/ganaderia/temas/zootecnia/razas-ganaderas/razas/catalogo/ consulted between March and July, 2017			

Table S2. List of local livestock breeds included in this work.

Breed Name	Livestock Type	Status	Code
Asturiana de los Valles	Bovine	Increasing	B1
Avileña Negra Ibérica	Bovine	Increasing	B2
Lidia	Bovine	Increasing	B3
Morucha	Bovine	Increasing	B4
Parda de Montaña	Bovine	Increasing	B5
Pirenaica	Bovine	Increasing	B6
Retinta	Bovine	Increasing	B7
Rubia Gallega	Bovine	Increasing	B8
Avileña Negra Ibérica Bociblanca	Bovine	Danger of Extinction	B9
Alistano-Sanabresa	Bovine	Danger of Extinction	B10
Albera	Bovine	Danger of Extinction	B11
Asturiana de Montaña	Bovine	Danger of Extinction	B12
Berrenda en Colorado	Bovine	Danger of Extinction	B13
Berrenda en Negro	Bovine	Danger of Extinction	B14
Betizu	Bovine	Danger of Extinction	B15
Blanca Cacereña	Bovine	Danger of Extinction	B16
Bruna de los Pirineos	Bovine	Danger of Extinction	B17
Cachena	Bovine	Danger of Extinction	B18
Caldelá	Bovine	Danger of Extinction	B19
Cárdena Andaluza	Bovine	Danger of Extinction	B20
Frieiresa	Bovine	Danger of Extinction	B21
Limiá	Bovine	Danger of Extinction	B22
Marismeña	Bovine	Danger of Extinction	B23

Monchina	Bovine	Danger of Extinction	B24
Morucha Negra	Bovine	Danger of Extinction	B25
Murciano-Levantina	Bovine	Danger of Extinction	B26
Negra Andaluza	Bovine	Danger of Extinction	B27
Pajuna	Bovine	Danger of Extinction	B28
Pallaresa	Bovine	Danger of Estinction	B29
Pasiega	Bovine	Danger of Extinction	B30
Sayaguesa	Bovine	Danger of Extinction	B31
Serrana Negra	Bovine	Danger of Extinction	B32
Serrana de Teruel	Bovine	Danger of Extinction	B33
Terreña	Bovine	Danger of Extinction	B34
Tudanca	Bovine	Danger of Extinction	B35
Vianesa	Bovine	Danger of Extinction	B36
Berciana	Bovine	Extinct	B37
Campoo	Bovine	Extinct	B38
Colorada Extremeña	Bovine	Extinct	B39
Lebaniega	Bovine	Extinct	B40
Mantequera Leonesa	Bovine	Extinct	B41
Rubia Andaluza	Bovine	Extinct	B42
Verinesa	Bovine	Extinct	B43
Vaca del Pirineo Catalán	Bovine	Extinct	B44
Castellana	Ovine	Increasing	O1
Churra	Ovine	Increasing	O2
Latxa	Ovine	Increasing	O3
Manchega	Ovine	Increasing	O4

Merino	Ovine	Increasing	O5
Navarra	Ovine	Increasing	O6
Ojinegra de Teruel	Ovine	Increasing	O7
Rasa Aragonesa	Ovine	Increasing	O8
Segureña	Ovine	Increasing	O9
Alcarreña	Ovine	Danger of Extinction	O10
Ansotana	Ovine	Danger of Extinction	O11
Aranesa	Ovine	Danger of Extinction	O12
Carranzana	Ovine	Danger of Extinction	O13
Carranzana Negra	Ovine	Danger of Extinction	O14
Cartera	Ovine	Danger of Extinction	O15
Castellana Negra	Ovine	Danger of Extinction	O16
Chamarita	Ovine	Danger of Extinction	O17
Churra Lebrijana	Ovine	Danger of Extinction	O18
Churra Tensina	Ovine	Danger of Extinction	O19
Colmenareña	Ovine	Danger of Extinction	O20
Galega	Ovine	Danger of Extinction	O21
Guirra	Ovine	Danger of Extinction	O22
Lojeña	Ovine	Danger of Extinction	O23
Maellana	Ovine	Danger of Extinction	O24
Manchega Negra	Ovine	Danger of Extinction	O25
Merino de Grazalema	Ovine	Danger of Extinction	O26
Merina Negra	Ovine	Danger of Extinction	O27
Merino de los Montes Universales	Ovine	Danger of Extinction	O28

Montesina	Ovine	Danger of Extinction	O29
Ojalada	Ovine	Danger of Extinction	O30
Ripollesa	Ovine	Danger of Extinction	O31
Roya Bilbilitana	Ovine	Danger of Extinction	O32
Rubia del Molar	Ovine	Danger of Extinction	O33
Sasi Ardi	Ovine	Danger of Extinction	O34
Talaverana	Ovine	Danger of Extinction	O35
Xalda	Ovine	Danger of Extinction	O36
Xisqueta	Ovine	Danger of Extinction	O37
Blanca del Bierzo	Ovine	Extinct	O38
Florida	Caprine	Increasing	C1
Malagueña	Caprine	Increasing	C2
Murciano-Granadina	Caprine	Increasing	C3
Agrupación de las Mesetas	Caprine	Danger of Extinction	C4
Azpi Gorri	Caprine	Danger of Extinction	C5
Bermeya	Caprine	Danger of Extinction	C6
Blanca Andaluza	Caprine	Danger of Extinction	C7
Blanca Celtibérica	Caprine	Danger of Extinction	C8
Blanca de Rasquera	Caprine	Danger of Extinction	C9
Galega	Caprine	Danger of Extinction	C10
Guadarrama	Caprine	Danger of Extinction	C11
Moncaina	Caprine	Danger of Extinction	C12
Negra Serrana	Caprine	Danger of Extinction	C13
Payoya	Caprine	Danger of Extinction	C14

Pirenaica	Caprine	Danger of Extinction	C15
Retinta	Caprine	Danger of Extinction	C16
Verata	Caprine	Danger of Extinction	C17
Guisandesa	Caprine	Extinct	C18
Jurdana	Caprine	Extinct	C19
Española	Equid	Increasing	E1
Asno Andaluz	Equid	Danger of Extinction	E2
Asno de las Encartaciones	Equid	Danger of Extinction	E3
Asno Catalán	Equid	Danger of Extinction	E4
Asno Zamorano-Leonés	Equid	Danger of Extinction	E5
Caballo Asturcón	Equid	Danger of Extinction	E6
Caballo de Burguete	Equid	Danger of Extinction	E7
Caballo de Monte del País Vasco	Equid	Danger of Extinction	E8
Caballo Marismeño	Equid	Danger of Extinction	E9
Cavall Pirenenc Català	Equid	Danger of Extinction	E10
Caballo Hispano-Árabe	Equid	Danger of Extinction	E11
Caballo Hispano Bretón	Equid	Danger of Extinction	E12
Jaca Navarra	Equid	Danger of Extinction	E13
Caballo de las Retuertas	Equid	Danger of Extinction	E14
Caballo Losino	Equid	Danger of Extinction	E15
Caballo Monchino	Equid	Danger of Extinction	E16
Pottoka	Equid	Danger of Extinction	E17
Cabalo Pura Raza Galega	Equid	Danger of Extinction	E18

Table S3. Classification ranges of continuous environmental variables (the upper value of each class is indicated).

Environmental Variable	Unit	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8	Class 9	Class 10
Annual Mean Temperature	ºC	5.99	8.24	10.5	12.76	15.01	17.27	19.53	20.75		
Isotermality	%	32.62	35.75	38.88	42.01	45.14	48.27	51.4	55.57		
Temperature Seasonality	ºC	299.74	401.88	504.03	606.17	708.31	763.01				
Temperature Anual Range	ºC	15.52	18.52	21.52	24.52	27.52	30.52	33.52	34.09		
Mean Temp. Warmest Quarter	ºC	14.26	16.15	18.03	19.92	21.81	23.7	25.58	26.01		
Mean Temp Coldest Quarter	ºC	0.58	2.43	4.28	6.13	7.98	9.83	11.68	13.53	17.84	
Annual Mean Precipitation	mm	339.85	546	752.15	958.3	1164.5	1370.6	1576.7	1802.9		
Precipitation Seasonality	%	22.31	29.33	36.35	43.37	50.39	57.41	64.43	71.45	78.47	90.39
Precipitation Wettest Quarter	mm	92.93	185.89	278.86	371.82	464.79	557.75	650.72	712.81		
Precipitation Driest Quarter	mm	18.62	39.8	60.98	82.16	103.34	124.52	145.7	166.88	265.83	
Altitude	masl	159.15	369.640	580.13	790.63	1001.1	1211.6	1.42	2360.4		
Slope	º	0.96	2.13	3.3	4.47	5.64	6.8	7.97	9.14	10.31	18.54
Interannual Prec Variation		1.88	2.87	3.87	4.87	5.86	7.73				
Inter-winter Prec Variation		1.69	2.86	4.03	5.2	7.04					
Inter-spring Prec Variation		2.03	3.43	4.83	6.23	14.11					
Inter-summer Prec Variation		2.79	3.78	4.77	5.76	6.74	7.73	8.72	9.71	10.700	21.65
Inter-autumn Prec Variation		1.68	2.88	4.07	5.07	5.27	7.33				
Mean Vegetation Productivity		0.11	0.22	0.33	0.44	0.48					
Seasonal Vegetation Productivity		0.03	0.07	0.12	0.16	0.19					
Maximum Vegetation Productivity		0.17	0.33	0.49	0.65	0.71					
Minimum Vegetation Productivity		0.02	0.09	0.16	0.23	0.29					

Table S4. Lithology classification from 1995 Geological Map of Spain at a scale of 1:1,000,000.

Class	Lithology
Class 1	Two micas Granitoids Migmatites, marbles and undifferentiated granitoids Other granitoids
Class 2	Sandstones, slates and limestones Quartzites, slates, sandstones and limestones Gneisses Slates, grauwackas, quartzites and conglomerates
Class 3	Conglomerates, sandstones, limestones, plasters and versicolor clays Conglomerates, sandstones, shales and limestones. Carbon
Class 4	Limestones, dolomites and marls. Sandstones and conglomerates Dolomites, limestones and marls. Sandstone
Class 5	Sandstones, conglomerates, clays; limestones and evaporites Detritic limestones, calcarenites, marls, clays and limestone Conglomerates, sandstones and lutites Conglomerates, sandstones, clays and limestones. Evaporitas Detrital limestones, calcarenites, marls, clays and limestones
Class 6	Gravels, conglomerates, sands and silts
Class 7	Mica-schists, phyllites, sandstones, marbles, limestones, dolomites and marls
Class 8	Felstic volcanic rocks Mafic volcanic rocks Mafic and felsic volcanic rocks Serpentinites and peridotites. Basic and ultrabasic rocks Vulcanites and volcanoclastic rocks

Table S5. Vegetation Classification based on Spanish Forestry Map 1:50 000.

Class	Vegetation Type
Class 1	Beech forest (*Fagus sylvatica*)
Class 2	Oak forest (different species)
Class 3	Pyrenean oak forest (*Quercus pyrenaica*)
Class 4	Gall oak forest (*Quercus faginea*)
Class 5	Holm oak forest (*Quercus ilex*)
Class 6	Cork oak forest (*Quercus suber*)
Class 7	*Juniperus thurifera* forest
Class 8	*Pynus sylvestris* forest
Class 9	*Pinus halepensis* forest
Class 10	*Pinus nigra* forest
Class 11	Dehesas silvopastoral systems
Class 12	Reforestation
Class 13	Chesnuts forest (*Castanea sativa*)
Class 14	Agricultural crooplands
Class 15	Artificial
Class 16	Pasture-Scrublands
Class 17	Scrublands
Class 18	Meadows
Class 19	Grassland

Table S6. Bioclimatic Types classification from Vegetation Map of Spain by Rivas Martínez 1987.

Class	Type
Class 1	Supra and Orotemperate
Class 2	Mesotemperate
Class 3	Thermotemperate
Class 4	Cryoromediterranean and Oromediterranean
Class 5	Supramediterranean
Class 6	Mesomediterranean
Class 7	Thermomediterranean
Class 8	Alluvial

APPENDIX II

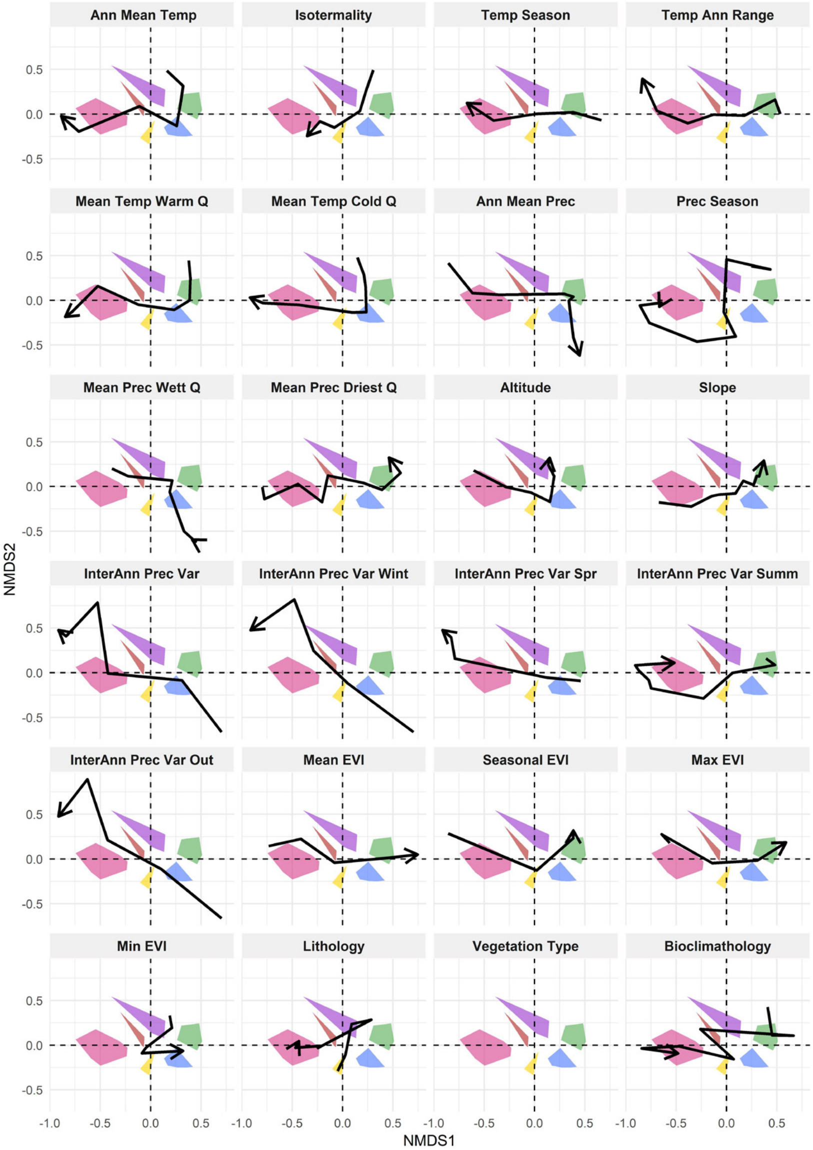

Figure S1. Bovine NMDS ordination, grouped in polygons according to the Hierarchical Cluster results (SI Appendix II, Figure S5) The arrows reflect the gradient of each environmental variable from lower to higher values.

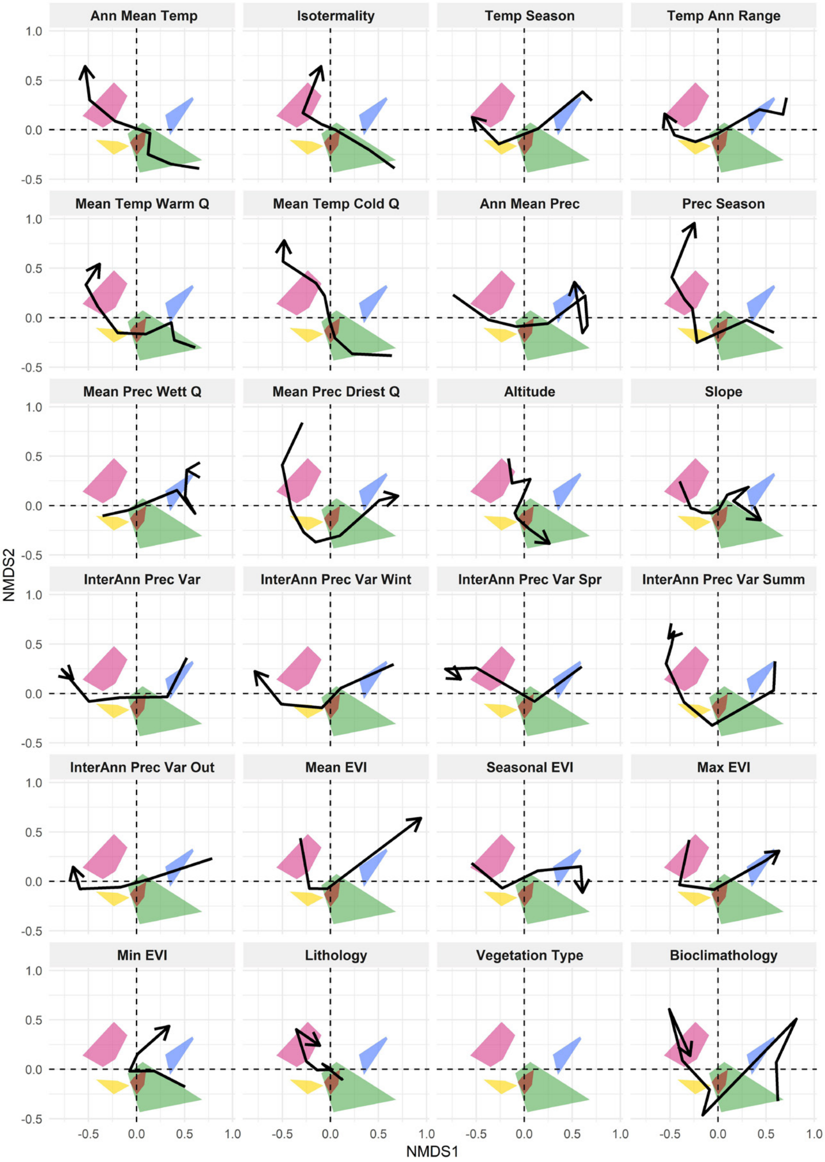

Figure S2. Ovine NMDS ordination grouped in polygons according to the Hierarchical Cluster results (SI Appendix II, Figure S6) The arrows reflect the gradient of each environmental variable from lower to higher values.

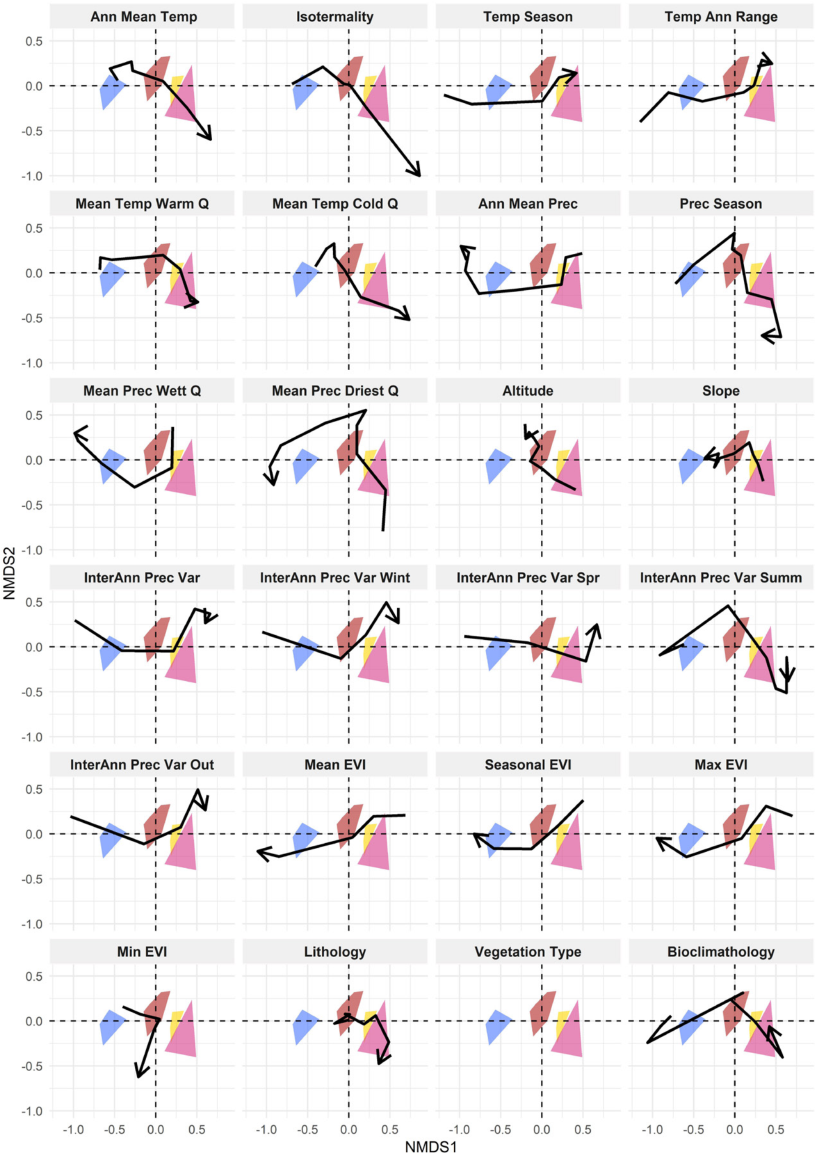

Figure S3. Caprine NMDS ordination grouped in polygons according to the Hierarchical Cluster results (SI Appendix II, Figure S7) The arrows reflect the gradient of each environmental variable from lower to higher values.

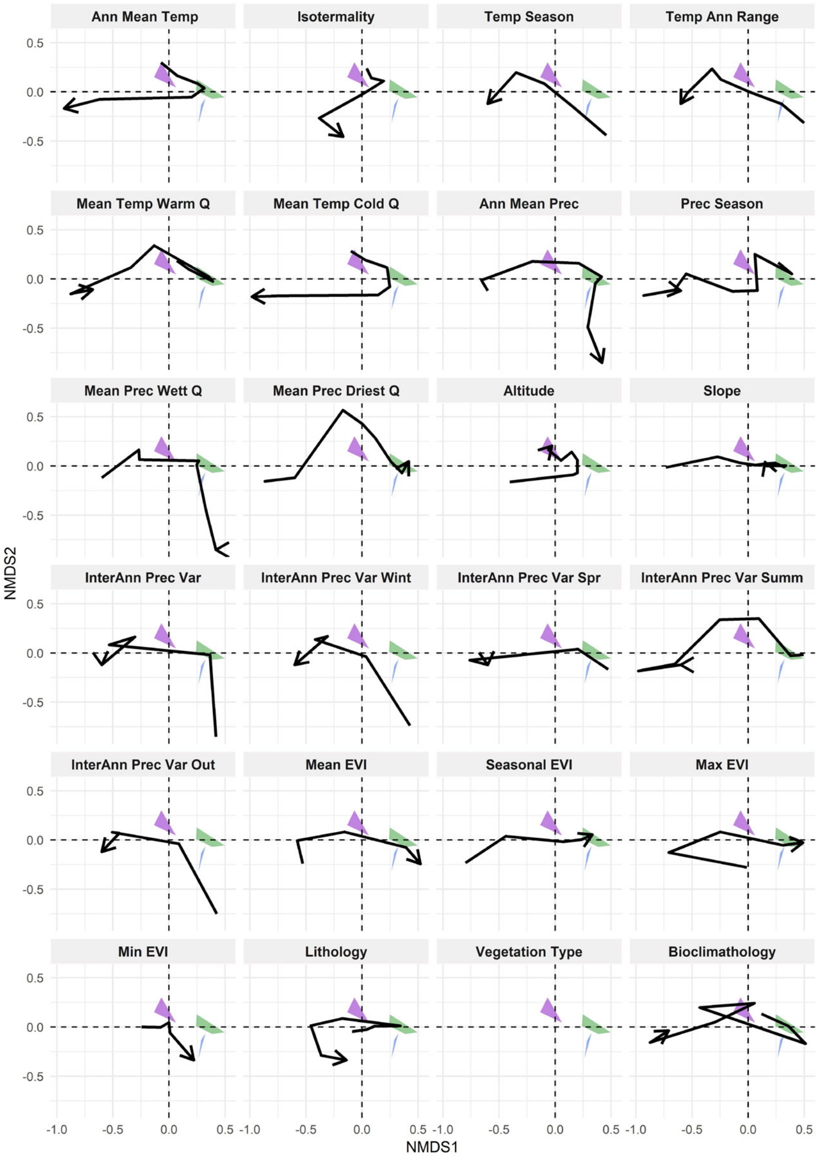

Figure S4. Equid NMDS ordination grouped in polygons according to the Hierarchical Cluster results (SI Appendix II, Figure S8) The arrows reflect the gradient of each environmental variable from lower to higher values.

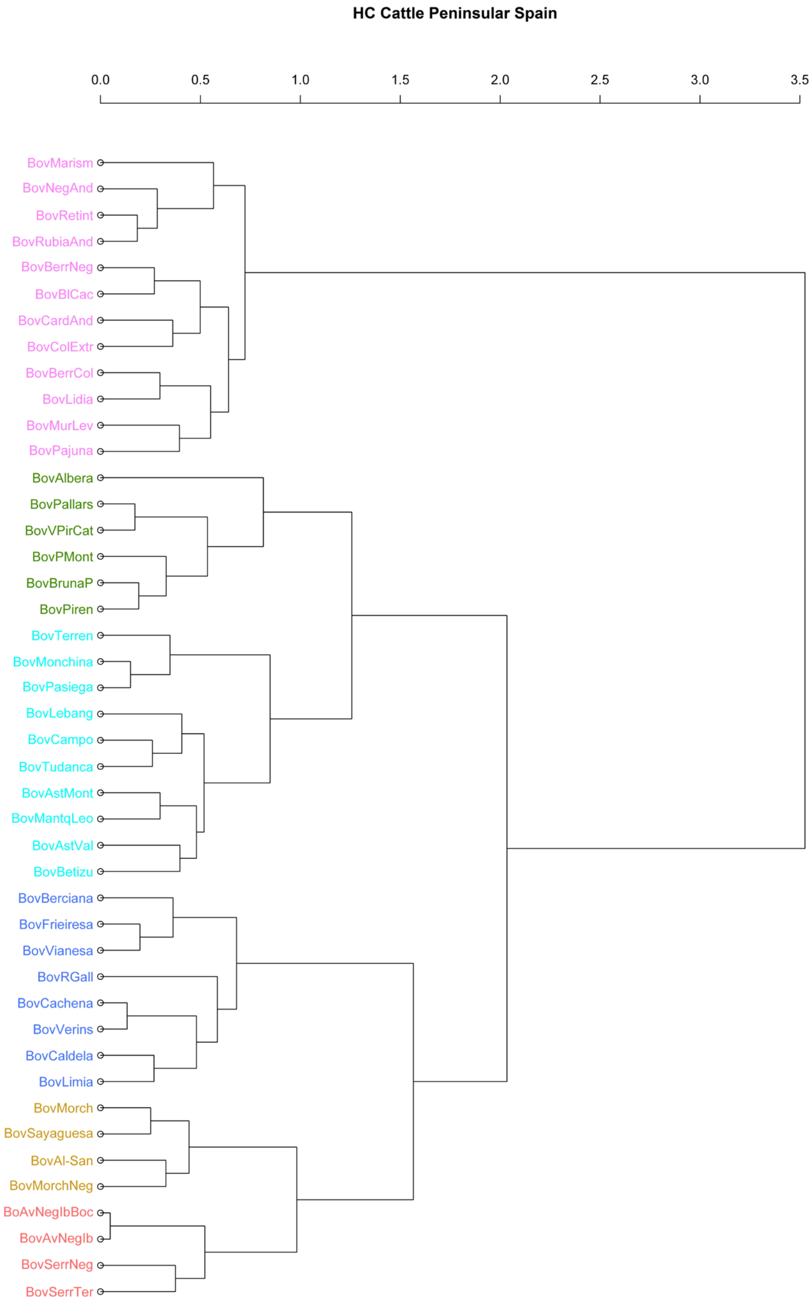

Figure S5. Bovine Hierarchical Cluster. The established groups are represented by different colours, which have been used in the representation of Figure 1a.

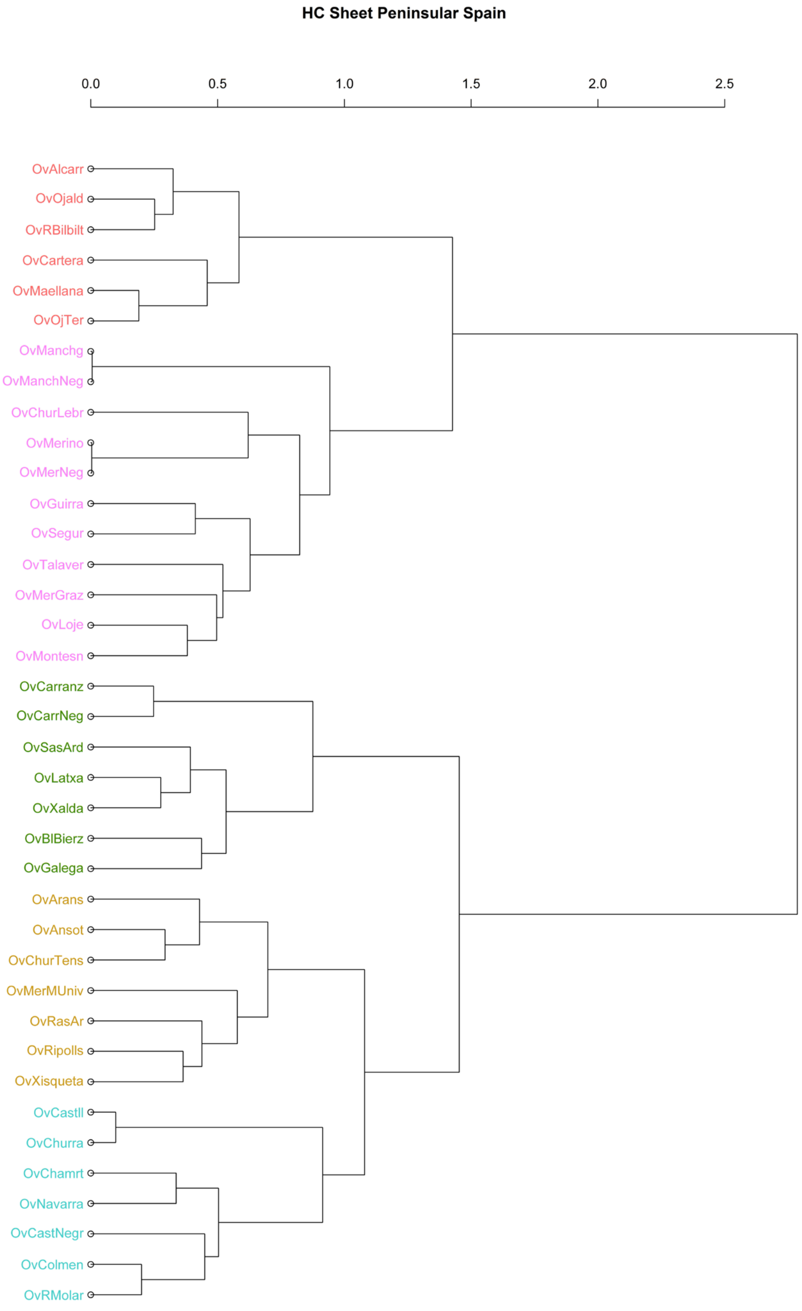

Figure S6. Ovine Hierarchical Cluster. The established groups are represented by different colours, which have been used in the representation of Figure 1b.

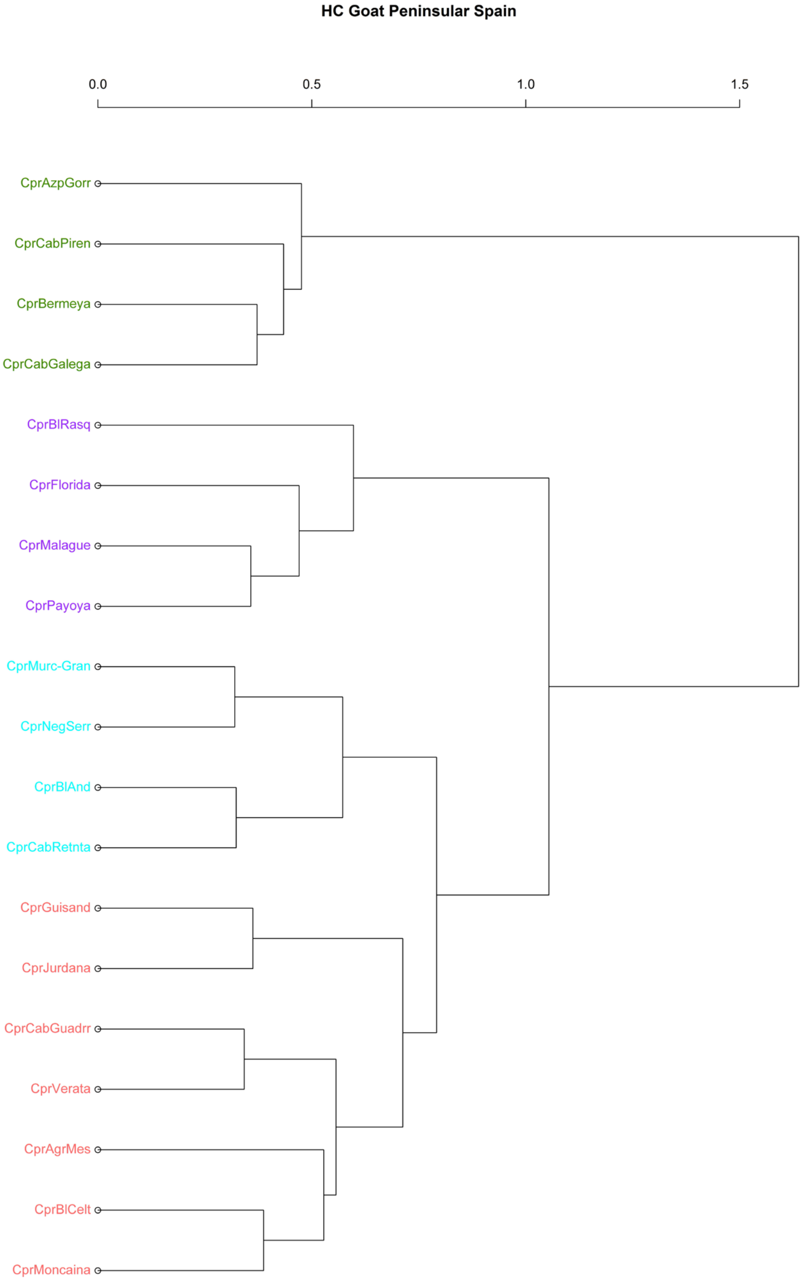

Figure S7. Caprine Hierarchical Cluster. The established groups are represented by different colours, which have been used in the representation of Figure 1c.

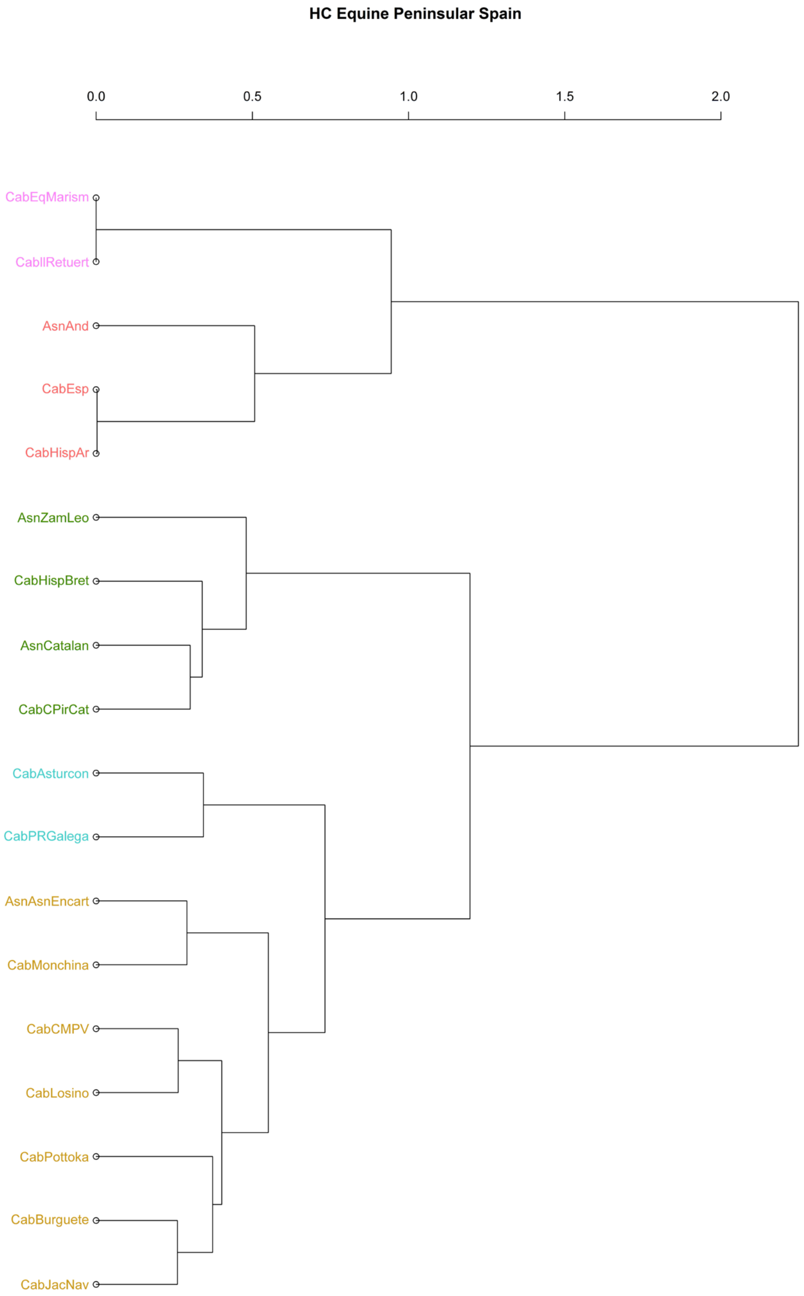

Figure S8. Equid Hierarchical Cluster. The established groups are represented by different colours, which have been used in the representation of Figure 1d.

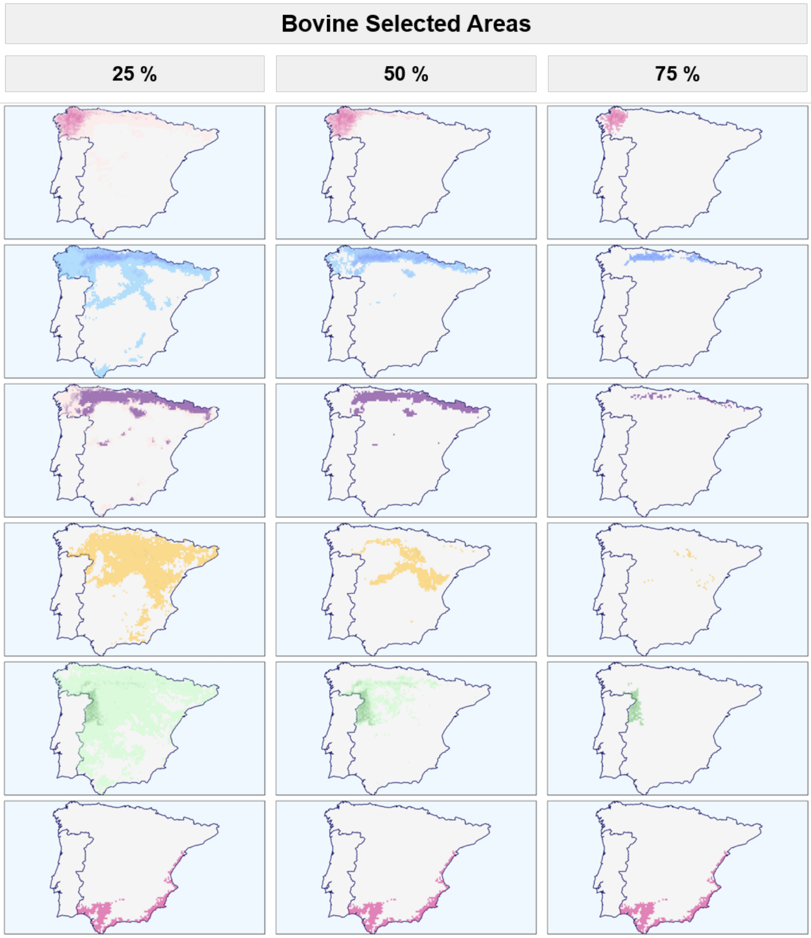

Figure S9. Livestock ecoregions maps representing those geographic regions where the environmental conditions coincide with at least 25%, 50% and 75% of the variable types preferred by each grouping of bovine local breeds, obtained through Hierarchical Cluster (SI Appendix II, Figure S5).

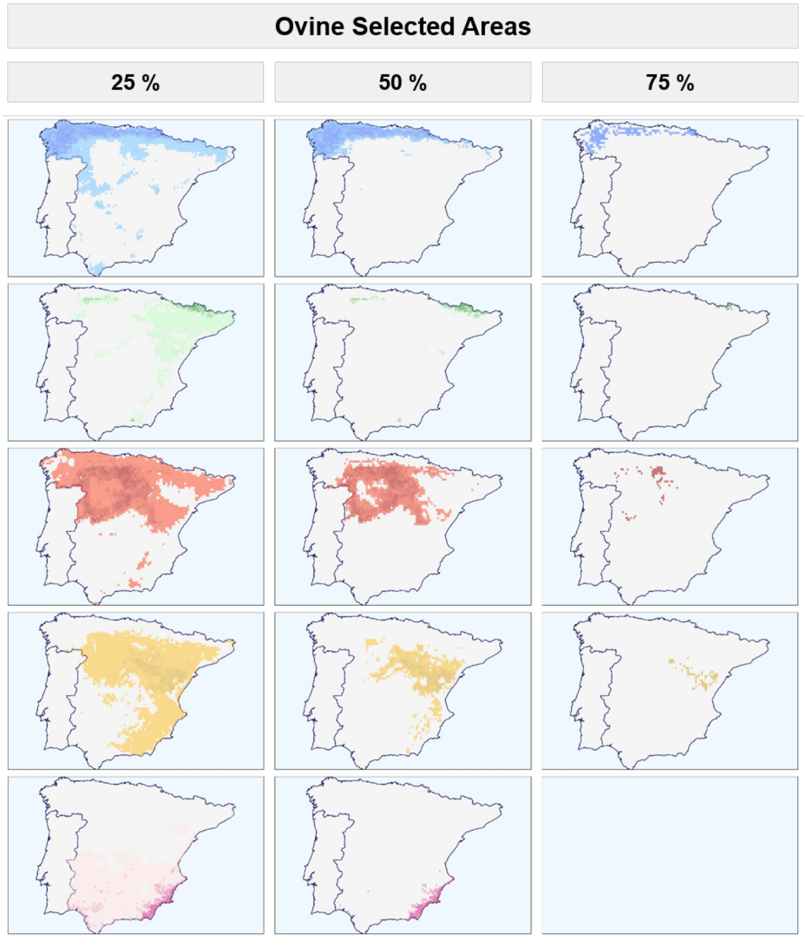

Figure S10. Livestock ecoregions maps representing those geographic regions where the environmental conditions coincide with at least 25%, 50% and 75% of the variable types preferred by each grouping of ovine local breeds, obtained through Hierarchical Cluster (SI Appendix II, Figure S6).

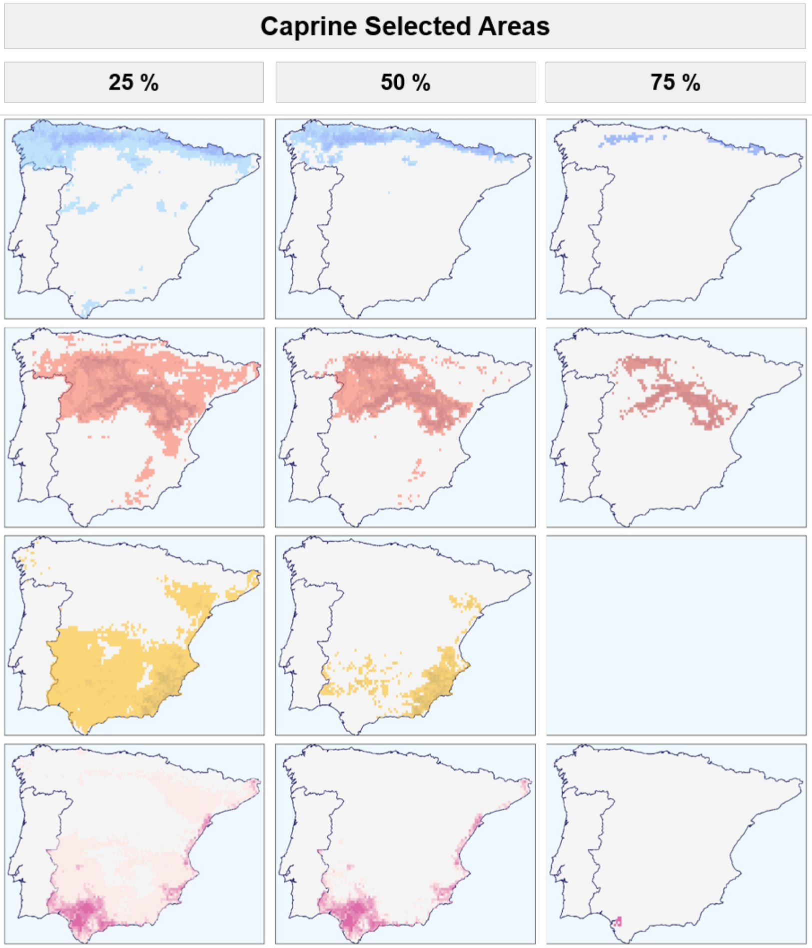

Figure S11. Livestock ecoregions maps representing those geographic regions where the environmental conditions coincide with at least 25%, 50% and 75% of the variable types preferred by each grouping of caprine local breeds, obtained through Hierarchical Cluster (SI Appendix II, Figure S7).

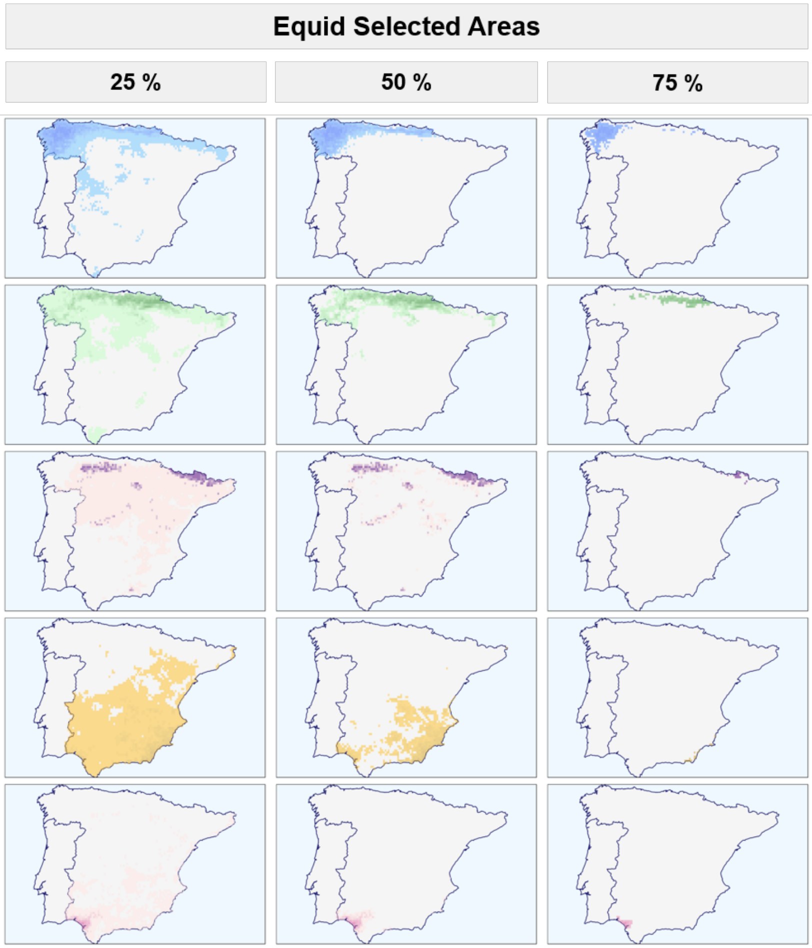

Figure S12. Livestock ecoregions maps representing those geographic regions where the environmental conditions coincide with at least 25%, 50% and 75% of the variable types preferred by each grouping of equid local breeds, obtained through Hierarchical Cluster (SI Appendix II, Figure 8).

CHAPTER 2

On the relationships between the distribution of wildlife and livestock diversity

Elena Velado-Alonso, Ignacio Morales-Castilla, Salvador Rebollo y Antonio Gómez-Sal

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 to these challenges and to other environmental factors in a similar fashion. Here, we examine the spatial relationships between the distributions of wild biodiversity and agrobiodiversity, to quantify how and where they covary across the geography, and therefore whether it would be useful to establish integrative conservation strategies.

Location:

Mainland Spain, a European region that harbours high values of both wild and domesticated diversity, a complex territory with marked contrasts in climate and topography.

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 —i.e. specific groups of amphibians, reptiles, birds, and mammals— as a function of local livestock breed richness —i.e. 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 display contrasting patterns, where cattle breeds associate positively to most wildlife vertebrates and sheep breeds show negative associations, but with relevant exceptions for specific groups of the analysed wild species.

Main Conclusion:

In the studied area, wildlife diversity distribution is significantly associated with livestock agrobiodiversity, varying depending on which group of local breeds and native vertebrates are considered. These spatial relationships are mediated by large-scale environmental gradients. Since wildlife and livestock diversity tend to co-occur spatially, future strategies for conservation in regions with agricultural uses for a long time could benefit from integrated approaches.

2.1. INTRODUCTION

Biodiversity conservation has been a key topic in research and policy for many years. In recent decades the conservation of agrobiodiversity has arisen as an additional dimension to that problem (COP 5, 2000). Yet, little is still known about the relationships between wild and domesticated components of biodiversity. There are few examples of integrated approaches where their conservation are considered together, either in research or in policy making (Attwood, Park, Marshall, & Fanshawe, 2017), even when that would be potentially beneficial in highly anthropogenic landscapes (Jackson, Pascual, & Hodgkin, 2007).

Changes toward intensification in agriculture over the last decades are compromising the conservation of wild species and their habitats (Foley et al., 2011; Godet & Devictor, 2018), 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 biodiversity conservation 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 derived from agrobiodiversity and does not guarantee that greater areas of land are geared towards natural zones (Rudel et al., 2009; Tscharntke et al., 2012).

Protected areas and large landscapes with a *wildlife friendly* management are necessary to promote biodiversity conservation (Kremen, 2015). In fact, highest values of biodiversity are not exclusively in protected areas, but also relatively high biodiversity can be found in the surrounding agricultural landscapes (López-López, Maiorano, Falcucci, Barba, & Luigi, 2011; Rey Benayas & de la Montaña, 2003). A number of ecological theories —e.g. intermediate disturbance (Hutchinson, 1953), the metacommunity theory (Leibold et al., 2004)— have been proposed to explain what drives biodiversity on these agroecosystems (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 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 abuse of fertilizers, shifts into intensive crop cultivation, or loss of sound 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 intra-specific diversification of those 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 locally adapted domesticated animals. Because of this, livestock diversity has helped shape plant structure and composition, which in turn influence 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 —e.g. food and resource provision, shelter and habitat maintenance for wild species—, which depend on different production systems and practices (Leroy et al., 2018).

The Mediterranean basin is considered a major "hotspot" of biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), characterised 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 breeds evolved long before industrialization, are unique and autochthonous of certain regions and have been regarded as *eco-cultural entities* (see e.g. Sponenberg, Martin, Couch, & Beranger, 2019), a product of the adaptation to local environmental and human conditions (Colino-Rabanal, Rodríguez-Díaz, Blanco-Villegas, Peris, & Lizana, 2018). Despite the long history of interactions and thus the potential influence of livestock on wildlife across the Mediterranean region, very little is known about if and how, both wildlife 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 peninsula topography (Blondel & Mourer-Chauviré, 1998). Much less is known about the distribution of local livestock breeds, but previous studies suggest that it 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 hypothesise the existence of a significant association between them at coarse scales. This association could be explained by two, nonexclusive mechanisms. First, the distributions of wild species and livestock breeds could be responding similarly to environmental and human factors and thus co-vary positively across the geography (Leroy, Boettcher, et al., 2016; Moreno-Rueda & Pizarro, 2009). Second, breed diversity would modify the structure and composition of 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 are the most positive for both types of biodiversity.

2.2. METHODS

2.2.1. Distributional and environmental data

We calculated several 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 costal grid cells to avoid edge effects. A total of 5,033 grid cells were used for analyses. To quantify diversity, we used species richness of terrestrial vertebrate groups —i.e. mammals, birds, amphibians and reptiles— and richness of local livestock breeds, calculated by summing the species (wildlife) or the breeds (livestock) present in each UTM grid cell.

We calculated livestock breed richness indices using all local breeds of bovine, ovine, caprine, asinine, equine, and porcine species. 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 recognised 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. These breeds were considered extinct by the FAO as Spanish Ministry doesn't account for breed extinction (Supporting Information

—SI— Appendix I, Table S1). Thus, our dataset encompasses all extant and recently extinct breeds, based on their historical distributions, prior to agricultural intensification that occurred during the recent decades (Tisdell, 2003). Thus, our measure of livestock diversity should be interpreted as historical or the long-term capacity of each grid cell to harbour breed diversity or as the diversity of land-based livestock systems, reliant on local natural resources (Colino-Rabanal et al., 2018; Gómez-Sal, 2001).

We documented a total of 128 local breeds: 44 bovine, 38 ovine, 19 caprine, 9 porcine, and 18 equine, including horses and donkeys (SI Appendix I, Table S2). With these breeds we computed 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 large number of local cattle and sheep breeds and to their markedly different distributional patterns (see Fig. 1e-g). The distribution of each breed corresponds to its area of origin —i.e. 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 SI Appendix I, 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.

Vertebrate species richness —i.e. 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 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. We additionally excluded species from aquatic environments for mammals, birds and reptiles (Fig.1a-d). Our dataset included a total of 76 mammal, 177 nesting bird, 41 reptile and 28 amphibian species (for more detail SI Appendix I, Tables S3-S6). Second, to deepen our understanding of relationships between wildlife and livestock, we further subsetted each vertebrate group based on their 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, as they feed on livestock carcasses. Reptiles were divided into those from rocky and shrubby habitats. Amphibians were separated

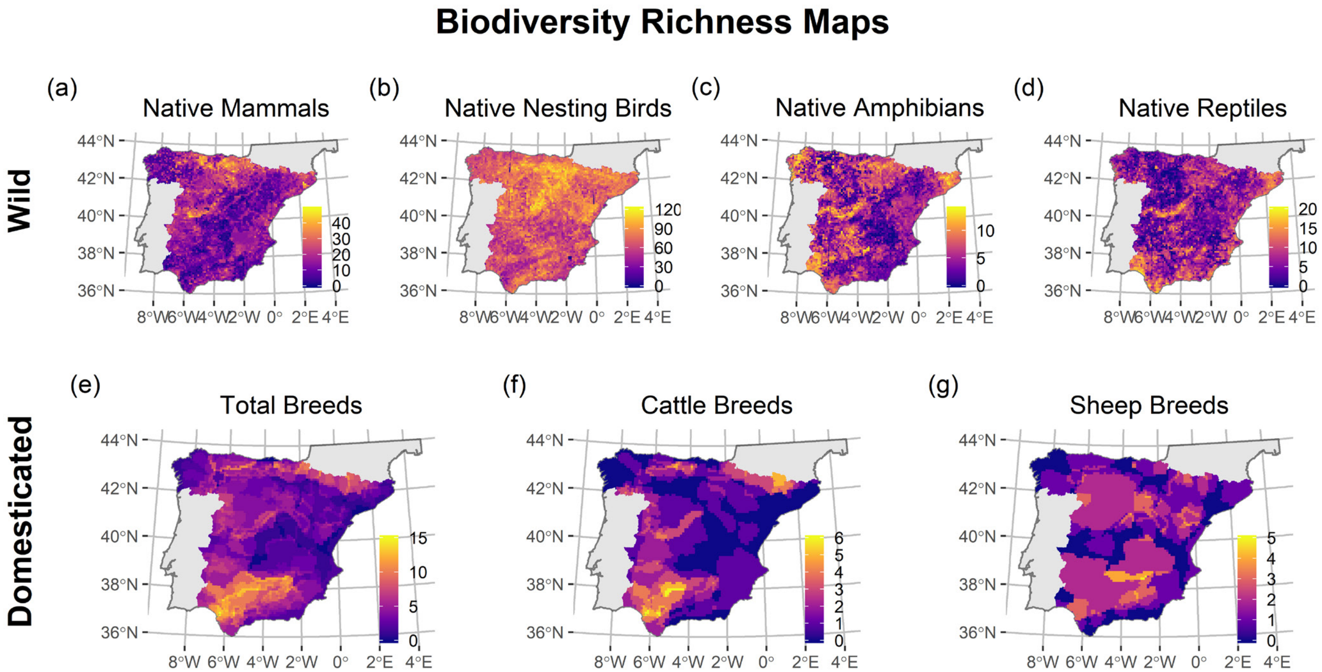

Figure 1. Diversity maps for wild and domesticated animals in Peninsular Spain. The panels are for species richness of wild native vertebrates including mammals (a), birds (b), amphibians (c) and reptiles (d) and for breed richness of domesticated livestock species, including total richness of cattle, 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 intra-specific breed (i.e. genetic) diversity.

into aquatic and land-based, according to whether their adult phase is developed or not in water bodies (for more detail SI Appendix I, Tables S7-S13).

To examine if the relationships between wild and domesticated biodiversity are mediated by 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, 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 characterise 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).

2.2.2. 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 —i.e. each 10 × 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% of the spatial units in our dataset (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 portioning (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, i.e. 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 $[P = 0] \leq 0.05$) 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.

2.3. 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 (Fig. 2). Model’s standardized global coefficients show that across over two thirds of the territory, an increase of 10 local breeds is associated 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 ($p < 0.05$; see SI Appendix II, Tables S1-S4 for details). These positive associations shift to negative ones in South western lowlands —i.e. the Guadalquivir Basin with lesser vertebrate species richness (Fig. 1a-d) and higher breed richness (Fig. 1e)— and North eastern of the Spain —i.e. the Ebro Basin, with a scarcity of livestock breeds (Fig. 1e) and high vertebrate species richness (Fig. 1a-d)— for all groups, except birds in the north east (Fig. 2b).

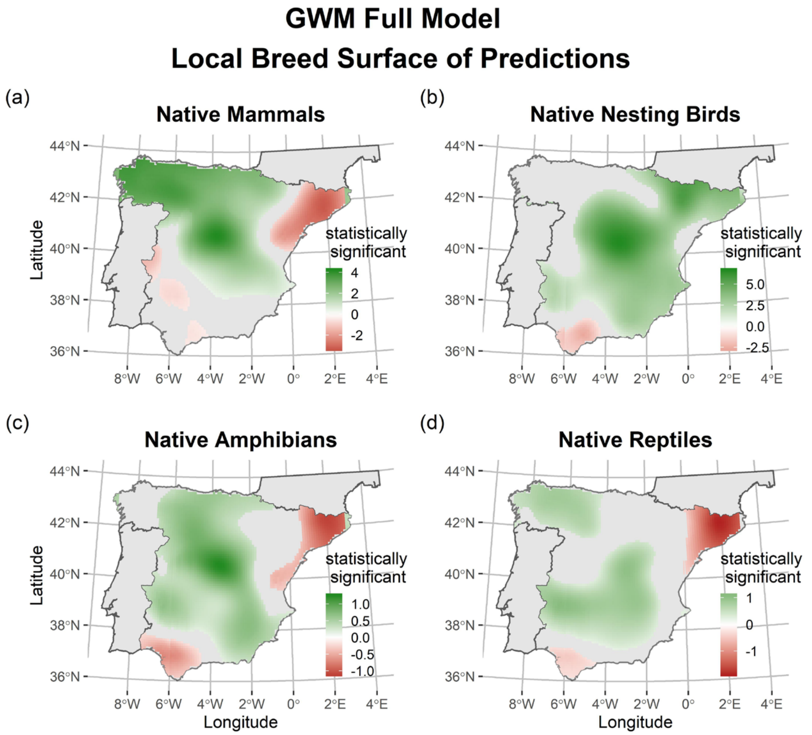

Figure 2. Maps of regression coefficients resulting from Geographically Weighted Regression models fitting the relationships between species richness of mammals (a), nesting birds (b), amphibians (c), and reptiles (d), using as predictors annual mean temperature, annual precipitation, precipitation seasonality, human footprint and total breed richness. Depicted coefficients are for total breed richness and are only coloured when statistically significant at $[P = 0] \leq 0.05$. 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 livestock.

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 0.19 to 0.39; Table 1). However, sequentially adding predictors does not increase the explained variation as compared 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).

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	0.40	0.32	0.35	0.42	0.41	0.44
	Native Nesting Birds	0.35	0.28	0.29	0.37	0.37	0.38
	Native Amphibians	0.24	0.20	0.21	0.26	0.26	0.28
	Native Reptiles	0.26	0.19	0.20	0.28	0.27	0.29
AIC	Native Mammals	33,217.22	33,856.62	33,602.5	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

Full models using any of the three indicators for livestock diversity —i.e. total breed, cattle breed and sheep breed richness— display similar ability to explain variation in the diversity of each wild vertebrate group in terms of quasi-R^2 (Table 2). Yet, cattle and sheep breed richness show markedly different distributions (Fig. 1f and 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 (Fig. 3, for more details see SI Appendix II, Tables S5-S19).

On the one hand, cattle breed richness shows positive significant associations with wild 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 Fig. 3b, e, h, k). On the other hand, the sheep breed richness is significantly 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) (Fig. 3c, f, i, l). These links are also significant but less intense for the rest of wild fauna groups analysed —lagomorphs, scavengers, aquatic amphibians and shrubby habitat reptiles— (for more details see SI Appendix II, 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 (Fig. 3b), whereas in the case of steppe birds and sheep breeds happen across central Iberian plateaus. In the case of native land-based amphibians and cattle breeds, we observe a positive and increasing effect following the aridity gradient (Fig. 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 (Fig. 3k).

2.4. 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 —i.e. shifting in magnitude and direction across the geography, in response to environmental gradients—, and differs when considering different

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	0.35	0.35	0.32
Native Nesting Birds	0.28	0.28	0.27
Native Amphibians	0.21	0.21	0.20
Native Reptiles	0.20	0.22	0.20

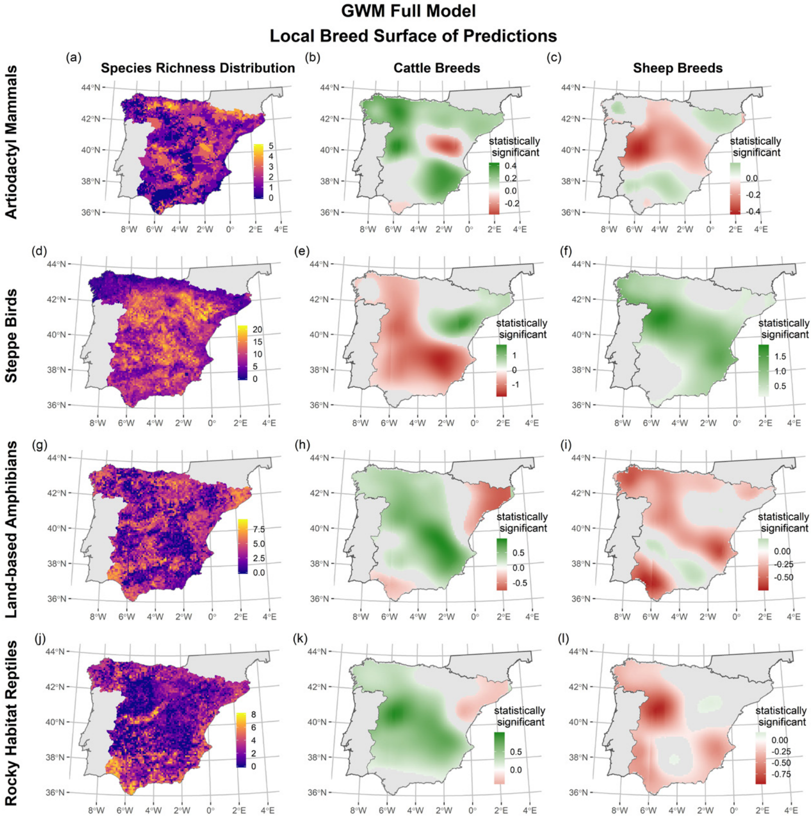

Figure 3. Maps of regression coefficients resulting from Geographically Weighted Regression models fitting the relationships between species richness of specific groups artiodactyl mammals (a), steppe birds (d), land-based amphibians (g), and rocky habitat reptiles (j), using as predictors annual mean 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] ≤ 0.05. 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 livestock.

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 studied area for all vertebrates (see Fig. 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, measures aimed at conserving one component of biodiversity —i.e. 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 Fig. 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 mesoscale considered here captures how livestock systems and practices would have promoted environmental heterogeneity, which could have indirectly fostered vertebrate species richness.

The positive associations between wild artiodactyls and cattle breed richness probably reflects similarities in their habitat preferences. Notably, the interaction between cattle and grasslands in extensive traditional livestock systems influences the distribution and composition of vegetation and fauna 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 homogenises 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 at coarse scales, then it could indirectly favour the diversity of wild artiodactyls. While our analyses do not allow establishing the causal direction of wild-domesticated diversity associations, exploring it may be an interesting avenue for future investigations.

Steppe birds and sheep breed diversity show positive associations in central Spain (see Fig. 3), possibly due to traditional sheep grazing practices promoting steppe bird preferred habitat. 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 a 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 may represent a threat for steppe bird 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 (Fig. 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, Lõhmus, & Briggs, 2009), especially in the driest areas. Livestock activities could influence amphibian diversity through different mechanisms such as influencing water quality, predator occurrence or 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 (Fig. 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 e.g. Moreno-Rueda & Pizarro, 2009) and the latter to human migrations and activities (Hall, 2004; Mason, 1973). Instead, in regions like the Mediterranean basin countries, long dominated by agricultural landscapes, both livestock biodiversity and relevant components of wild diversity may feedback and respond similarly to environmental drivers. That suggests that the integration of agrobiodiversity into wildlife conservation schemes could be mutually beneficial. Examples of integrative conservation measures would include: 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 sustainable dynamics surrounding protected areas (DeFries, Hansen, Newton, & Hansen, 2005; Ervin et al., 2010; Laurance et al., 2012; Rey Benayas & de la Montaña, 2003). At any rate, more research is needed to fully understand the causal relationships between wild biodiversity and livestock agrobiodiversity at different geographic and time scales.

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, characteristic of regions with higher local breed richness represent an opportunity to aid wildlife conservation, as they can harbour more wild biodiversity than industrialised agricultural lands (Kleijn et al., 2011). This is shown by the positive covariation between wild species and livestock breeds (see Fig. 2). Agricultural landscapes play a critical role for biodiversity conservation in Spain (Maldonado, Ramos-López, & Aguilera, 2019), a country with a long history of agriculture and some examples of sustainable uses —e.g. it is the country with the highest number of UNESCO's Biosphere Reserves, which are specifically designed to protect examples of sustainable development. Our pioneering work poses new scientific questions. For example, could results for Spain be easily extrapolated or do they only apply to world regions with a long history of livestock domestication and diversification? In any case, our findings propose a major conservation avenue for a very large part of the humanized biosphere. By suggesting that wild biodiversity and agrobiodiversity can be integrated, both to improve the sustainability of livestock farming systems and the conservation of wildlife.

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2.6. SUPPORTING INFORMATION

APPENDIX I

Table S1. List of bibliographic sources reviewed for Spanish livestock local breed areas of origin identification.

Authors	**Year**	**Edition**	**Title**
Faelli, F.	1932	Edición Española- Revista Veterinaria de España (1ªEdición 1902)	Razas Bovinas, Equinas, Porcinas, Ovinas y Caprinas. Traducción anotada por Tomás de la Fuente Muñoz.
Aparicio, G.	1947	Segunda Edición (1ª Edición 1944)	Zootecnia Especial. Etnología compendiada.
Esteban Muñoz, C. & Tejón Tejón, D.	1980	Primera Edición	Catálogo de Razas Autóctonas Españolas. I-Especies Ovina y Caprina
Sánchez Belda, A.,	1984	Primera Edición	Razas Bovinas Españolas
Sámchez Belda, A. & Sánchez Trujillano, M.C.	1986	Segunda Edición (Primera Edición 1974).	Razas Ovinas Españolas
García Dory, M.A., Martínez Vicente, S. & Orozco Piñán, F.	1990	Primera Edición	Guía de Campo de las Razas Autóctonas de España
Sáncehz Belda, A.	2002	Primera Edición	Razas Ganaderas Españolas Bovinas
Esteban Muñoz, C.	2003	Primera Edición	Razas Ganaderas Españolas Ovinas
Yanes García, J.E.	2005	Primera Edición	Razas Asnales Autóctonas Españolas
Esteban Muñoz, C.	2008	Primera Edición	Razas Ganaderas Españolas Caprinas
Sánchez Belda, A.	2012	Primera Edición	Razas Ganaderas Españolas Caballares

Information available on the ARCA (Breed Information National System) website of the MAPA (Ministry of Agriculture, Fisheries and Food) has also been consulted: http://www.mapama.gob.es/es/ganaderia/temas/zootecnia/razas-ganaderas/razas/catalogo/ consulted between March and July, 2017

Table S2. List of local livestock breeds included in this work.

Breed Name	Livestock Type	Status
Asturiana de los Valles	Bovine	Increasing
Avileña Negra Ibérica	Bovine	Increasing
Lidia	Bovine	Increasing
Morucha	Bovine	Increasing
Parda de Montaña	Bovine	Increasing
Pirenaica	Bovine	Increasing
Retinta	Bovine	Increasing
Rubia Gallega	Bovine	Increasing
Avileña Negra Ibérica Bociblanca	Bovine	Danger of Extinction
Alistano-Sanabresa	Bovine	Danger of Extinction
Albera	Bovine	Danger of Extinction
Asturiana de Montaña	Bovine	Danger of Extinction
Berrenda en Colorado	Bovine	Danger of Extinction
Berrenda en Negro	Bovine	Danger of Extinction
Betizu	Bovine	Danger of Extinction
Blanca Cacereña	Bovine	Danger of Extinction
Bruna de los Pirineos	Bovine	Danger of Extinction
Cachena	Bovine	Danger of Extinction
Caldelá	Bovine	Danger of Extinction
Cárdena Andaluza	Bovine	Danger of Extinction
Frieiresa	Bovine	Danger of Extinction
Limia	Bovine	Danger of Extinction
Marismeña	Bovine	Danger of Extinction
Monchina	Bovine	Danger of Extinction
Morucha Negra	Bovine	Danger of Extinction
Murciano-Levantina	Bovine	Danger of Extinction
Negra Andaluza	Bovine	Danger of Extinction
Pajuna	Bovine	Danger of Extinction
Pallaresa	Bovine	Danger of Estinction
Pasiega	Bovine	Danger of Extinction
Sayaguesa	Bovine	Danger of Extinction
Serrana Negra	Bovine	Danger of Extinction

Serrana de Teruel	Bovine	Danger of Extinction
Terreña	Bovine	Danger of Extinction
Tudanca	Bovine	Danger of Extinction
Vianesa	Bovine	Danger of Extinction
Berciana	Bovine	Extinct
Campoo	Bovine	Extinct
Colorada Extremeña	Bovine	Extinct
Lebaniega	Bovine	Extinct
Mantequera Leonesa	Bovine	Extinct
Rubia Andaluza	Bovine	Extinct
Verinesa	Bovine	Extinct
Vaca del Pirineo Catalán	Bovine	Extinct
Castellana	Ovine	Increasing
Churra	Ovine	Increasing
Latxa	Ovine	Increasing
Manchega	Ovine	Increasing
Merino	Ovine	Increasing
Navarra	Ovine	Increasing
Ojinegra de Teruel	Ovine	Increasing
Rasa Aragonesa	Ovine	Increasing
Segureña	Ovine	Increasing
Alcarreña	Ovine	Danger of Extinction
Ansotana	Ovine	Danger of Extinction
Aranesa	Ovine	Danger of Extinction
Carranzana	Ovine	Danger of Extinction
Carranzana Negra	Ovine	Danger of Extinction
Cartera	Ovine	Danger of Extinction
Castellana Negra	Ovine	Danger of Extinction
Chamarita	Ovine	Danger of Extinction
Churra Lebrijana	Ovine	Danger of Extinction
Churra Tensina	Ovine	Danger of Extinction
Colmenareña	Ovine	Danger of Extinction
Galega	Ovine	Danger of Extinction
Guirra	Ovine	Danger of Extinction

Lojeña	Ovine	Danger of Extinction
Maellana	Ovine	Danger of Extinction
Manchega Negra	Ovine	Danger of Extinction
Mererino de Grazalema	Ovine	Danger of Extinction
Merina Negra	Ovine	Danger of Extinction
Merinno de los Montes Universales	Ovine	Danger of Extinction
Montesina	Ovine	Danger of Extinction
Ojalada	Ovine	Danger of Extinction
Ripollesa	Ovine	Danger of Extinction
Roya Bilbilitana	Ovine	Danger of Extinction
Rubia del Molar	Ovine	Danger of Extinction
Sasi Ardi	Ovine	Danger of Extinction
Talaverana	Ovine	Danger of Extinction
Xalda	Ovine	Danger of Extinction
Xisqueta	Ovine	Danger of Extinction
Blanca del Bierzo	Ovine	Extinct
Florida	Caprine	Increasing
Malagueña	Caprine	Increasing
Murciano-Granadina	Caprine	Increasing
Agrupación de las Mesetas	Caprine	Danger of Extinction
Azpi Gorri	Caprine	Danger of Extinction
Bermeya	Caprine	Danger of Extinction
Blanca Andaluza	Caprine	Danger of Extinction
Blanca Celtibérica	Caprine	Danger of Extinction
Blanca de Rasquera	Caprine	Danger of Extinction
Galega	Caprine	Danger of Extinction
(Cabra del) Guadarrama	Caprine	Danger of Extinction
Moncaina	Caprine	Danger of Extinction
Negra Serrana	Caprine	Danger of Extinction
Payoya	Caprine	Danger of Extinction
Pirenaica	Caprine	Danger of Extinction
Retinta	Caprine	Danger of Extinction
Verata	Caprine	Danger of Extinction
Guisandesa	Caprine	Extinct

Jurdana	Caprine	Extinct
Española	Equid	Increasing
Asno Andaluz	Equid (Donkey)	Danger of Extinction
Asno de las Encartaciones	Equid (Donkey)	Danger of Extinction
Asno Catalán	Equid (Donkey)	Danger of Extinction
Asno Zamorano-Leonés	Equid (Donkey)	Danger of Extinction
Caballo Asturcón	Equid	Danger of Extinction
Caballo de Burguete	Equid	Danger of Extinction
Caballo de Monte del País Vasco	Equid	Danger of Extinction
Caballo Marismeño	Equid	Danger of Extinction
Cavall del Pirenenc Català	Equid	Danger of Extinction
Caballo Hispano-Árabe	Equid	Danger of Extinction
Caballo Hispano Bretón	Equid	Danger of Extinction
Jaca Navarra	Equid	Danger of Extinction
Caballo de las Retuertas	Equid	Danger of Extinction
Caballo Losino	Equid	Danger of Extinction
Caballo Monchino	Equid	Danger of Extinction
Pottoka	Equid	Danger of Extinction
Cabalo Pura Raza Galega	Equid	Danger of Extinction
Ibérico	Porcine	Increasing
Celta	Porcine	Danger of Extinction
Chato Murciano	Porcine	Danger of Extinction
Euskal Txerria	Porcine	Danger of Extinction
Gochu Asturcelta	Porcine	Danger of Extinction
Baztanesa	Porcine	Extinct
Cerdo de Vich	Porcine	Extinct
Chato Vitoriano	Porcine	Extinct
Lermeña	Porcine	Extinct

Table S3. List of native terrestrial mammals included in the study.

Species Name	Taxonomic Group (Order)
Apodemus flavicollis	Rodentia
Apodemus sylvaticus	Rodentia
Arvicola terrestris	Rodentia
Barbastella barbastellus	Chiroptera
Canis lupus	Carnivora
Capra pyrenaica	Artiodactyla
Capreolus capreolus	Artiodactyla
Cervus elaphus	Artiodactyla
Chionomys nivalis	Rodentia
Crocidura russula	Soricomorpha
Crocidura suaveolens	Soricomorpha
Eliomys quercinus	Rodentia
Eptesicus serotinus	Chiroptera
Erinaceus europaeus	Erinaceomorpha
Felis silvestris	Carnivora
Glis glis	Rodentia
Hypsugo savii	Chiroptera
Lepus castroviejoi	Lagomorpha
Lepus europaeus	Lagomorpha
Lepus granatensis	Lagomorpha
Lynx pardinus	Carnivora
Marmota marmota	Rodentia
Martes foina	Carnivora
Martes martes	Carnivora
Meles meles	Carnivora
Micromys minutus	Rodentia
Microtus agrestis	Rodentia
Microtus arvalis	Rodentia
Microtus cabrerae	Rodentia
Microtus duodecimcostatus	Rodentia
Microtus gerbei	Rodentia
Microtus lusitanicus	Rodentia
Miniopterus schreibersii	Chiroptera
Mus musculus	Rodentia

Mus spretus	Rodentia
Mustela erminea	Carnivora
Mustela nivalis	Carnivora
Mustela putorius	Carnivora
Myodes glareolus	Rodentia
Myotis alcathoe	Chiroptera
Myotis bechsteinii	Chiroptera
Myotis blythii	Chiroptera
Myotis emarginatus	Chiroptera
Myotis myotis	Chiroptera
Myotis mystacinus	Chiroptera
Myotis nattereri / M. escalerai	Chiroptera
Nyctalus lasiopterus	Chiroptera
Nyctalus leisleri	Chiroptera
Nyctalus noctula	Chiroptera
Oryctolagus cuniculus	Lagomorpha
Pipistrellus kuhlii	Chiroptera
Pipistrellus nathusii	Chiroptera
Pipistrellus pipistrellus	Chiroptera
Pipistrellus pygmaeus	Chiroptera
Plecotus auritus	Chiroptera
Plecotus austriacus	Chiroptera
Plecotus macrobullaris	Chiroptera
Rattus norvegicus	Rodentia
Rattus rattus	Rodentia
Rhinolophus euryale	Chiroptera
Rhinolophus ferrumequinum	Chiroptera
Rhinolophus hipposideros	Chiroptera
Rhinolophus mehelyi	Chiroptera
Rupicapra pyrenaica	Artiodactyla
Sciurus vulgaris	Rodentia
Sorex araneus	Soricomorpha
Sorex coronatus	Soricomorpha
Sorex granarius	Soricomorpha
Sorex minutus	Soricomorpha
Suncus etruscus	Soricomorpha
Sus scrofa	Artiodactyla

Tadarida teniotis	Chiroptera
Talpa europaea	Soricomorpha
Talpa occidentalis	Soricomorpha
Ursus arctos	Carnivora
Vulpes vulpes	Carnivora

Table S4. List of terrestrial native nesting birds included in the study.

Species Name
Aegolius funereus
Anthus spinoletta
Charadrius morinellus
Dendrocopos leucotos
Dendrocopos medius
Dryocopus martius
Lagopus muta
Luscinia svecica
Montifringilla nivalis
Perdix perdix
Prunella collaris
Pyrrhocorax graculus
Tetrao urogallus
Turdus torquatus
Tichodroma muraria
Accipiter gentilis
Accipiter nisus
Aegithalos caudatus
Asio otus
Carduelis chloris
Carduelis spinus
Certhia brachydactyla
Certhia familiaris
Coccothraustes coccothraustes
Cyanopica cyana
Dendrocopos major
Dendrocopos minor
Erithacus rubecula
Ficedula hypoleuca

Fringilla coelebs
Garrulus glandarius
Jynx torquilla
Loxia curvirostra
Luscinia megarhynchos
Muscicapa striata
Oriolus oriolus
Parus ater
Parus caeruleus
Parus cristatus
Parus major
Parus palustris
Pernis apivorus
Phoenicurus phoenicurus
Phylloscopus bonelli
Phylloscopus ibericus
Phylloscopus trochilus
Pyrrhula pyrrhula
Regulus ignicapilla
Regulus regulus
Scolopax rusticola
Serinus citrinella
Serinus serinus
Sitta europaea
Strix aluco
Troglodytes troglodytes
Aegypius monachus
Alauda arvensis
Alectoris rufa
Anthus campestris
Anthus pratensis
Anthus trivialis
Apus apus
Apus caffer
Apus melba
Apus pallidus
Aquila adalberti

Aquila chrysaetos
Asio flammeus
Athene noctua
Bubo bubo
Bucanetes githagineus
Burhinus oedicnemus
Buteo buteo
Calandrella brachydactyla
Calandrella rufescens
Calandrella rufescens aptezii
Calandrella rufescens polatzekii
Calandrella rufescens rufescens
Caprimulgus europaeus
Caprimulgus ruficollis
Carduelis cannabina
Carduelis carduelis
Cecropis daurica
Cercotrichas galactotes
Chersophilus duponti
Ciconia ciconia
Ciconia nigra
Circaetus gallicus
Circus cyaneus
Circus pygargus
Cisticola juncidis
Clamator glandarius
Columba domestica
Columba livia
Columba livia/domestica
Columba oenas
Columba palumbus
Coracias garrulus
Corvus corax
Corvus corone
Corvus frugilegus
Corvus monedula
Coturnix coturnix

Cuculus canorus
Delichon urbicum
Elanus caeruleus
Emberiza calandra
Emberiza cia
Emberiza cirlus
Emberiza citrinella
Emberiza hortulana
Falco naumanni
Falco peregrinus
Falco subbuteo
Falco tinnunculus
Galerida cristata
Galerida theklae
Gypaetus barbatus
Gyps fulvus
Hieraaetus fasciatus
Hieraaetus pennatus
Hippolais polyglotta
Hirundo rustica
Lanius collurio
Lanius meridionalis
Lanius minor
Lanius senator
Lullula arborea
Melanocorypha calandra
Merops apiaster
Milvus migrans
Milvus milvus
Monticola saxatilis
Monticola solitarius
Motacilla alba
Motacilla cinerea
Motacilla flava
Neophron percnopterus
Oenanthe hispanica
Oenanthe leucura

Oenanthe oenanthe
Otis tarda
Otus scops
Passer domesticus
Passer hispaniolensis
Passer montanus
Petronia petronia
Phoenicurus ochruros
Phylloscopus collybita/ibericus
Pica pica
Picus viridis
Prunella modularis
Pterocles alchata
Pterocles orientalis
Ptyonoprogne rupestris
Pyrrhocorax pyrrhocorax
Saxicola rubetra
Saxicola torquatus
Streptopelia decaocto
Streptopelia turtur
Sturnus unicolor
Sturnus vulgaris
Sylvia atricapilla
Sylvia borin
Sylvia cantillans
Sylvia communis
Sylvia conspicillata
Sylvia hortensis
Sylvia melanocephala
Sylvia undata
Tetrax tetrax
Turdus merula
Turdus philomelos
Turdus viscivorus
Turnix sylvaticus
Tyto alba
Upupa epops

Table S5. List of terrestrial native amphibians included in the study.

Species Name
Pelodytes punctatus
Discoglossus jeanneae
Rana iberica
Alytes cisternasii
Rana temporaria
Alytes dickhilleni
Calotriton asper
Pelophylax perezi
Discoglossus galganoi
Lissotriton boscai
Mesotriton alpestris
Alytes obstetricans
Pleurodeles waltl
Pelobates cultripes
Rana dalmatina
Triturus marmoratus
Hyla arborea
Lissotriton helveticus
Calotriton arnoldi
Pelodytes ibericus
Triturus pygmaeus
Salamandra salamandra
Bufo calamita
Hyla meridionalis
Euproctus asper
Chioglossa lusitanica
Rana pyrenaica
Bufo spinosus

Table S6. List of terrestrial native reptiles included in the study.

Species Name
Iberolacerta martinezricai
Iberolacerta monticola

Iberolacerta aranica
Tarentola mauritanica
Vipera latastei
Psammodromus algirus
Macroprotodon brevis
Vipera seoanei
Podarcis muralis
Malpolon monspessulanus
Blanus cinereus
Lacerta bilineata
Timon lepidus
Iberolacerta bonnali
Vipera aspis
Algyroides marchi
Coronella girondica
Iberolacerta galani
Anguis fragilis
Testudo hermanni
Hierophis viridiflavus
Chalcides striatus
Podarcis hispanica
Podarcis vaucheri
Zamenis longissimus
Podarcis carbonelli
Coronella austriaca
Chalcides bedriagai
Chamaeleo chamaeleon
Acanthodactylus erythrurus
Podarcis bocagei
Lacerta schreiberi
Lacerta agilis
Hemidactylus turcicus
Rhinechis scalaris
Hemorrhois hippocrepis
Natrix astreptophora
Iberolacerta aurelioi
Psammodromus hispanicus

Iberolacerta cyreni
Testudo graeca

Table S7. List of native lagomorphs included in the study.

Species Name
Lepus castroviejoi
Lepus granatensis
Oryctolagus cuniculus
Lepus europaeus

Table S8. List of native artiodactyls included in the study.

Species Name
Rupicapra pyrenaica
Capreolus capreolus
Capra pyrenaica
Sus scrofa
Cervus elaphus

Table S9. List of native steppe birds included in the study.

Species Name
Otis tarda
Pterocles orientalis
Calandrella rufescens
Emberiza calandra
Anthus spinoletta
Chersophilus duponti
Burhinus oedicnemus
Circus cyaneus
Galerida theklae
Circus pygargus
Anthus campestris
Oenanthe leucura
Calandrella rufescens
Pterocles alchata
Calandrella rufescens

Tetrax tetrax
Alauda arvensis
Falco naumanni
Bucanetes githagineus
Calandrella rufescens
Calandrella brachydac
Merops apiaster
Oenanthe oenanthe
Galerida cristata
Melanocorypha calandr
Coracias garrulus
Oenanthe hispanica

Table S10. List of native scavenger birds included in the study.

Species Name
Aegypius monachus
Gypaetus barbatus
Gyps fulvus
Neophron percnopterus

Table S10. List of native rocky habitat reptiles included in the study.

Species Name
Iberolacerta martinezricai
Iberolacerta monticola
Iberolacerta aranica
Tarentola mauritanica
Vipera latastei
Macroprotodon brevis
Vipera seoanei
Podarcis muralis
Iberolacerta bonnali
Vipera aspis
Algyroides marchi
Iberolacerta galani
Podarcis hispanica

Podarcis vaucheri
Chalcides bedriagai
Podarcis bocagei
Lacerta schreiberi
Hemidactylus turcicus
Hemorrhois hippocrepis
Iberolacerta aurelioi
Iberolacerta cyreni

Table S11. List of native shrub habitat reptiles included in the study

Species Name
Tarentola mauritanica
Psammodromus algirus
Macroprotodon brevis
Vipera seoanei
Malpolon monspessulanus
Timon lepidus
Coronella girondica
Anguis fragilis
Hierophis viridiflavus
Chalcides striatus
Podarcis carbonelli
Coronella austriaca
Chalcides bedriagai
Chamaeleo chamaeleon
Acanthodactylus erythrurus
Podarcis bocagei
Lacerta schreiberi
Lacerta agilis
Hemidactylus turcicus
Rhinechis scalaris
Hemorrhois hippocrepis
Natrix astreptophora
Psammodromus hispanicus
Testudo graeca

Table S12. List of native aquatic amphibians —those that adult phase is necessarily developed in water bodies— included in the study.

Species Name
Rana iberica
Calotriton asper
Pelophylax perezi
Lissotriton boscai
Mesotriton alpestris
Pleurodeles waltl
Triturus marmoratus
Hyla arborea
Lissotriton helveticus
Calotriton arnoldi
Triturus pygmaeus
Hyla meridionalis
Euproctus asper
Chioglossa lusitanica
Rana pyrenaica

Table S13. List of native land-based amphibians —those whose adult phase is not necessarily developed in water bodies— included in the study.

Species Name
Pelodytes punctatus
Discoglossus jeanneae
Alytes cisternasii
Rana temporaria
Alytes dickhilleni
Discoglossus galganoi
Alytes obstetricans
Pelobates cultripes
Rana dalmatina
Pelodytes ibericus
Salamandra salamandra
Bufo calamita
Bufo spinosus

APPENDIX II

Table S1. Summary of GWR coefficient estimates (β) for the terrestrial native mammal full model.

Native Mammals	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept	5.913	11.064	14.804	16.720	23.427	14.734
Annual Mean Temperature	-8.899	-3.146	-1.311	0.067	4.133	-2.005
Annual Precipitation	-6.188	-0.147	1.471	3.929	12.728	0.328
Precipitation Seasonality	-9.314	-5.962	-4.247	-1.040	10.971	-1.957
Human Footprint	-0.035	0.801	1.237	1.871	3.773	1.428
Total Breed Richness	-3.336	-0.292	0.866	2.543	4.222	1.464

Table S2. Summary of GWR coefficient estimates (β) for the terrestrial native nesting bird full model.

Nesting Birds	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	53.211	65.006	69.663	72.979	77.806	70.790
Annual Mean Temperature	-33.923	-11.124	-7.925	-5.958	1.590	-7.394
Annual Precipitation	-36.124	-8.363	-4.668	-2.280	18.437	-2.383
Precipitation Seasonality	-22.172	-7.730	-3.479	4.344	21.525	-2.509
Human Footprint	-2.082	-0.204	1.523	2.798	5.021	1.109
Total Breed Richness	-2.704	0.940	2.282	3.509	6.651	1.535

Table S3. Summary of GWR coefficient estimates (β) for the terrestrial native amphibian full model.

Native Amphibians	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	2.176	4.275	4.731	5.155	7.054	5.141
Annual Mean Temperature	-7.908	-1.220	-0.771	-0.083	1.588	-0.204
Annual Precipitation	-9.419	-0.152	0.443	1.010	3.022	0.639
Precipitation Seasonality	-2.989	-0.545	0.084	1.159	6.191	0.115
Human Footprint	-0.809	-0.239	0.383	0.641	1.088	0.233
Total Breed Richness	-1.104	0.018	0.366	0.568	1.252	0.360

Table S4. Summary of GWR coefficient estimates (β) for the terrestrial native reptile full model.

Native Reptiles	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-1.879	3.376	4.454	6.272	7.384	6.316
Annual Mean Temperature	-12.141	-3.332	-1.313	-0.303	1.036	-0.193
Annual Precipitation	-16.141	-4.089	0.249	0.846	2.060	-0.047
Precipitation Seasonality	-3.896	-0.309	1.228	3.212	12.837	0.341
Human Footprint	-0.257	0.154	0.603	0.862	1.271	0.605
Total Breed Richness	-1.871	-0.019	0.263	0.663	1.081	0.463

Table S5. Summary of GWR coefficient estimates (β) for the artiodactyl full model with cattle richness as agrobiodiversity index.

Artiodactyls	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	0.665	1.329	1.553	1.846	2.885	1.595
Annual Mean Temperature	-0.859	-0.481	-0.380	-0.188	0.337	-0.262
Annual Precipitation	-0.886	-0.104	0.048	0.300	1.802	-0.048
Precipitation Seasonality	-1.184	-0.423	-0.213	-0.007	0.825	-0.177
Human Footprint	-0.559	-0.244	-0.172	-0.131	-0.002	-0.250
Cattle Breed Richness	-0.360	0.046	0.158	0.248	0.423	0.161

Table S6. Summary of GWR coefficient estimates (β) for the artiodactyl full model with sheep richness as agrobiodiversity index.

Artiodactyls	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	0.585	1.237	1.512	1.837	2.709	1.595
Annual Mean Temperature	-0.948	-0.577	-0.414	-0.313	0.177	-0.327
Annual Precipitation	-0.832	-0.099	0.035	0.258	1.755	-0.058
Precipitation Seasonality	-1.018	-0.422	-0.161	0.068	1.020	-0.073
Human Footprint	-0.544	-0.256	-0.190	-0.138	-0.014	-0.252
Sheep Breed Richness	-0.426	-0.163	-0.043	0.073	0.168	-0.063

Table S6. Summary of GWR coefficient estimates (β) for the steppe bird full model with cattle richness as agrobiodiversity index.

Steppe Birds	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	4.379	8.890	9.574	10.269	11.277	8.542
Annual Mean Temperature	-2.448	-0.835	-0.078	1.128	4.485	-0.850
Annual Precipitation	-8.354	-3.674	-2.941	-0.226	4.160	-2.449
Precipitation Seasonality	-3.630	-0.752	0.060	1.319	4.146	0.582
Human Footprint	-0.560	-0.026	0.246	0.732	1.859	0.235
Cattle Breed Richness	-1.754	-0.898	-0.469	0.132	1.619	-0.467

Table S7. Summary of GWR coefficient estimates (β) for the steppe bird full model with sheep richness as agrobiodiversity index.

Steppe Birds	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	4.974	8.382	9.564	10.121	11.475	8.542
Annual Mean Temperature	-2.649	-0.414	0.359	0.991	3.983	-0.473
Annual Precipitation	-6.992	-3.526	-2.474	-0.793	4.240	-2.268
Precipitation Seasonality	-4.479	-1.278	-0.533	0.357	3.696	0.115
Human Footprint	-0.338	0.030	0.368	0.831	1.737	0.263
Sheep Breed Richness	-0.226	0.214	0.575	1.027	1.845	0.648

Table S8. Summary of GWR coefficient estimates (β) for land-based amphibian full model with cattle richness as agrobiodiversity index.

Land-based amphibians	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	1.496	2.339	2.523	2.775	3.736	2.928
Annual Mean Temperature	-5.291	-1.018	-0.636	-0.362	0.572	-0.235
Annual Precipitation	-6.133	-0.607	-0.017	0.227	1.348	0.100
Precipitation Seasonality	-1.602	-0.184	0.275	0.620	4.273	0.039
Human Footprint	-0.416	-0.117	0.231	0.385	0.599	0.160
Cattle Breed Richness	-0.713	0.003	0.275	0.464	0.924	0.184

Table S9. Summary of GWR coefficient estimates (β) for the land-based amphibian full model with sheep richness as agrobiodiversity index.

Land-based amphibians	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	1.684	2.320	2.516	2.897	4.216	2.928
Annual Mean Temperature	-4.964	-1.182	-0.731	-0.443	1.011	-0.350
Annual Precipitation	-5.433	-0.595	-0.068	0.220	1.585	0.056
Precipitation Seasonality	-1.170	0.006	0.523	0.893	3.960	0.194
Human Footprint	-0.446	-0.124	0.227	0.378	0.644	0.153
Cattle Breed Richness	-0.731	-0.332	-0.194	-0.022	0.215	-0.173

Table S10. Summary of GWR coefficient estimates (β) for the rocky habitat reptile full model with cattle richness as agrobiodiversity index.

Rocky habitat reptiles	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-1.331	0.787	1.291	2.071	3.379	2.205
Annual Mean Temperature	-5.252	-1.433	-0.649	-0.303	0.559	-0.152
Annual Precipitation	-7.075	-1.961	0.404	0.553	1.834	0.139
Precipitation Seasonality	-0.801	-0.049	0.309	1.684	5.678	0.322
Human Footprint	-0.193	0.079	0.195	0.280	0.527	0.233
Cattle Breed Richness	-0.364	0.053	0.290	0.514	0.998	0.272

Table S11. Summary of GWR coefficient estimates (β) for the rocky habitat reptile full model with sheep richness as agrobiodiversity index.

Rocky habitat reptiles	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-1.225	0.810	1.212	2.035	2.976	2.205
Annual Mean Temperature	-4.986	-1.528	-0.965	-0.306	0.373	-0.307
Annual Precipitation	-6.691	-1.830	0.202	0.548	1.251	0.086
Precipitation Seasonality	-0.798	0.134	0.629	1.883	5.693	0.537
Human Footprint	-0.121	0.077	0.187	0.296	0.513	0.224
Sheep Breed Richness	-0.947	-0.337	-0.145	-0.025	0.140	-0.218

Table S12. Summary of GWR coefficient estimates (β) for the lagomorph full model with cattle richness as agrobiodiversity index.

Lagomorphs	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	1.012	1.327	1.556	1.924	3.035	1.449
Annual Mean Temperature	-0.373	-0.059	0.038	0.219	1.130	-0.017
Annual Precipitation	-0.394	-0.163	0.004	0.565	2.072	-0.124
Precipitation Seasonality	-1.564	-0.460	-0.114	0.126	0.706	0.001
Human Footprint	-0.047	0.054	0.117	0.161	0.245	0.051
Cattle Breed Richness	-0.123	-0.027	0.024	0.076	0.160	0.019

Table S13. Summary of GWR coefficient estimates (β) for the lagomorph full model with sheep richness as agrobiodiversity index.

Lagomorphs	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-0.242	1.017	1.632	2.256	3.692	1.656
Annual Mean Temperature	-0.393	-0.126	-0.011	0.188	1.118	-0.043
Annual Precipitation	-0.002	-0.001	0.000	0.002	0.007	-0.001
Precipitation Seasonality	-0.114	-0.033	-0.009	0.013	0.056	0.002
Human Footprint	-0.058	0.042	0.104	0.150	0.232	0.048
Sheep Breed Richness	-0.245	-0.166	-0.036	0.000	0.193	-0.054

Table S14. Summary of GWR coefficient estimates (β) for the scavenger full model with cattle richness as agrobiodiversity index.

Scavengers	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	0.077	0.376	0.498	0.609	1.318	0.509
Annual Mean Temperature	-0.485	-0.147	0.060	0.152	0.960	0.006
Annual Precipitation	-0.686	-0.064	0.077	0.334	1.259	-0.002
Precipitation Seasonality	-1.304	-0.498	-0.284	-0.049	0.300	-0.247
Human Footprint	-0.431	-0.169	-0.113	-0.071	0.053	-0.136
Cattle Breed Richness	-0.134	0.055	0.181	0.277	0.422	0.209

Table S15. Summary of GWR coefficient estimates (β) for the scavenger full model with sheep richness as agrobiodiversity index.

Scavengers	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-0.391	0.250	0.437	0.555	1.230	0.509
Annual Mean Temperature	-0.534	-0.175	-0.067	0.073	0.824	-0.047
Annual Precipitation	-0.750	-0.030	0.088	0.346	1.261	0.009
Precipitation Seasonality	-1.109	-0.578	-0.254	0.039	0.431	-0.139
Human Footprint	-0.395	-0.177	-0.115	-0.059	0.046	-0.136
Sheep Breed Richness	-0.262	-0.098	-0.020	0.072	0.208	-0.006

Table S16. Summary of GWR coefficient estimates (β) for the aquatic amphibian full model with cattle richness as agrobiodiversity index.

Aquatic amphibians	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	0.315	1.665	2.160	2.590	3.639	2.213
Annual Mean Temperature	-2.655	-0.294	-0.062	0.297	1.084	0.022
Annual Precipitation	-3.345	0.138	0.437	1.023	2.099	0.527
Precipitation Seasonality	-1.666	-0.505	-0.164	0.314	1.853	0.080
Human Footprint	-0.401	-0.116	0.080	0.244	0.443	0.067
Cattle Breed Richness	-0.461	0.012	0.119	0.308	0.992	0.237

Table S17. Summary of GWR coefficient estimates (β) for the aquatic amphibian full model with sheep richness as agrobiodiversity index.

Aquatic amphibians	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	0.994	1.579	2.148	2.604	3.549	2.213
Annual Mean Temperature	-2.450	-0.564	-0.156	0.237	1.082	-0.049
Annual Precipitation	-2.974	0.045	0.508	0.946	2.064	0.532
Precipitation Seasonality	-1.242	-0.496	0.014	0.677	1.692	0.213
Human Footprint	-0.404	-0.103	0.098	0.249	0.503	0.065
Sheep Breed Richness	-0.444	-0.199	-0.089	-0.001	0.165	-0.033

Table S18. Summary of GWR coefficient estimates (β) for the shrub habitat reptile full model with cattle richness as agrobiodiversity index.

Shrub habitat reptiles	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-1.825	2.478	3.373	4.508	5.652	4.336
Annual Mean Temperature	-8.464	-2.294	-0.426	0.243	0.918	0.181
Annual Precipitation	-12.067	-3.787	-0.008	0.441	2.146	0.021
Precipitation Seasonality	-1.800	0.080	0.706	2.490	9.363	0.399
Human Footprint	-0.189	0.105	0.404	0.555	0.684	0.386
Cattle Breed Richness	-0.843	0.129	0.470	0.789	1.730	0.233

Table S19. Summary of GWR coefficient estimates (β) for the shrub habitat reptile full model with sheep richness as agrobiodiversity index.

Shrub habitat reptiles	Min.	1st Qu.	Median	3rd Qu.	Max.	Global
Intercept.	-1.251	2.485	3.188	4.305	5.605	4.336
Annual Mean Temperature	-8.108	-2.303	-0.949	0.115	1.096	-0.042
Annual Precipitation	-11.482	-3.642	-0.078	0.352	1.705	-0.098
Precipitation Seasonality	-1.020	0.296	1.515	3.138	9.056	0.662
Human Footprint	-0.157	0.120	0.370	0.528	0.783	0.368
Sheep Breed Richness	-1.491	-0.493	-0.287	-0.131	0.273	-0.410

CHAPTER 3

Humans decouple livestock diversity relationship with environment. Analysis over time of spatial patterns of Spanish livestock diversity.

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ABSTRACT

Local livestock breeds, i.e. those autochthonous to a specific region, are locally adapted domesticated animals that conserve genetic resources, guaranty food security and provide agroecosystem services. Local breeds are largely threatened worldwide by agricultural intensification and rural area abandonment processes related to current production schemes and planning. Yet, our gap of knowledge regarding livestock breed-environment relationships may prevent the design of successful conservation measures. In this work, we analyse the links between livestock diversity —i.e. richness of local breeds— and environmental factors, from a temporal perspective. We compare breeds' distributional patterns before and after agricultural intensification, in the context of land-use change in mainland Spain. Our results confirm the existence of strong associations between the distribution of local livestock breeds and environmental factors. These links, however, weaken for contemporary distributions. In fact, changes in breed distribution reflect a shift towards more productive environments. Finally, we found that the areas having higher historical breed richness are undergoing land abandonment processes. Succeeding in the conservation of threatened local breeds will require going beyond merely genetic and production-oriented views. Ecological and sociocultural perspectives should also be accounted for as global change processes are determining livestock agrobiodiversity.

3.1. INTRODUCTION

Understanding the distribution of biodiversity is a major goal of ecology. An extensive literature has proposed numerous hypotheses to explain biodiversity gradients, usually linked to environmental factors such as ambient energy, water availability, vegetation productivity or environmental heterogeneity (Field et al., 2009; Stein, Gerstner, & Kreft, 2014). Most of this work has focused on wild species. Much less is known about the distribution of agrobiodiversity —i.e. the variation within and across agricultural plants and domesticated animals—, especially in the case of livestock (Robinson et al., 2011). Yet, knowing which factors underlie the distribution of agrobiodiversity is critical to understand the adaptation processes responsible for generating it and to plan conservation actions where needed.

Local livestock breeds are those autochthonous and locally adapted to a specific region (Hoffmann, 2013). They are homogeneous intraspecific groups with inheritable external traits (FAO, 2000), resulting from differentiation processes of domesticated animals (Felius et al., 2014; Larson & Fuller, 2014). In these processes, human intended and non-intended selection, as well as other factors such as genetic and geographic isolation, inbreeding, ecological and historical processes or human geography, have been key to create and maintain local breeds over time (Hall, 2004; Hoffmann, 2013; Mignon-Grasteau et al., 2005). Thus, both natural and artificial selection are involved in the diversification of local breeds (Hall, 2004). In addition, livestock breeds are considered management and conservation units of livestock agrobiodiversity (FAO, 2007a; Felius, Theunissen, & Lenstra, 2015).

For these reasons, local livestock breeds represent important ecocultural —i.e. culturally and environmentally mediated— entities to preserve (Sponenberg, Beranger, Martin, & Couch, 2018). First, they help maintaining animal genetic resources and diversity and thus guarantee food security (Sponenberg et al., 2018; Taberlet et al., 2008). Second, their conservation prevents the loss of rare and unique phenotypes of current or potential future importance (Leroy, Besbes, et al., 2016). Third, local breeds act as drivers and providers of agroecosystem services (Leroy et al., 2018), which are expected to be secured or increased with higher diversity rates. However, livestock breed diversity is largely threatened. Currently, there are 7,136 catalogued local livestock breeds worldwide, of which 27% are endangered and 65% have an unknown status (FAO, 2019).

Althought the value of local livestock breeds is widely recognised (World Bank, 2009), major shortfalls in our knowledge about them remain. For example, even if local breeds being highly locally adapted is claimed as a chief reason for their worth, especially in the context of climate change (Hoffmann, 2011), little is known about the mechanisms involved in breeds adaptations (Boettcher et al., 2014; FAO, 2015). Besides, even when *in situ* is supposedly the preferred conservation option (FAO, 2007b), most research focuses on breed genetics and animal production. Therefore, ecological perspectives are neglected (Hoffmann, 2011), limiting our understanding of breed-environment interactions.

Wild and domesticated diversity have followed markedly different evolutionary pathways (Zeder, 2015). While climate and biogeography exert major influences on wild diversity (Hawkins et al., 2003), the distribution of domesticated diversity and its drivers are less well known. For example, we know that the distribution of domesticated animals is associated with human migrations, through a complex process where local adaptation and blending with wild populations seems to have been frequent (Zeder, 2017b). Wildlife diversity is also known to be limited by human pressures (Davies et al., 2006; Pimm et al., 2014), especially in regions deeply modified by humans such as the Mediterranean basin (Blondel, Aronson, Bodiou, & Boeuf, 2010; López-López, Maiorano, Falcucci, Barba, & Luigi, 2011) over a historical process of at least 7,000 years. There is also evidence that bioclimatic factors have determined regions where the genome of livestock breeds would have endured stronger selective pressures (Bertolini et al., 2018).

Environmental heterogeneity has been proposed as a driver of wild species richness, since it would increase the available niche options, enhancing species coexistence, providing refuges, promoting species persistence and increasing the probability of speciation events resulting from isolation or adaptation (Stein et al., 2014). In the case of domesticated animals, heterogeneity could have played a similar role, though acting through different mechanisms. Firstly, human needs and human-modified environments should have fostered heterogeneity, promoting diversity among domestication pathways (Zeder, 2012), through processes such as human-animal cultural coevolution (Zeder, 2017a). Secondly, during post-domestication specialization processes, prompting the diversification of local and regional populations, responding to new demands in the context of traditional agriculture (Larson & Fuller, 2014).

Climatic conditions should have played an additional role in shaping the distributional ranges of domesticated animals based on their physiological requirements and the availability of resources (Ethier et al., 2017), as in the case of wild species (Hawkins et al., 2003). They should also have had, both direct and indirect effects, on the adaptation of breeds to local environments through physiological mechanisms (Lv et al., 2014; Xu et al., 2015). In addition, the relaxation of intra- and interspecific competition, due to human control of natural selection (e.g. predator pressure), may have facilitated the emergence of new phenotypes.

Conversely, human factors —e.g. diversity of production systems, agricultural area and land cover types— are positively correlated with the number of breeds reported by each country (Leroy, Boettcher, et al., 2016). Nonetheless, human factors have been also identified as core drivers of livestock diversity erosion, mainly related to recent agricultural intensification, due to replacement with highly productive breeds, crossbreeding or lack of economic profitability of the local breeds (FAO, 2015). The conservation of livestock diversity is largely threatened by under-utilization, contrary to the case of wild diversity which usually is more related to overuse, e.g. overhunting or habitat degradation (Hoffmann, 2011). In this context, the apparently opposite processes of land-use intensification and abandonment are factors that currently threaten (or at times foster) wildlife diversity (Newbold et al., 2015), and might also be key for agrobiodiversity (FAO, 2015).

The goal of this work is twofold. First, to quantify changes in the associations between the distribution of livestock agrobiodiversity —i.e. different estimates of local breed richness— and environmental factors in mainland Spain, a remarkable area of livestock breed richness in Europe. We hypothesise that environmental factors are associated with livestock breeds richness, which would respond to them in a similar way to wild biodiversity. That is, based on the water-energy hypothesis (Hawkins et al., 2003), we expect positive relationships between local livestock breed richness and predictors such as temperature and precipitation (Hawkins et al., 2003). Second, we explore how the current distribution of livestock diversity relates to land-use changes occurred in recent decades. We determine where in the current land use context is more likely to find higher richness of local livestock breeds. We hypothesise that present local breed distribution relates to rural abandonment, and is affected by agricultural intensification (FAO, 2015).

3.2. RESULTS

Our results show a major effect of environmental factors on the distribution of local livestock breed diversity both for past —i.e. before agricultural intensification— and current distributions —i.e. after agricultural intensification (see methods for more detail). This pattern is robust across all the studied domesticated species. Environmental factors explain up to three quarters of the variation in species diversity for past distributions (i.e. from global quasi-R^2_{ovine} = 0.39 to global quasi-R^2_{equine} = 0.73; see Table 1), and up to half the variation for current distributions (i.e. from global quasi-R^2_{ovine} = 0.20 to global quasi-R^2_{bovine} = 0.43; see Table 1). Consistently, environmental factors explain more variation in total breed richness for the past distributions than for contemporary distributions of livestock (global quasi-R^2_{past} = 0.64; global quasi-$R^2_{present}$ = 0.46; see Table 1). This pattern of stronger associations between the environment and past distributions is constant across species —i.e. bovine, ovine, caprine, equids, porcine (see Table 1)—, sampling grain size —i.e. 10×10, 20×20 and 50×50 km (see Table 2, more detail in Supporting Information —SI—, Appendix II-1)— and analysis extent —i.e. 2.5%, 5%, 10%, 20% of data bandwidth (see methods section). These results are also robust to a sensitivity test excluding extinct or new local breeds from the analysis (for more details see SI, Appendix II-3).

The distribution of local livestock breed diversity has changed over time and so has its associations with environmental factors (see Fig. 1). Overall, when considering total breed richness, the distribution has shifted from hotspot areas southern part of the studied area (Guadalquivir Basin and surrounding mountains), and the north eastern part of mainland Spain (Pyrenees Mountain range), to areas placed in southwestern and western Spain, close to Portuguese border, and the Atlantic regions, north and north-western Spain (see Fig. 1e, j).

GWR models show a contrasting effect of environmental factors on the past and present distributions of total local breed richness. In general, past breed richness is negatively, neutral or non-significantly associated with temperature and precipitation across most of the studied territory (Fig. 1f, g). There is an exception in the southern corner of Spain, where positive coefficients coincide with the diversity hotspot of Guadalquivir Basin (Fig. 1e). In contrast, the contemporary distribution of livestock diversity is positively associated with these environmental factors across most of the Spanish geography (Fig. 1k, l). The climatic seasonality seems to have had general positive effects on livestock richness distribution in the past (Fig. 1h, i). Precipitation seasonality presents higher positive coefficients in central mainland Spain where intermediate local breed richness values are found (Fig. 1e), and the seasonality of vegetation productivity shows greater positive coefficients in the central-north and central eastern Spain, coinciding with the Iberian mountain range. In the contemporary distributions, the association with the seasonality of vegetation productivity remains positive (Fig. 1n), but precipitation seasonality becomes strongly negatively associated over northernmost and

Table 1: Global quasi R^2 values of the Geographically Weighted Regression fitted models, with an analysis extent of 5% of the total data as bandwidth, for each studied livestock species richness (i.e. bovine, ovine, caprine, equid —horses and donkeys—, porcine and total, sampled at 10×10 km UTM grid cell), in past and present distributions, using as predictors: annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality (see more detail in SI Appendix II).

	Global Quasi-R^2	
	Past	**Present**
Bovine	0.63	0.45
Ovine	0.39	0.20
Caprine	0.40	0.29
Equid	0.73	0.41
Porcine	0.66	0.35
Total	0.64	0.46

Table 2: Global quasi R^2 values of the Geographically Weighted Regression fitted models with an analysis extent of 5% of the total data as bandwidth, considering different sampling scales (20×20, 50x50 km UTM grid cell) for each studied livestock species richness (i.e. bovine, ovine, caprine, equid —horses and donkeys—, porcine and total) in past and present distribution, using as predictors annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality. (see more detail in SI, Appendix II).

	Sample Size	**Global Quasi-R^2**	
		Past	**Past**
Bovine	20X20	0.65	0.37
	50x50	0.66	0.48
Ovine	20x20	0.43	0.16
	50x50	0.57	0.24
Caprine	20x20	0.43	0.23
	50x50	0.46	0.35
Equid	20x20	0.73	0.42
	50x50	0.75	0.47
Porcine	20x20	0.66	0.24
	50x50	0.70	0.38
Total	20x20	0.65	0.41
	50x50	0.68	0.51

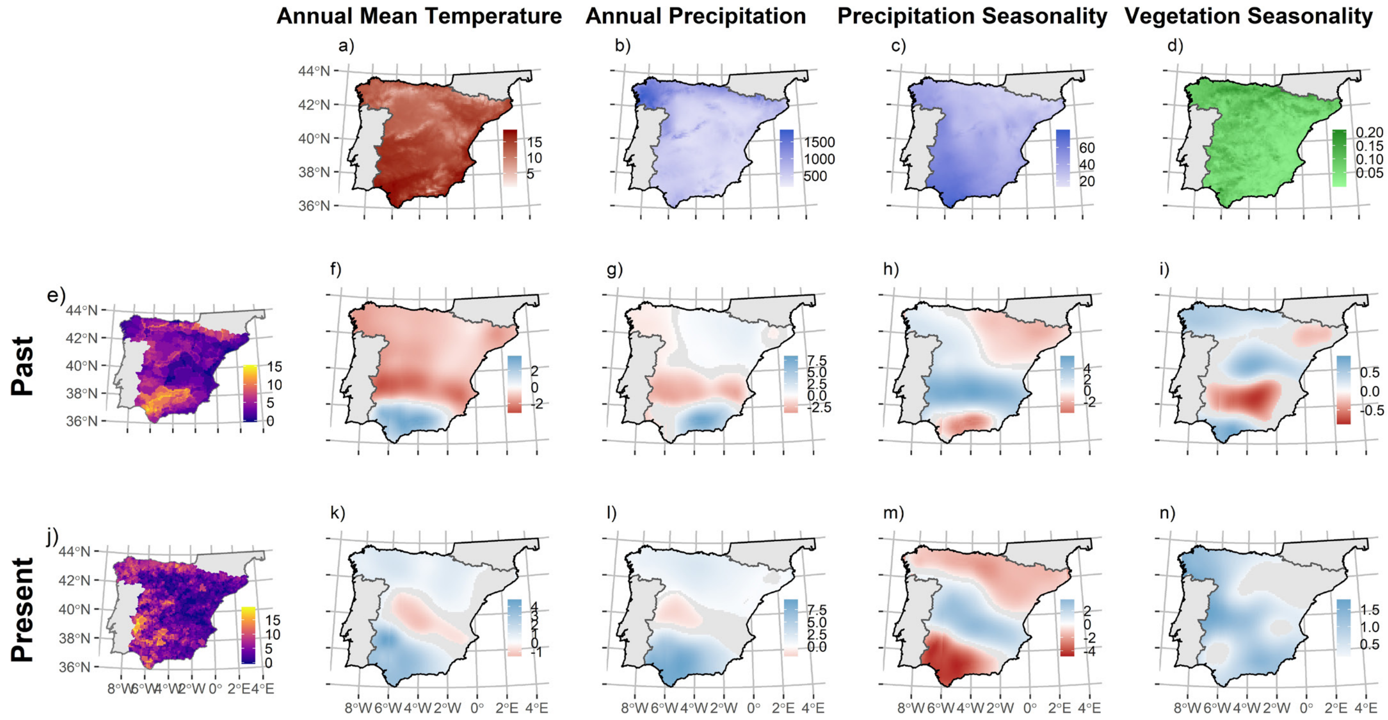

Figure 1: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models, fitting the relationships between total local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

southernmost ends of mainland Spain (Fig. 1m). Coarse extent analyses —i.e. 20% of data as bandwidth— show that the four environmental factors become positively associated to contemporary total livestock breed richness (for more details see SI, Appendix II-2, Fig. S1).

GWR models fitted separately for breed diversity of each studied species reveals contrasting patterns. In general, ruminant species —i.e. bovine, ovine and caprine— present a common pattern where mean temperature, annual precipitation and seasonality of the vegetation productivity are mostly negative or invariant in their associations with the past distribution of breed richness (Fig. 2). Regarding contemporary distributions, stronger positive coefficients are found for the environmental factors, except for precipitation seasonality, in bovine and ovine, but not in caprine species distribution (Fig. 2). On the contrary, the associations of the distributions of porcine and equine breed richness with environmental factors remain invariant regardless whether past or present distributions are considered. Mean temperature, annual precipitation and seasonality of the vegetation productivity are mostly positive for porcine breeds, whereas for equine breeds are positive northern Spain and negative southern Spain (Fig. 3). These patterns change for precipitation seasonality, which shows positive associations southwards and negative northwards (Fig. 3). Similarly to the patterns for all livestock species together, using coarser analysis extents, differences across species weaken and tend to become positive for contemporary distributions (see SI, Appendix II-2, Fig. S2-S6).

The results on current local breed distribution in relation to land use changes show that livestock breed richness is higher in areas undergoing agricultural farm abandonment. Our models —e.g. Ordinal Logistic Regressions, OLR— show that municipalities experiencing afforestation linked to farm abandonment —i.e. land-use change class 1— are twice more likely to harbour high than low diversity of breeds (Fig. 4). When compared against municipalities undergoing different land-use processes —i.e. land-use change classes 2 to 7, ranging from farm extensification to artificialization—, the former is up to three times more likely to have higher livestock breed richness (see Fig. 4). In locations going through agriculture extensification —i.e. class 2— it is slightly more likely to find high local livestock breed richness. In contrast, within municipalities subjected to agricultural intensification —i.e. classes 3 to 7— finding high breed richness is decreasingly probable (Fig. 4). These patterns are robust when considering the studied species separately, except for equids, where ORL models are not significant (SI, Appendix III).

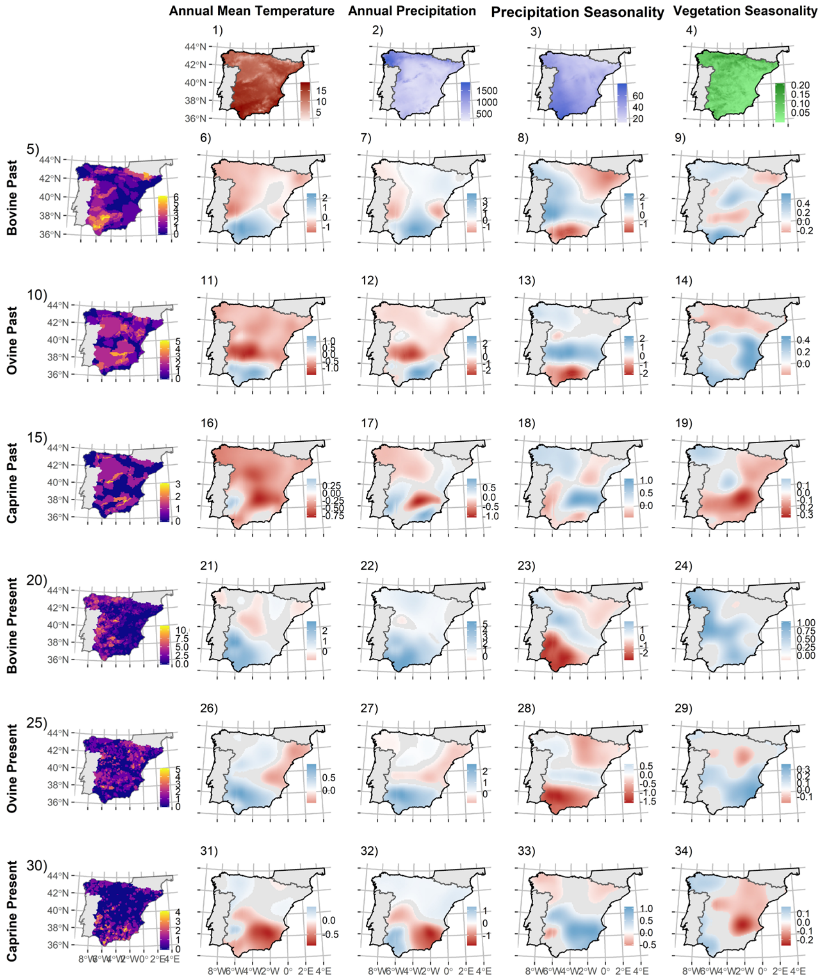

Figure 2: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 5% of the data as bandwidth, fitting the relationships between bovine (5, 10), ovine (10, 25) and caprine (15, 30) local breed richness —sampled at 10×10 km UTM grid cell— for past (5-19) and present (20-34) distributions, using as predictors annual mean temperature (1), annual precipitation (2), precipitation seasonality (3) and vegetation productivity seasonality (4). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

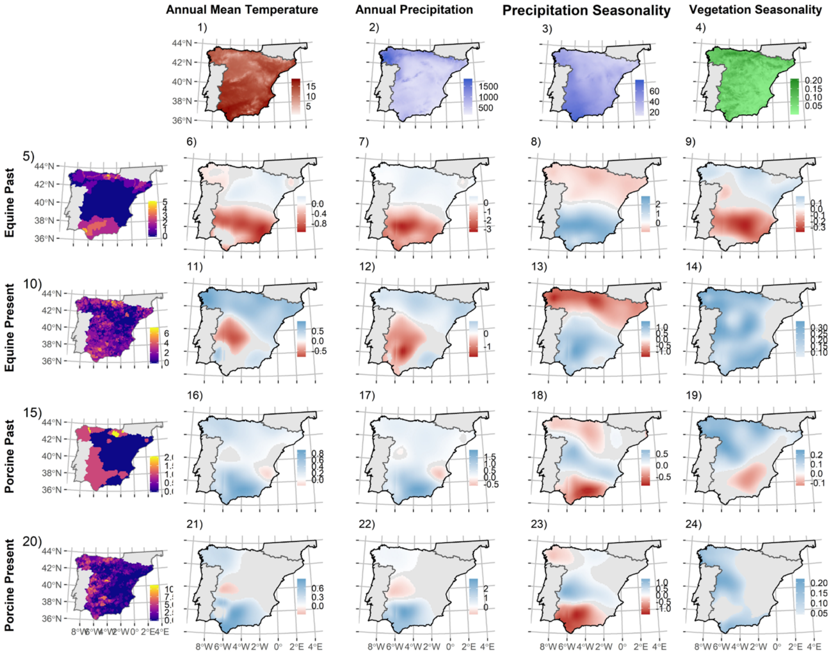

Figure 3. Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 5% of the data as bandwidth, fitting the relationships between equid —horses and donkeys— (5, 10) and porcine (15, 20) local breed richness (sampled at 10×10 km UTM grid cell) for past (5-9, 15-19) and present distributions (10-14, 20-24), using as predictors annual mean temperature (1), annual precipitation (2), precipitation seasonality (3) and vegetation productivity seasonality (4). Depicted coefficients are only coloured when statistically significant at [P = 0] ≤0.05. Blue colour represents positive coefficients and red colour represents negative associations.

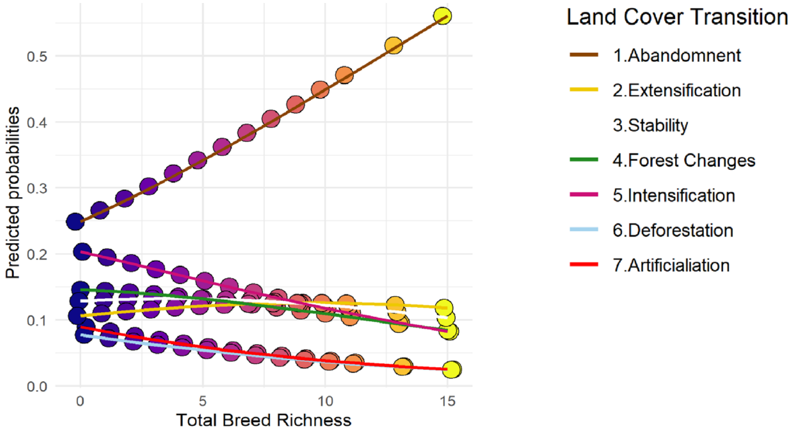

Figure 4. Predicted probabilities of total breed richness —based on current distribution by municipality— (from 0 to 15) in each land cover transition class (see legend), calculated from Ordinal Logistic Regression model (consult SI Appendix III for more detail).

3.3. DISCUSSION

Our results show that, despite the major role played by humans on the differentiation and distribution of livestock breeds (Hall, 2004), the environment also has an imprint on the distribution of livestock diversity. The distribution of livestock agrobiodiversity is significantly associated with environmental factors, but the strength of the associations has decreased for contemporary distributions. As proven for wildlife diversity and hypothesized for agrobiodiversity, variables linked to the water-energy hypothesis seem to be suitable predictors to explain both distributions. However, we find that the direction of model coefficients has shifted with time. Overall, the areas where past distribution —i.e. before agricultural intensification— was negatively associated with mean temperature and annual precipitation, become positively or not associated in the present (more so at coarser scales, see SI Appendix II-2). This pattern indicates that a) past distribution of livestock diversity was associated with low productivity zones, determined by climatic and topographic factors, b) the current distribution of livestock tends to concentrate in more productive environments. In addition, the highest values of local breed richness are found in areas undergoing farm abandonment processes. Taken together, our results confirm that beyond human determinants —e.g. economically oriented management criteria— the distribution of local livestock breeds is related to environmental influences as well.

The relationships between environmental factors and wildlife diversity have been amply studied (Field et al., 2009; Hawkins et al., 2003; Stein et al., 2014; Willig, Kaufman, & Stevens, 2003; Wright, 1993), but they have rarely been studied for livestock diversity, under the untested assumption that human drivers would explain all variation (Mason, 1973). Our study pioneers the attempts to quantify livestock agrobiodiversity-environment relationships from a biogeographic perspective and including several domesticated species. However, our approach faces data limitations, for example the lack of higher resolution in breeds distributional data so it can be tied to more precise periods of time, and a lack of a clearer definition of the breed concept in the literature, which has prompted the official recognition of new breeds formerly considered varieties. We have circumvented these limitations by conducting exhaustive sensitivity analyses —i.e. at multiple grain sizes or resolutions, multiple analysis extents, and varying breed grouping approaches. The observed patterns are robust regardless the approaches (see SI, Appendix II-1).

Predictors linked to the water-energy hypotheses explain much of the distribution of local livestock breed richness (see Tables 1-2) but the underlying mechanisms may differ from those determining wild diversity distributions. For example, diversity gradients for wild species commonly co-vary with temperature and water availability positively —i.e. increasing productivity (Hawkins et al., 2003; Rosenzweig, 1987, but see Morales-Castilla, Davies, & Rodríguez, 2019)— but past distributions of livestock diversity were negatively associated with these predictors in large portions of the Northern half of Spain (see Fig. 1-2; see SI Appendix II for more details) and in general positively associated with vegetation productivity seasonality. This is likely due to humans having forced domesticated livestock species away from their environmental optima (Zeder, 2017b).

It seems that past distributions of livestock diversity were kept away from their supposed *climatic equilibrium* (Gaston, 2003) —i.e. possibly a reason underlying intra-specific diversification, as adaptation to new and challenging environments (Hoffmann, 2013; Milla et al., 2018)—, while the weaker associations between current distributions and climate (Table 1) would suggest that livestock diversity is undergoing a redistribution process strongly conditioned by human activities, in the context of current land-use change. Observed shifts in the tendency of environmental factors at present distribution suggest that local breeds occupy more productive environments than before. A small number of local breeds that are currently expanding their distributions are playing a main role in the geographic reshuffle of livestock diversity following agricultural intensification; as for example breeds from bovine, equid and porcine species, such as "*Rubia Gallega*" or "*Asturiana*" cattle, "*Pura Raza Español*" horse or the recently recognised breeds of "*Iberico*" pig (former varieties).

The livestock sector has suffered a rapid transformation during recent decades. The increasing demand for livestock products triggered a "livestock revolution" and the expansion of more homogenous and industrialised livestock systems (Steinfeld, 2004). That process has also affected local breed distributions in Spain (see Fig. 3 and SI, Appendix II-2). Thus, the observed changes in breed distribution can be interpreted as a result of increasing anthropic pressures, relaxing breed-environment interaction, and changing the nature of this relationship. These changes represent a threat to domesticated animal diversity conservation. On the one hand, intensification of local livestock breeds and separation of their traditional environments could diminish their ability to adapt to local and challenging environments, which is one of the reasons given for their value (Sponenberg et al., 2018). On the other hand, this separation of livestock diversity from the environment could break the adaptation processes to land-based extensive production systems, triggering evolvability of local breeds to tightly controlled artificial environments, or at least fewer challenging environments.

Finally, two major opposite processes of land-use change —i.e. farm abandonment and intensification of the agricultural production systems— are influencing the distribution of agrobiodiversity and thus, should be accounted for by any conservation efforts. Areas of abandonment coincide with livestock diversity hotspots (Fig. 3). In contrast, areas of intensification, known to compromise the conservation of natural habitats and wild species (Chappell & LaValle, 2011; Green, Cornell, Scharlemann, & Balmford, 2005; Tscharntke et al., 2012), also have a negative impact on livestock agrobiodiversity (Hoffmann, 2011) (Fig. 3). The fact that more than 80% of the studied Spanish local breeds are currently at risk of extinction (MAPA, 2019) calls for conservation actions to avoid breed disappearance related with those mentioned land-use change processes.

Our results highlight the importance of both environmental and human factors in the distribution of local livestock breed. Overall, the focus of the little research relating livestock biodiversity and the environment has been on competition of livestock for natural resources and distribution of diseases and parasites (FAO, 2015). This study represents a first attempt to document livestock agrobiodiversity-environment interactions from an ecological perspective; however, further efforts are needed. On the one hand, it is important to understand how global change will affect livestock agrobiodiversity since two major components —i.e. climate change and land use change— could affect local livestock breeds. On the other hand, breed conservation planning needs to integrate the processes described in this work, taking a more holistic perspective on livestock conservation and management that expands the focus from genetic and productive aspects to include also ecological and sociocultural dimensions.

3.4. METHODS

3.4.1. Distributional and environmental data: local livestock breeds in mainland Spain

The area of study is mainland Spain, located in the Iberian Peninsula. This is a territory characterised by old agricultural uses — for at least the last millennium (López-López et al., 2011)— and great heterogeneity of landscapes (Gómez-Sal, 2017), that have led to a significant agrobiodiversity. Livestock activities in mainland Spain have had historical —there are archaeological evidences of livestock activities since 7,500 years (Zeder, 2017b)— and economic importance (Gómez-Sal, 2001), driving the differentiation of a substantial number of local livestock breeds (MAPA, 2019). For the present work we have used all extant (118) and extinct (15) local breeds from the bovine, ovine, caprine, asinine, equine and porcine species in mainland Spain. We used the Official Catalogue of Livestock Breeds (MAPA, 2019) to identify all currently recognised local breeds. We selected those listed as extinct in the FAO Domesticated Animal Diversity-Information System (FAO DAD-IS, 2017), also mentioned in the Spanish livestock breeds a literature. In total, they represent 133 breeds: 44 bovine, 38 ovine, 19 caprine, 4 asinine, 14 equine and 14 porcine (SI Appendix I, Table S1).

To determine the geographic distribution of each breed over time we follow two different pathways. First, to stablish the distribution in the past, as there are not available data on the dynamics of breed distributions over time, we identify the area of origin of each breed through a literature review of the main catalogues of Spanish breeds (SI Appendix I, Table S2). We considered as area of origin the zone where each breed was first described, claimed as origin area. If that was not clear, we assigned the oldest region of distribution, except for the new Ibérico porcine breeds. These were in the past considered as varieties and any specific information was found for them. We assume that the areas of origin represent closely the distribution of local breeds before agricultural intensification, representing the historical and natural domains of each local breed (Colino-Rabanal, Rodríguez-Díaz, Blanco-Villegas, Peris, & Lizana, 2018). Areas of origin were digitally mapped using QGIS 2.18.26 “Las Palmas” software (QGIS Development Team, 2017).

To determine the current geographic distribution, as it is only available in detailed resolution at administrative NUTS 3 units, we used the information of the National Programme for the Conservation, Improvement and Promotion of the Spanish Livestock Breeds. We collected all the farm identification numbers of those farms that were collaborating with the conservation program during the period 2017-2019. This information was provided by different sources: mainly by the National Breed Information System of the Spanish Agriculture Ministry and some Autonomous Community Administrations. In cases where the administration could not offer data on the breeds we requested, we would directly contact with the Breeding Associations. Lastly, for four specific breeds which was impossible to collect any information by this mean, we used the listed farms available on their specific conservation program, that did not precede the year 2015 of publication. Only one porcine local breed information was impossible to collect, the one for Euskal Txerria pig.

The first five digits of the farm identification number correspond to the municipality (LAU2 administrative level). By this way we mapped the areas of distribution in the present, i.e. after agricultural intensification, of Spanish local livestock breeds by municipalities using R software (R Core Team, 2019). For those breeds in danger of extinction (more than 80% of studied breeds), 100% of farms are collaborating with the conservation program, however for those increasing in number (less than 20%) that is not the case. To see the percentage of farms included in the study for those increasing in number local breeds see SI Appendix I, Table S3.

Then, for both present and past distributions, we calculated several richness indices (for each species and total livestock breeds), considering richness as the sum of all breeds present in each UTM grid cell. Since present distributions have a finer scale —i.e. municipalities— than past distributions —i. e. based on areas of origin—. We calculated the richness indices at 3 different scales, i.e. 10×10, 20×20 and 50×50 km UTM sampling grain, in order to test data scale bias.

In addition, to stablish to what degree the distribution of local livestock breed is determined by environmental factors, we calculated average values of a suite of variables within the 10×10, 20×20 and 50×50 km UTM cell. We used annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality. Climatic data was obtained from the 30s BIO1, BIO12 and BIO15 layers of WorldClim version 2 (Fick & Hijmans, 2017) and vegetation productivity seasonality was calculated from the coefficient of variation of the Enhanced Vegetation Index —satellite-derived Ecosystem Functional Attributes— (Alcaraz-Segura, Cabello, & Paruelo, 2009; Alcaraz-Segura, Paruelo, & Cabello, 2006) on the basis of the Global MOD13Q1 for the 2001-2017 period. That descriptor has been utilised to study diversity richness in mainland Spain at similar scales (Moreno-Rueda & Pizarro, 2009). The descriptors were chosen as they help to characterise the water-energy dynamics on the system, are good indicators of primary productivity in warm and dry climates as the Mediterranean (Hawkins et al., 2003), as well as being dynamic variables that are expected to change under the ongoing global change (IPCC, 2018). All variables were standardised through normalization, in order to improve the interpretability and facilitate the comparison within and between models (Schielzeth, 2010).

Lastly, in order to explore the relationship between the current distribution of local breeds and land use changes, we used the map proposed by Fernández-Nogueira and Corbelle-Rico of land cover transitions based on Corine Land Cover in 1990, 2000 and 2012 by municipalities in Spain (LAU2 level) (Fernández-Nogueira & Corbelle-Rico, 2018). In order to facilitate the interpretation of these results, we have classified the transitions from less to more intensified, based on the dominant transition in the municipalities from 1.Abandonment —those municipalities where afforestation dominates, related to agricultural abandonment in tension with conversion to agriculture—, 2.Extensification —agriculture extensification—, 3.Stability —municipalities where stability along the 22 years period dominates—, 4.Forest Changes —afforestation and changes on forest composition—, 5.Intensification —agricultural intensification—, 6.Deforestation —deforestation—, to 7.Artificialization —increase of urban areas. Finally, we calculated current local breed richness indices in each municipality.

3.4.2. STATISTICAL ANALYSIS

To test to what extent environmental factors are determining the distribution of local livestock breeds richness distribution, we performed a set of Geographically Weighted Regression models (GWR), a frequent technique used to modelling spatial non-stationarity on the distribution of wildlife (Brunsdon, Fotheringham, & Charlton, 1996; da Silva Cassemiro, de Souza Barreto, Rangel, & Diniz-Filho, 2007; Osborne, Foody, & Suárez-Seoane, 2007). This GWR fits a regression considering each spatial unit with the geographically weighted (based on a distance function) neighbouring units up to a given bandwidth, i.e. analysis extent. GWR models allow to identify spatial shifts in the direction of the associations among response and predictor variables, taking into consideration the spatial variation (non-stationarity) (Bini et al., 2009; Legendre, 1993).

Firstly, to test possible effects of sampling scale we performed a set of GWR for each domesticated species and total local breed richness indices, using an adaptative bandwidth including 5% of the spatial units in our dataset (i.e. ca. 100 km bandwidth), for the 10×10, 20×20 and 50×50 km UTM cell local breed sampling, for the past and present distributions. Also, we performed a sensitivity test, removing those extinct and new local livestock breeds for the analysis. Secondly, to account for the spatial heterogeneity and non-stationarity of the environmental gradients, we performed the GWR models varying the adaptative bandwidth, considering also 2.5%, 10%, 20% (i.e. ca. 50, 200 and 400 km bandwidth respectively) (Bickford & Laffan, 2006). We chose an adaptative bandwidth, in order to facilitate result comparison within and between models.

We evaluated model accuracy using global quasi-R^2 to assess the global explained variance to compare past and present richness distribution model performances. The global quasi-R^2 is calculated from the coefficients in the local models, not by aggregating the local R^2 (Fotheringham, 2002). Lastly, we documented the spatial variation in regression coefficients and their statistical significance (at $[P = 0] \leq 0.05$) to map only significant results and quantify their ratio.

Finally, to analyse the relations between land used changes and local livestock breeds, we performed Ordinal Logistic Regression (OLR) models (McCullagh, 1980), where land cover intensification transition gradient was the response variable and local breed richness indices were the predictors. This technique has been proposed to analyses land uses changes, as it assumes ordinality of the outcomes and it is favourable when land cover change patterns can be interpreted as an ordinal process (Rutherford, Guisan, & Zimmermann, 2007) —in our case, ordered sequence of change in land cover types from extensification to intensification. Lastly, we calculated the predicted probabilities for each of the levels of the predictors —i.e. breed richness by municipality.

All data processing and analyses were performed in R v3.6.0 software (R Core Team, 2019) using the “sf” (Pebesma, 2018) and “tidyverse” (Wickham, 2017) to process local livestock breed data, “raster” package (Hijmans, 2019) to process the environmental data, “spgwr” package (Bivand & Yu, 2017) to perform GWR, “MASS” (Venables & Ripley, 2002) package to perform OLR and “sf” (Pebesma, 2018) and “ggplot2” (Wickham, 2016) for result visualization.

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3.6. SUPPORTING INFORMATION

Appendix 1. Local Livestock Breed Data

Table S1. List of local livestock breeds included in this work.

Breed Name	Livestock Type	Status
Asturiana de los Valles	Bovine	Increasing
Avileña Negra Ibérica	Bovine	Increasing
Lidia	Bovine	Increasing
Morucha	Bovine	Increasing
Parda de Montaña	Bovine	Increasing
Pirenaica	Bovine	Increasing
Retinta	Bovine	Increasing
Rubia Gallega	Bovine	Increasing
Albera	Bovine	Danger of Extinction
Alistano-Sanabresa	Bovine	Danger of Extinction
Asturiana de Montaña	Bovine	Danger of Extinction
Avileña Negra Ibérica Bociblanca	Bovine	Danger of Extinction
Berrenda en Colorado	Bovine	Danger of Extinction
Berrenda en Negro	Bovine	Danger of Extinction
Betizu	Bovine	Danger of Extinction
Blanca Cacereña	Bovine	Danger of Extinction
Bruna de los Pirineos	Bovine	Danger of Extinction
Cachena	Bovine	Danger of Extinction
Caldelá	Bovine	Danger of Extinction
Cárdena Andaluza	Bovine	Danger of Extinction
Frieiresa	Bovine	Danger of Extinction
Limia	Bovine	Danger of Extinction
Marismeña	Bovine	Danger of Extinction
Monchina	Bovine	Danger of Extinction
Morucha Negra	Bovine	Danger of Extinction
Murciano-Levantina	Bovine	Danger of Extinction
Negra Andaluza	Bovine	Danger of Extinction
Pajuna	Bovine	Danger of Extinction
Pallaresa	Bovine	Danger of Estinction
Pasiega	Bovine	Danger of Extinction

Sayaguesa	Bovine	Danger of Extinction
Serrana Negra	Bovine	Danger of Extinction
Serrana de Teruel	Bovine	Danger of Extinction
Terreña	Bovine	Danger of Extinction
Tudanca	Bovine	Danger of Extinction
Vianesa	Bovine	Danger of Extinction
Berciana	Bovine	Extinct
Campoo	Bovine	Extinct
Colorada Extremeña	Bovine	Extinct
Lebaniega	Bovine	Extinct
Mantequera Leonesa	Bovine	Extinct
Rubia Andaluza	Bovine	Extinct
Vaca del Pirineo Catalán	Bovine	Extinct
Verinesa	Bovine	Extinct
Castellana	Ovine	Increasing
Churra	Ovine	Increasing
Latxa	Ovine	Increasing
Manchega	Ovine	Increasing
Merino	Ovine	Increasing
Navarra	Ovine	Increasing
Ojinegra de Teruel	Ovine	Increasing
Rasa Aragonesa	Ovine	Increasing
Segureña	Ovine	Increasing
Alcarreña	Ovine	Danger of Extinction
Ansotana	Ovine	Danger of Extinction
Aranesa	Ovine	Danger of Extinction
Carranzana	Ovine	Danger of Extinction
Carranzana Negra	Ovine	Danger of Extinction
Cartera	Ovine	Danger of Extinction
Castellana Negra	Ovine	Danger of Extinction
Chamarita	Ovine	Danger of Extinction
Churra Lebrijana	Ovine	Danger of Extinction
Churra Tensina	Ovine	Danger of Extinction
Colmenareña	Ovine	Danger of Extinction
Galega	Ovine	Danger of Extinction

Guirra	Ovine	Danger of Extinction
Lojeña	Ovine	Danger of Extinction
Maellana	Ovine	Danger of Extinction
Manchega Negra	Ovine	Danger of Extinction
Mererino de Grazalema	Ovine	Danger of Extinction
Merina Negra	Ovine	Danger of Extinction
Merinno de los Montes Universales	Ovine	Danger of Extinction
Montesina	Ovine	Danger of Extinction
Ojalada	Ovine	Danger of Extinction
Ripollesa	Ovine	Danger of Extinction
Roya Bilbilitana	Ovine	Danger of Extinction
Rubia del Molar	Ovine	Danger of Extinction
Sasi Ardi	Ovine	Danger of Extinction
Talaverana	Ovine	Danger of Extinction
Xalda	Ovine	Danger of Extinction
Xisqueta	Ovine	Danger of Extinction
Blanca del Bierzo	Ovine	Extinct
Florida	Caprine	Increasing
Malagueña	Caprine	Increasing
Murciano-Granadina	Caprine	Increasing
Agrupación de las Mesetas	Caprine	Danger of Extinction
Azpi Gorri	Caprine	Danger of Extinction
Bermeya	Caprine	Danger of Extinction
Blanca Andaluza	Caprine	Danger of Extinction
Blanca Celtibérica	Caprine	Danger of Extinction
Blanca de Rasquera	Caprine	Danger of Extinction
Galega	Caprine	Danger of Extinction
(Cabra del) Guadarrama	Caprine	Danger of Extinction
Moncaina	Caprine	Danger of Extinction
Negra Serrana	Caprine	Danger of Extinction
Payoya	Caprine	Danger of Extinction
Pirenaica	Caprine	Danger of Extinction
Retinta	Caprine	Danger of Extinction
Verata	Caprine	Danger of Extinction
Guisandesa	Caprine	Extinct

Jurdana	Caprine	Extinct
Española	Equid	Increasing
Asno Andaluz	Equid (Donkey)	Danger of Extinction
Asno de las Encartaciones	Equid (Donkey)	Danger of Extinction
Asno Catalán	Equid (Donkey)	Danger of Extinction
Asno Zamorano-Leonés	Equid (Donkey)	Danger of Extinction
Caballo Asturcón	Equid	Danger of Extinction
Caballo de Burguete	Equid	Danger of Extinction
Caballo Hispano-Árabe	Equid	Danger of Extinction
Caballo Hispano Bretón	Equid	Danger of Extinction
Caballo Losino	Equid	Danger of Extinction
Caballo Marismeño	Equid	Danger of Extinction
Caballo de Monte del País Vasco	Equid	Danger of Extinction
Caballo Monchino	Equid	Danger of Extinction
Jaca Navarra	Equid	Danger of Extinction
Cavall del Pirenenc Català	Equid	Danger of Extinction
Caballo Pottoka	Equid	Danger of Extinction
Cabalo Pura Raza Galega	Equid	Danger of Extinction
Caballo de las Retuertas	Equid	Danger of Extinction
Ibérico	Porcine	Increasing
Ibérico Entrepelado (*new breed*)	Porcine	Increasing
Ibérico Retinto (*new breed*)	Porcine	Increasing
Ibérico Lampiño (*new breed*)	Porcine	Danger of Extinction
Ibérico Manchado de Jabugo (*new breed*)	Porcine	Danger of Extinction
Ibérico Torbiscal (*new breed*)	Porcine	Danger of Extinction
Celta	Porcine	Danger of Extinction
Chato Murciano	Porcine	Danger of Extinction
Euskal Txerria	Porcine	Danger of Extinction
Gochu Asturcelta	Porcine	Danger of Extinction
Baztanesa	Porcine	Extinct
Cerdo de Vich	Porcine	Extinct
Chato Vitoriano	Porcine	Extinct
Lermeña	Porcine	Extinct

Table S2. List of bibliographic sources reviewed for Spanish livestock local breed areas of origin identification.

Authors	Year	Edition	Title
Faelli, F.	1932	Edición Española- Revista Veterinaria de España (1ªEdición 1902)	Razas Bovinas, Equinas, Porcinas, Ovinas y Caprinas. Traducción anotada por Tomás de la Fuente Muñoz.
Aparicio, G.	1947	Segunda Edición (1ª Edición 1944)	Zootecnia Especial. Etnología compendiada.
Esteban Muñoz, C. & Tejón Tejón, D.	1980	Primera Edición	Catálogo de Razas Autóctonas Españolas. I-Especies Ovina y Caprina
Sánchez Belda, A.,	1984	Primera Edición	Razas Bovinas Españolas
Sámchez Belda, A. & Sánchez Trujillano, M.C.	1986	Segunda Edición (Primera Edición 1974).	Razas Ovinas Españolas
García Dory, M.A., Martínez Vicente, S. & Orozco Piñán, F.	1990	Primera Edición	Guía de Campo de las Razas Autóctonas de España
Sáncehz Belda, A.	2002	Primera Edición	Razas Ganaderas Españolas Bovinas
Esteban Muñoz, C.	2003	Primera Edición	Razas Ganaderas Españolas Ovinas
Yanes García, J.E.	2005	Primera Edición	Razas Asnales Autóctonas Españolas
Esteban Muñoz, C.	2008	Primera Edición	Razas Ganaderas Españolas Caprinas
Sánchez Belda, A.	2012	Primera Edición	Razas Ganaderas Españolas Caballares

Information available on the ARCA (Breed Information National System) website of the MAPA (Ministry of Agriculture, Fisheries and Food) has also been consulted: http://www.mapama.gob.es/es/ganaderia/temas/zootecnia/razas-ganaderas/razas/catalogo/ consulted between March and July, 2017

Table S3. Percentage of farms included in this study for "*increasing in number*" local breeds obtained from the comparison between collaborating farms on the National Conservation Program and active farms on Official Breeding Books. For four breeds that comparison was not possible, due to that we are not sure about the exact percentage.

Breed Name (species)	Farm percentage
Asturiana de los Valles (Bovine)	100%
Castellana (Ovine)	100%
Churra (Ovine)	100%
Navarra (Ovine)	100%
Rubia Gallega (Bovine)	100%
Merina (Ovine)	89%
Marchega (Ovine)	86%
Murciano-Granadina (Caprine)	85%
Latxa (Ovine)	83%
Lidia (Bovine)	81%
Rasa Aragonesa (Ovine)	77%
Pirenaica (Bovine)	73%
Retinta (Bovine)	68%
Parda de Montaña (Bovine)	65%
Florida (Caprine)	60%
Segureña (Ovine)	50%
Avileña-Negra Ibérica (Bovine)	50%
Ojinegra de Teruel	34%
Pirenaica (Bovine)	30%
Carranzana (Ovine)	24%
Morucha (Bovine)	21%
Española (Equid)	Unsure
Ibérico (Porcine)	Unsure
Ibérico Entrepelado (Porcine)	Unsure
Ibérico Retinto (Porcine)	Unsure

APPENDIX II GEOGRAPHIC WEIGHTED REGRESSION MODELS

II-1) Sampling Effects

Table S1. Quasi-global R^2 Geographically Weighted Regression (analyses extent: 5% of data) fitted models performed for 3 different sampling scales (10×10, 20×20, 50x50 km UTM grid cell) of the local breed richness (bovine, ovine, caprine, equid —hoses and donkeys—, porcine species and total) for past and present distribution, using as predictors annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality.

	UTM	**Past**	**Present**
		Quasi- Global R^2	**Quasi- Global** R^2
Bovine	10x10	0.63	0.45
	20X20	0.65	0.37
	50x50	0.66	0.48
Ovine	10x10	0.39	0.20
	20x20	0.43	0.16
	50x50	0.57	0.24
Caprine	10x10	0.40	0.29
	20x20	0.43	0.23
	50x50	0.46	0.35
Equid	10x10	0.73	0.41
	20x20	0.73	0.42
	50x50	0.75	0.47
Porcine	10x10	0.66	0.35
	20x20	0.66	0.24
	50x50	0.70	0.38
Total	10x10	0.64	0.46
	20x20	0.65	0.41
	50x50	0.68	0.51

Table S2. Summary of GWR coefficient estimates *(β)* for past distribution of total livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.65.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.2101	2.614	3.420	4.256	13.229	4.923
Annual Mean Temperature	-3.609	-2.182	-1.391	-0.730	3.536	-1.273
Annual Precipitation	-4.151	-1.202	-0.226	0.894	8.606	-0.413
Precipitation Seasonality	-4.217	-0.819	0.890	2.919	6.307	2.036
Seasonality of Vegetation Productivity	-1.105	-0.102	0.152	0.426	1.312	0.903

Table S3. Summary of GWR coefficient estimates *(β)* for past distribution of total livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.68.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-1.377	3.369	4.188	5.270	15.503	6.278
Annual Mean Temperature	-6.011	-3.587	-2.382	-1.377	2.708	-1.757
Annual Precipitation	-6.823	-2.553	-0.833	0.018	7.576	0.773
Precipitation Seasonality	-4.903	-0.708	1.066	3.968	8.645	2.239
Seasonality of Vegetation Productivity	-1.011	-0.056	0.537	1.160	2.033	1.374

Table S4. Summary of GWR coefficient estimates *(β)* for present distribution of total livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.41$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.606	1.436	1.987	2.606	7.0295	2.488
Annual Mean Temperature	-1.166	-0.051	0.615	1.318	5.228	0.632
Annual Precipitation	-2.584	-0.141	0.521	1.370	6.136	0.403
Precipitation Seasonality	-4.310	-0.965	-0.056	0.784	2.875	0.622
Seasonality of Vegetation Productivity	0.008	0.271	0.634	0.9801	1.922	0.873

Table S5. Summary of GWR coefficient estimates *(β)* for present distribution of total livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.51$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.310	1.744	2.409	3.189	10.308	3.081
Annual Mean Temperature	-0.654	0.116	0.946	1.853	4.104	0.875
Annual Precipitation	-3.094	-0.133	0.584	1.318	8.553	0.534
Precipitation Seasonality	-4.421	-1.489	-0.519	0.648	3.490	0.622
Seasonality of Vegetation Productivity	-0.151	0.303	0.641	1.156	2.437	1.021

Table S6. Summary of GWR coefficient estimates (β) for past distribution of bovine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.65$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.895	0.306	0.918	1.477	4.898	1.52
Annual Mean Temperature	-1.664	-0.841	-0.391	-0.056	2.340	-0.438
Annual Precipitation	-1.839	-0.331	0.145	0.510	4.060	-0.162
Precipitation Seasonality	-2.136	-0.694	0.220	0.985	2.385	0.796
Seasonality of Vegetation Productivity	-0.247	-0.025	0.096	0.201	0.753	0.478

Table S7. Summary of GWR coefficient estimates (β) for past distribution of bovine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.66$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-1.298	0.619	1.221	1.833	6.048	2.000
Annual Mean Temperature	-2.664	-1.337	-0.671	-0.290	2.014	-0.606
Annual Precipitation	-2.602	-0.950	-0.261	0.135	3.163	-0.2512
Precipitation Seasonality	-2.547	-0.455	0.646	1.454	3.116	0.988
Seasonality of Vegetation Productivity	-0.500	0.081	0.299	0.532	1.253	0.719

Table S8. Summary of GWR coefficient estimates (β) for present distribution of bovine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.37.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	Global
Intercept	-0.177	0.429	0.798	1.301	3.3467	0.856
Annual Mean Temperature	-0.539	-0.016	0.154	0.544	2.401	0.183
Annual Precipitation	-0.383	0.070	0.395	0.841	3.892	0.270
Precipitation Seasonality	-2.169	-0.580	-0.149	0.218	1.093	0.209
Seasonality of Vegetation Productivity	-0.015	0.108	0.297	0.538	1.082	0.416

Table S9. Summary of GWR coefficient estimates (β) for present distribution of bovine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.48.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.390	0.512	0.882	1.802	4.763	1.064
Annual Mean Temperature	-0.249	0.138	0.369	1.077	3.753	0.357
Annual Precipitation	-1.222	0.212	0.515	1.210	5.623	0.347
Precipitation Seasonality	-3.306	-0.954	-0.370	0.007	1.653	0.182
Seasonality of Vegetation Productivity	-0.307	0.034	0.184	0.556	1.510	0.470

Table S10. Summary of GWR coefficient estimates (β) for past distribution of ovine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.43.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.163	1.147	1.503	1.928	4.478	1.503
Annual Mean Temperature	-1.846	-0.840	-0.660	-0.511	1.1129	-0.571
Annual Precipitation	-2.757	-0.660	-0.412	-0.188	2.811	-0.423
Precipitation Seasonality	-2.076	0.017	0.338	0.676	2.519	0.413
Seasonality of Vegetation Productivity	-0.263	-0.143	0.020	0.244	0.527	0.079

Table S11. Summary of GWR coefficient estimates (β) for past distribution of ovine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.57.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.363	1.221	1.584	2.227	5.141	1.932
Annual Mean Temperature	-2.436	-1.291	-1.076	-0.845	0.275	-0.859
Annual Precipitation	-2.859	-1.520	-0.516	-0.313	3.062	-0.605
Precipitation Seasonality	-1.605	-0.002	0.357	0.924	2.715	0.460
Seasonality of Vegetation Productivity	-0.548	-0.127	0.066	0.259	0.739	0.064

Table S12. Summary of GWR coefficient estimates (β) for present distribution of ovine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.16.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.036	0.262	0.409	0.564	1.611	0.384
Annual Mean Temperature	-0.295	-0.045	0.134	0.205	0.758	0.061
Annual Precipitation	-0.754	-0.219	0.032	0.150	1.120	-0.001
Precipitation Seasonality	-1.016	-0.247	-0.079	0.052	0.411	-0.046
Seasonality of Vegetation Productivity	-0.161	0.018	0.066	0.177	0.362	0.082

Table S13. Summary of GWR coefficient estimates (β) for present distribution of ovine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.24.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.430	0.162	0.433030	0.670	2.131	0.458
Annual Mean Temperature	-0.759	-0.067	0.049	0.128	0.589	0.056
Annual Precipitation	-1.557	-0.465	-0.048	0.048	1.163	-0.060
Precipitation Seasonality	-0.928	-0.500	-0.147	0.020	0.674	-0.068
Seasonality of Vegetation Productivity	-0.463	0.036	0.129	0.197	0.474	0.121

Table S14. Summary of GWR coefficient estimates (β) for past distribution of caprine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.43$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.0.67	0.434	0.720	0.937	1.778	0.655
Annual Mean Temperature	-0.819	-0.549	-0.425	-0.323	0.624	-0.498
Annual Precipitation	-0.783	-0.244	-0.054	0.135	1.232	-0.196
Precipitation Seasonality	-0.625	-0.087	0.190	0.416	1.030	0.319
Seasonality of Vegetation Productivity	-0.451	-0.169	-0.105	0.002	0.225	-0.007

Table S15. Summary of GWR coefficient estimates (β) for past distribution of caprine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.46$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.320	0.663	0.812	1.073	2.957	0.858
Annual Mean Temperature	-1.433	-0.804	-0.588	-0.439	0.062	-0.571
Annual Precipitation	-1.077	-0.367	-0.192	-0.051	1.846	-0.258
Precipitation Seasonality	-0.494	0.038	0.293	0.496	1.202	0.382
Seasonality of Vegetation Productivity	-0.549	-0.181	-0.079	0.046	0.256	0.017

Table S16. Summary of GWR coefficient estimates (β) for present distribution of caprine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.23.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.444	0.030	0.118	0.226	0.696	0.234
Annual Mean Temperature	-0.475	-0.156	-0.0136	0.045	0.320	0.016
Annual Precipitation	-1.363	-0.171	0.084	0.168	0.549	0.025
Precipitation Seasonality	-0.372	-0.022	0.061	0.258	0.650	0.080
Seasonality of Vegetation Productivity	-0.149	0.024	0.026	0.067	0187	0.025

Table S17. Summary of GWR coefficient estimates (β) for present distribution of caprine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.35.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.578	0.060	0.142	0.392	0.925	0.285
Annual Mean Temperature	-0.766	-0.289	-0.092	0.008	0.247	-0.023
Annual Precipitation	-1.584	-0.209	0.107	0.217	0.676	0.047
Precipitation Seasonality	-0.384	0.073	0.244	0.364	0.863	0.107
Seasonality of Vegetation Productivity	-0.415	-0.043	0.035	0.148	0.410	0.005

Table S18. Summary of GWR coefficient estimates (β) for past distribution of equine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.73$.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-2.598	-0.234	0.172	0.338	0.930	0.779
Annual Mean Temperature	-1.215	-0.405	-0.139	0.161	0.409	0.058
Annual Precipitation	-3.228	-1.212	0.123	0.444	0.904	0.140
Precipitation Seasonality	-0.910	-0.444	-0.130	1.584	2.686	0.359
Seasonality of Vegetation Productivity	-0.454	-0.134	0.018	0.096	0.279	0.195

Table S19. Summary of GWR coefficient estimates (β) for past distribution of equine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.76$.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-2.139	-0.130	0.264	0.468	1.546	0.919
Annual Mean Temperature	-1.355	-0.529	-0.069	0.279	1.078	0.104
Annual Precipitation	-2.545	-0.954	0.097	0.370	0.974	0.133
Precipitation Seasonality	-1.663	-0.608	-0.297	1.321	3.078	0.292
Seasonality of Vegetation Productivity	-0.566	-0.149	0.026	0.249	0.826	0.340

Table S20. Summary of GWR coefficient estimates (β) for present distribution of equine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.41.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.570	0.424	0.583	0.739	1.327	0.839
Annual Mean Temperature	-0.377	0.097	0.251	0.480	1.478	0.294
Annual Precipitation	-1.651	-0.371	0.088	0.280	0.560	0.070
Precipitation Seasonality	-0.940	-0.013	0.220	0.413	1.162	0.252
Seasonality of Vegetation Productivity	-0.040	0.088	0.175	0.235	0.462	0.270

Table S21. Summary of GWR coefficient estimates (β) for present distribution of equine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.47.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.276	0.517	0.889	1.090	2.855	1.048
Annual Mean Temperature	-0.266	0.097	0.300	0.553	0.823	0.355
Annual Precipitation	-1.149	-0.240	0.156	0.385	1.005	0.115
Precipitation Seasonality	-1.148	-0.277	0.130	0.505	1.064	0.250
Seasonality of Vegetation Productivity	-0.164	0.077	0.240	0.355	0.531	0.299

Table S22. Summary of GWR coefficient estimates (β) for past distribution of porcine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.66$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.198	0.190	0.386	0.619	1.827	0.466
Annual Mean Temperature	-0.201	0.056	0.216	0.329	0.873	0.176
Annual Precipitation	-0.645	0.106	0.277	0.393	1.975	0.229
Precipitation Seasonality	-0.941	-0.153	-0.021	0.179	0.670	0.149
Seasonality of Vegetation Productivity	-0.175	-0.002	0.066	0.191	0.320	0.157

Table S23. Summary of GWR coefficient estimates (β) for past distribution of porcine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.70$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.490	0.209	0.542	0.805	1.509	0.570
Annual Mean Temperature	-0.342	0.0753	0.185	0.318	0.680	0.176
Annual Precipitation	-0.99	0.110	0.189	0.286	1.309	0.208
Precipitation Seasonality	-0.713	-0.179	-0.013	0.180	0.684	0.116
Seasonality of Vegetation Productivity	-0.087	0.014	0.088	0.284	0.435	0.235

Table S24. Summary of GWR coefficient estimates (β) for present distribution of porcine livestock breed richness sampled at 20 × 20 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.24.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.178	0.007	0.066	0.192	2.127	0.175
Annual Mean Temperature	-0.265	0.000	0.025	0.175	0.691	0.078
Annual Precipitation	-0.616	-0.001	0.009	0.572	1.560	0.039
Precipitation Seasonality	-0.952	-0.178	0.001	0.064	0.882	0.127
Seasonality of Vegetation Productivity	-0.010	0.002	0.029	0.071	0.192	0.079

Table S25. Summary of GWR coefficient estimates (β) for present distribution of porcine livestock breed richness sampled at 50 × 50 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.38.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.502	0.000	0.0094	0.025	1.795	0.227
Annual Mean Temperature	-0.731	0.000	0.0257	0.241	0.751	0.129
Annual Precipitation	-1.284	0.000	0.031	0.205	1.399	0.085
Precipitation Seasonality	-0.827	-0.161	0.038	0.034	2.021	0.152
Seasonality of Vegetation Productivity	-0.234	0.000	0.018	0.102	0.467	0.126

II-2) Analysis Extent Effects

Table S26: Quasi-global R^2 from the Geographically Weighted Regression fitted models performed at 4 analysis extent (2.5%, 5%, 10%, 20% of the total data as bandwidth) of the local breed richness (bovine, ovine, caprine, equid —hoses and donkeys—, porcine species and total, sampled at 10×10 km UTM grid cell) for past and present distributions, using as predictors annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality.

Sampling size: 10×10 UTM cell	**Analysis Extent (data %)**	**Quasi- Global** R^2	
		Past	**Present**
Bovine	*2.50%*	0.71	0.52
	5%	0.63	0.45
	10%	0.54	0.38
	20%	0.45	0.31
Ovine	*2.50%*	0.54	0.28
	5%	0.39	0.2
	10%	0.26	0.14
	20%	0.18	0.08
Caprine	*2.50%*	0.51	0.35
	5%	0.4	0.29
	10%	0.31	0.23
	20%	0.26	0.17
Equid	*2.50%*	0.8	0.46
	5%	0.73	0.41
	10%	0.65	0.35
	20%	0.54	0.31
Porcine	*2.50%*	0.72	0.43
	5%	0.66	0.35
	10%	0.6	0.28
	20%	0.54	0.22
Total	*2.50%*	0.73	0.53
	5%	0.64	0.46
	10%	0.55	0.4
	20%	0.46	0.35

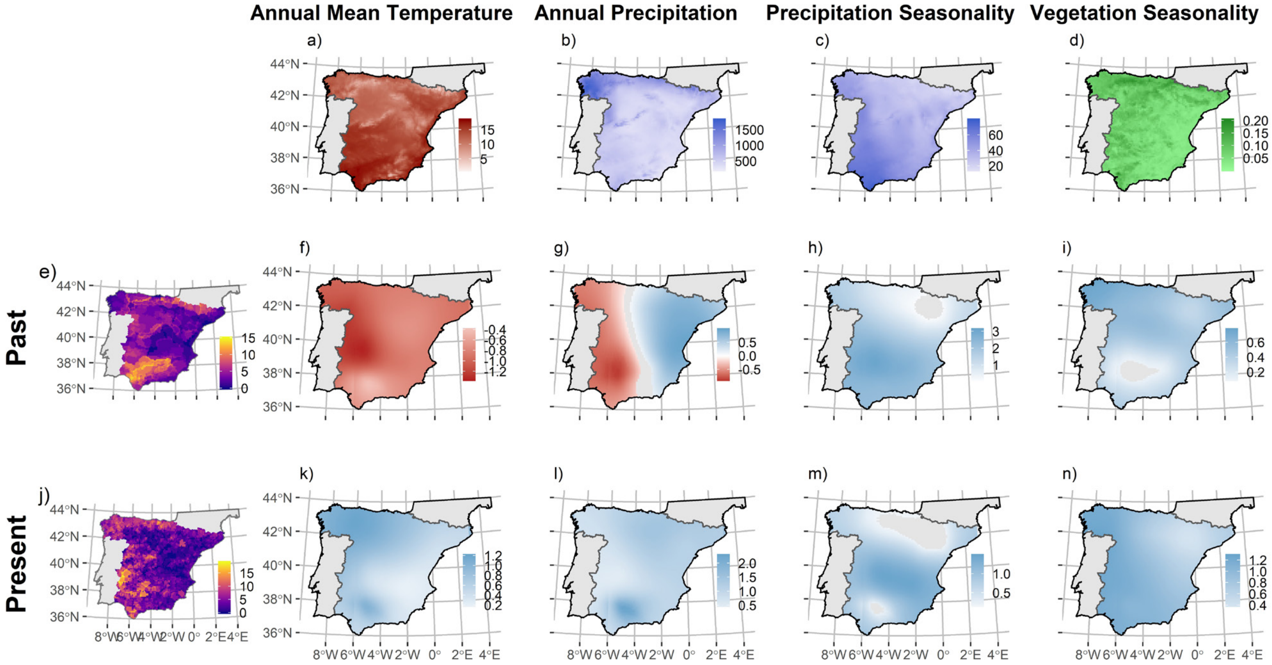

Figure S1: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between total local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [P = 0] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S27. Summary of GWR coefficient estimates *(β)* for past distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global R^2 =0.73.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-4.180	1.379	2.400	4.175	4.175	4.356
Annual Mean Temperature	4.681	-1.518	-1.026	-0.482	0.481	-0.980
Annual Precipitation	-10.005	-0.903	0.147	1.1345	1.135	1.837
Precipitation Seasonality	9.576	-1.444	-0.004	2.127	2.127	1.837
Seasonality of Vegetation Productivity	-0.917	-0.215	0.069	0.402	0.404	0.759

Table S28. Summary of GWR coefficient estimates *(β)* for past distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 = 0.55.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	1.73	2.78	3.55	3.87	5.83	4.36
Annual Mean Temperature	-2.44	-1.31	-0.96	-0.71	1.41	-0.98
Annual Precipitation	-2.38	-0.66	0.23	0.74	1.94	-0.32
Precipitation Seasonality	-1.45	0.11	1.40	2.65	4.64	1.84
Seasonality of Vegetation Productivity	-0.36	0.04	0.27	0.39	0.70	0.76

Table S29. Summary of GWR coefficient estimates (β) for past distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 =0.46.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	3.13	3.72	3.95	4.12	4.65	4.36
Annual Mean Temperature	-1.36	-1.01	-0.83	-0.77	-0.40	-0.98
Annual Precipitation	-0.88	-0.52	0.08	0.68	0.97	-0.32
Precipitation Seasonality	-0.13	0.92	1.78	2.43	3.11	1.84
Seasonality of Vegetation Productivity	0.04	0.31	0.43	0.55	0.77	0.76

Table S30. Summary of GWR coefficient estimates (β) for present distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global R^2 = 0.53.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.06	2.07	3.66	5.99	15.91	4.66
Annual Mean Temperature	-2.72	-0.19	0.38	1.16	8.70	0.61
Annual Precipitation	-6.07	0.12	1.13	2.57	10.34	0.88
Precipitation Seasonality	-6.51	-2.27	-1.26	1.22	4.38	0.95
Seasonality of Vegetation Productivity	-0.52	0.06	0.46	1.08	2.27	1.02

Table S31. Summary of GWR coefficient estimates *(β)* for present distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 =0.40.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	1.91	3.63	4.52	5.15	10.58	4.66
Annual Mean Temperature	-0.30	0.30	0.78	1.16	3.18	0.61
Annual Precipitation	-0.47	0.75	1.09	1.70	7.76	0.88
Precipitation Seasonality	-3.46	-0.91	-0.03	1.11	2.37	0.95
Seasonality of Vegetation Productivity	0.06	0.43	0.77	1.02	1.48	1.02

Table S30. Summary of GWR coefficient estimates *(β)* for present distribution of total livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 = 0.35.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	3.50	4.38	4.72	4.89	6.09	4.66
Annual Mean Temperature	0.19	0.43	0.65	0.90	1.20	0.61
Annual Precipitation	0.48	0.85	1.09	1.27	2.27	0.88
Precipitation Seasonality	-0.19	0.39	0.75	1.12	1.48	0.95
Seasonality of Vegetation Productivity	0.39	0.68	0.96	1.13	1.28	1.02

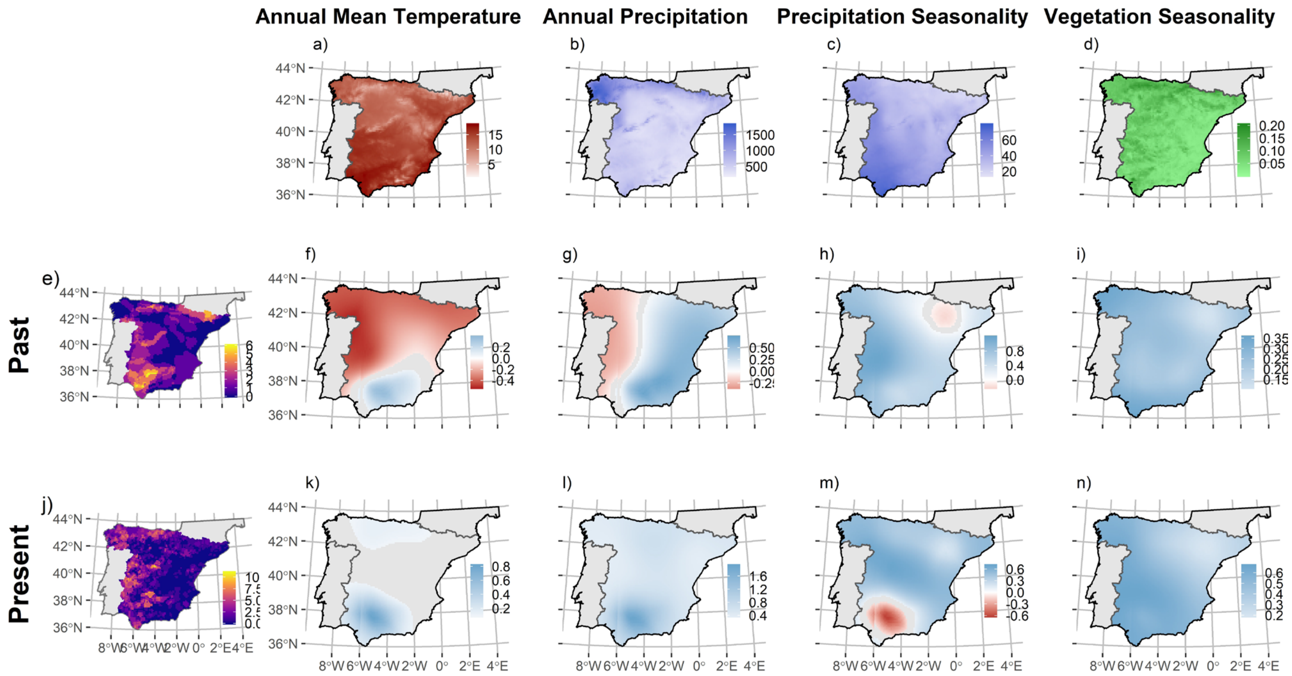

Figure S2: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between bovine local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S31. Summary of GWR coefficient estimates *(β)* for past distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global R^2 = 0.69.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-1.62	0.06	0.67	1.41	6.97	1.32
Annual Mean Temperature	-1.92	-0.73	-0.36	0.12	3.16	-0.34
Annual Precipitation	-3.80	-0.46	0.23	0.79	5.90	-0.14
Precipitation Seasonality	-3.78	-0.66	-0.09	0.96	3.24	0.71
Seasonality of Vegetation Productivity	-0.49	-0.08	0.03	0.14	0.81	0.38

Table S32. Summary of GWR coefficient estimates *(β)* for past distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 = 0.54

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.12	0.78	1.08	1.31	2.46	1.32
Annual Mean Temperature	-0.91	-0.51	-0.29	0.05	1.30	-0.34
Annual Precipitation	-0.66	-0.09	0.39	0.62	2.25	-0.14
Precipitation Seasonality	-0.95	-0.16	0.36	0.83	1.71	0.71
Seasonality of Vegetation Productivity	-0.05	0.07	0.14	0.20	0.37	0.38

Table S33. Summary of GWR coefficient estimates *(β)* for past distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 = 0.45

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.79	1.11	1.20	1.35	1.56	1.32
Annual Mean Temperature	-0.53	-0.39	-0.27	-0.05	0.39	-0.34
Annual Precipitation	-0.35	-0.13	0.24	0.50	0.73	-0.14
Precipitation Seasonality	-0.22	0.34	0.57	0.83	1.20	0.71
Seasonality of Vegetation Productivity	0.11	0.21	0.23	0.27	0.36	0.38

Table S33. Summary of GWR coefficient estimates *(β)* for present distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global R^2 = 0.52.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.36	0.73	1.36	2.82	6.96	1.62
Annual Mean Temperature	-1.69	-0.38	0.05	0.48	4.42	0.03
Annual Precipitation	-4.92	0.17	0.66	1.61	6.03	0.49
Precipitation Seasonality	-4.40	-0.90	-0.28	0.48	3.16	0.49
Seasonality of Vegetation Productivity	-0.40	0.00	0.20	0.57	1.38	0.49

Table S34. Summary of GWR coefficient estimates *(β)* for present distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 = 0.38.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.40	1.35	1.79	2.33	4.53	1.62
Annual Mean Temperature	-0.28	-0.04	0.06	0.41	2.07	0.03
Annual Precipitation	0.09	0.39	0.63	1.33	4.39	0.49
Precipitation Seasonality	-2.32	-0.27	0.05	0.47	1.07	0.49
Seasonality of Vegetation Productivity	0.02	0.19	0.39	0.57	0.80	0.49

Table S35. Summary of GWR coefficient estimates *(β)* for present distribution of bovine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 =0.31.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	1.16	1.57	1.81	1.92	2.71	1.62
Annual Mean Temperature	-0.08	0.00	0.07	0.13	0.81	0.03
Annual Precipitation	0.37	0.47	0.57	0.68	1.92	0.49
Precipitation Seasonality	-0.62	0.27	0.43	0.54	0.69	0.49
Seasonality of Vegetation Productivity	0.19	0.34	0.53	0.61	0.67	0.49

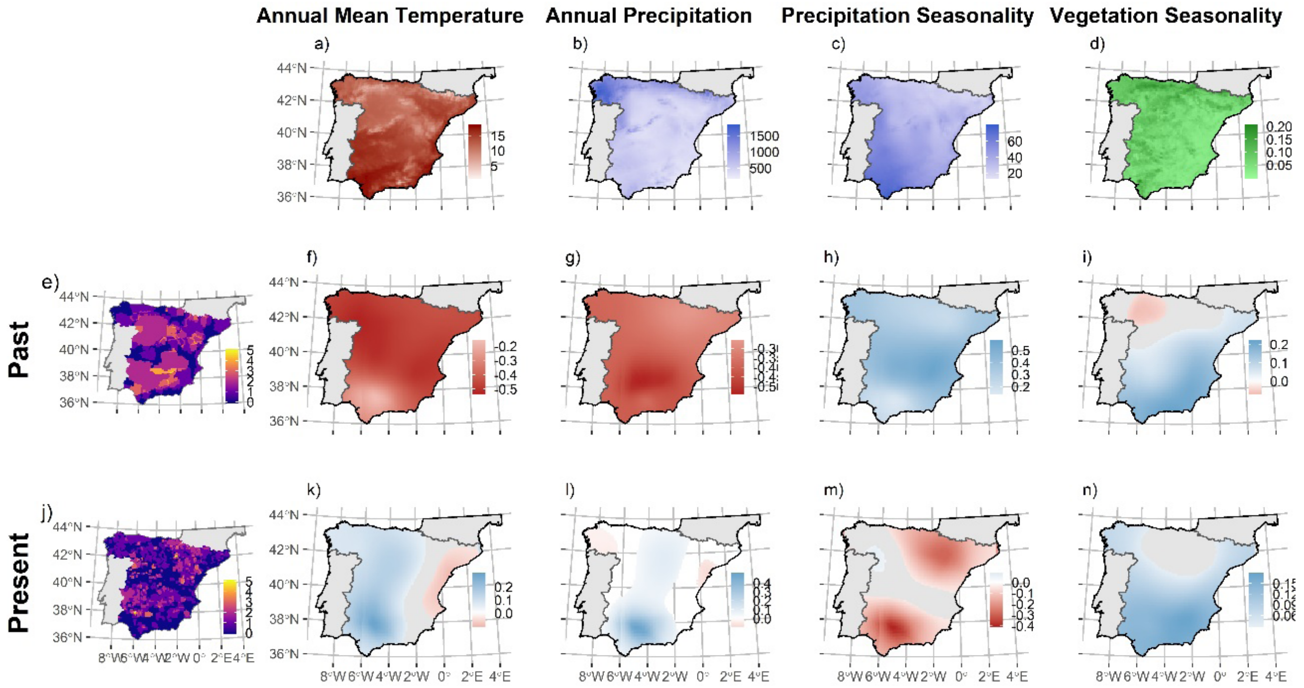

Figure S3: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between ovine local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S36. Summary of GWR coefficient estimates *(β)* for past distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global $R^2 = 0.54$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-1.87	0.74	1.38	2.04	6.39	1.35
Annual Mean Temperature	-2.93	-0.64	-0.38	0.00	2.46	-0.43
Annual Precipitation	-5.97	-0.60	-0.28	0.22	5.13	-0.38
Precipitation Seasonality	-3.83	-0.45	0.11	0.72	4.29	0.35
Seasonality of Vegetation Productivity	-0.30	-0.12	0.02	0.21	0.67	0.09

Table S37. Summary of GWR coefficient estimates *(β)* for past distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global $R^2 = 0.26$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.82	1.17	1.32	1.51	2.38	1.35
Annual Mean Temperature	-0.87	-0.57	-0.49	-0.44	0.46	-0.43
Annual Precipitation	-1.20	-0.45	-0.39	-0.31	0.58	-0.38
Precipitation Seasonality	-0.72	0.10	0.31	0.52	1.11	0.35
Seasonality of Vegetation Productivity	-0.15	-0.05	0.05	0.16	0.33	0.09

Table S38. Summary of GWR coefficient estimates *(β)* for past distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 =0.18.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	1.26	1.34	1.37	1.39	1.49	1.35
Annual Mean Temperature	-0.53	-0.49	-0.47	-0.44	-0.17	-0.43
Annual Precipitation	-0.54	-0.41	-0.38	-0.33	-0.26	-0.38
Precipitation Seasonality	0.15	0.28	0.36	0.43	0.57	0.35
Seasonality of Vegetation Productivity	-0.07	0.01	0.07	0.14	0.22	0.09

Table S39. Summary of GWR coefficient estimates *(β)* for present distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global R^2 = 0.28.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.21	0.41	0.80	1.26	3.51	0.78
Annual Mean Temperature	-0.85	-0.13	0.07	0.31	1.39	0.01
Annual Precipitation	-1.82	-0.28	0.00	0.57	3.33	-0.02
Precipitation Seasonality	-1.90	-0.68	-0.27	0.17	1.08	-0.06
Seasonality of Vegetation Productivity	-0.35	-0.04	0.05	0.15	0.44	0.10

Table S40. Summary of GWR coefficient estimates (β) for present distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global $R^2 = 0.14$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.52	0.67	0.82	0.96	2.22	0.78
Annual Mean Temperature	-0.26	0.00	0.10	0.22	0.68	0.01
Annual Precipitation	-0.36	-0.07	0.05	0.18	1.73	-0.02
Precipitation Seasonality	-1.16	-0.43	-0.18	0.06	0.18	-0.06
Seasonality of Vegetation Productivity	-0.08	0.00	0.07	0.13	0.28	0.10

Table S41. Summary of GWR coefficient estimates *(*β*)* for present distribution of ovine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global $R^2 = 0.08$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.68	0.79	0.82	0.84	1.15	0.78
Annual Mean Temperature	-0.10	0.02	0.10	0.14	0.30	0.01
Annual Precipitation	-0.09	-0.01	0.04	0.09	0.50	-0.02
Precipitation Seasonality	-0.40	-0.18	-0.09	-0.02	0.07	-0.06
Seasonality of Vegetation Productivity	-0.01	0.04	0.08	0.14	0.18	0.10

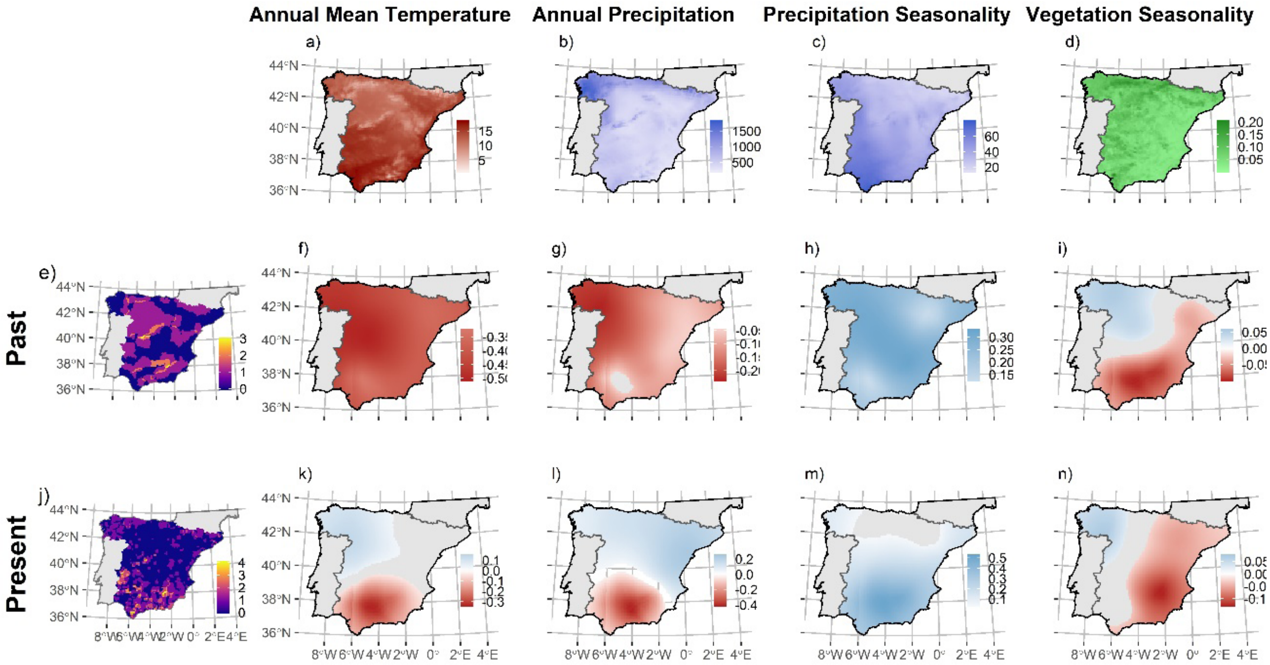

Figure S4: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between caprine local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [*P* = 0] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S42. Summary of GWR coefficient estimates *(β)* for past distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global R^2 =0.51.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-1.49	0.17	0.70	0.93	2.56	0.56
Annual Mean Temperature	-1.52	-0.45	-0.33	-0.17	0.88	-0.43
Annual Precipitation	-2.96	-0.27	0.00	0.33	2.49	-0.17
Precipitation Seasonality	-1.09	-0.37	-0.01	0.38	2.29	0.26
Seasonality of Vegetation Productivity	-0.36	-0.14	-0.07	0.01	0.25	0.01

Table S43. Summary of GWR coefficient estimates *(β)* for past distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 = 0.31.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.24	0.43	0.57	0.69	0.96	0.56
Annual Mean Temperature	-0.56	-0.47	-0.39	-0.32	-0.10	-0.43
Annual Precipitation	-0.34	-0.20	-0.09	-0.01	0.24	-0.17
Precipitation Seasonality	-0.11	0.05	0.22	0.32	0.54	0.26
Seasonality of Vegetation Productivity	-0.20	-0.10	-0.06	0.03	0.10	0.01

Table S44. Summary of GWR coefficient estimates *(β)* for past distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global $R^2 = 0.26$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.42	0.54	0.58	0.62	0.70	0.56
Annual Mean Temperature	-0.51	-0.47	-0.41	-0.38	-0.33	-0.43
Annual Precipitation	-0.24	-0.18	-0.12	-0.08	-0.02	-0.17
Precipitation Seasonality	0.13	0.21	0.26	0.30	0.33	0.26
Seasonality of Vegetation Productivity	-0.10	-0.05	-0.02	0.03	0.06	0.01

Table S45. Summary of GWR coefficient estimates *(β)* for present distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global $R^2 = 0.35$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-1.41	0.10	0.22	0.44	2.25	0.47
Annual Mean Temperature	-1.68	-0.29	-0.01	0.10	1.33	0.01
Annual Precipitation	-3.37	-0.20	0.19	0.36	1.98	0.06
Precipitation Seasonality	-1.40	-0.15	-0.01	0.27	1.64	0.19
Seasonality of Vegetation Productivity	-0.25	-0.08	-0.02	0.08	0.38	-0.01

Table S46. Summary of GWR coefficient estimates *(β)* for present distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 =0.23.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.05	0.20	0.28	0.36	1.08	0.47
Annual Mean Temperature	-0.59	-0.24	0.00	0.05	0.19	0.01
Annual Precipitation	-1.13	-0.15	0.13	0.18	0.44	0.06
Precipitation Seasonality	-0.14	-0.04	0.10	0.38	0.84	0.19
Seasonality of Vegetation Productivity	-0.20	-0.07	-0.04	0.05	0.12	-0.01

Table S47. Summary of GWR coefficient estimates *(β)* for present distribution of caprine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 =0.17.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.29	0.33	0.38	0.43	0.54	0.47
Annual Mean Temperature	-0.34	-0.09	0.01	0.06	0.15	0.01
Annual Precipitation	-0.41	-0.07	0.09	0.16	0.24	0.06
Precipitation Seasonality	0.00	0.06	0.16	0.33	0.52	0.19
Seasonality of Vegetation Productivity	-0.13	-0.06	-0.04	0.01	0.07	-0.01

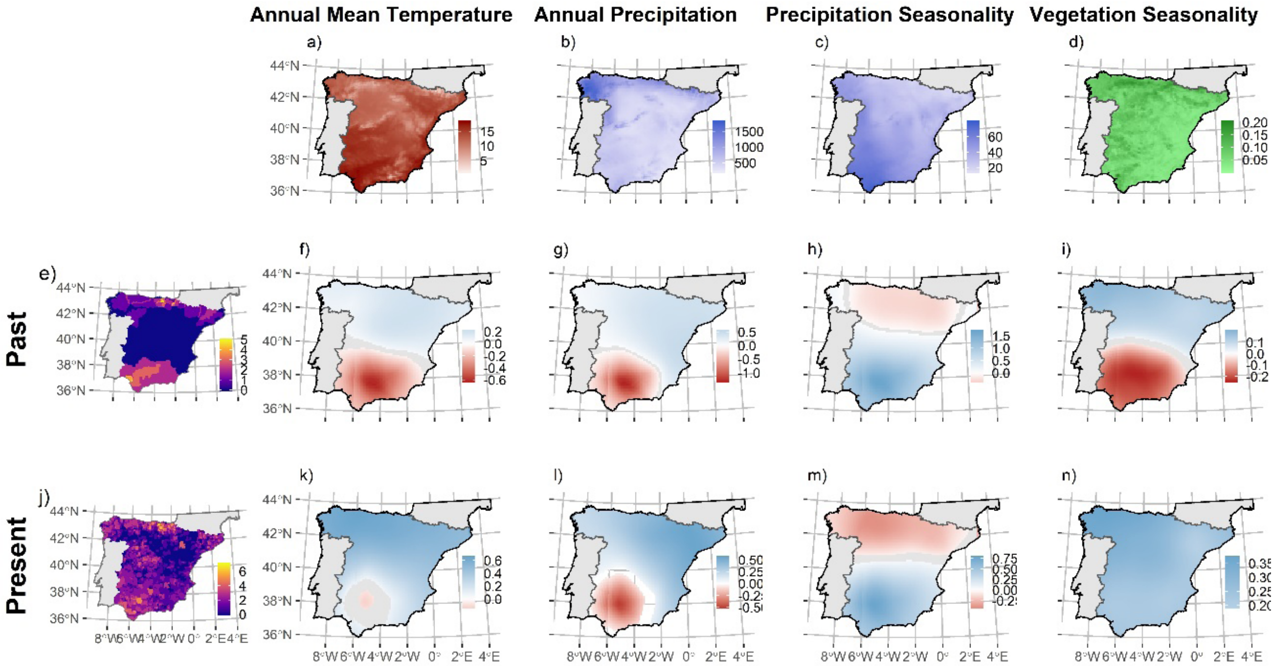

Figure S5: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between equine local breed richness —sampled at 10×10 km UTM grid cell-—for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S42. Summary of GWR coefficient estimates *(β)* for past distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global R^2 = 0.44.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-3.75	-0.45	0.02	0.24	2.85	0.70
Annual Mean Temperature	-1.85	-0.20	-0.01	0.12	1.18	0.05
Annual Precipitation	-4.66	-0.65	0.04	0.36	1.20	0.13
Precipitation Seasonality	-1.68	-0.50	-0.09	0.80	4.03	0.36
Seasonality of Vegetation Productivity	-0.42	-0.09	0.00	0.07	0.25	0.14

Table S43. Summary of GWR coefficient estimates *(β)* for past distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 =0.65.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-1.55	-0.32	0.13	0.25	0.88	0.70
Annual Mean Temperature	-0.91	-0.59	-0.01	0.16	0.23	0.05
Annual Precipitation	-2.60	-0.96	0.23	0.42	0.58	0.13
Precipitation Seasonality	-0.60	-0.41	-0.05	1.60	2.33	0.36
Seasonality of Vegetation Productivity	-0.31	-0.17	0.05	0.10	0.19	0.14

Table S44. Summary of GWR coefficient estimates *(β)* for past distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global $R^2 = 0.54$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.46	0.28	0.36	0.49	0.82	0.70
Annual Mean Temperature	-0.62	-0.16	0.09	0.17	0.21	0.05
Annual Precipitation	-1.32	-0.08	0.24	0.43	0.53	0.13
Precipitation Seasonality	-0.35	-0.17	0.14	0.89	1.69	0.36
Seasonality of Vegetation Productivity	-0.25	-0.14	0.08	0.13	0.20	0.14

Table S45. Summary of GWR coefficient estimates *(β)* for present distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global $R^2 = 0.46$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.80	0.48	0.89	1.34	2.83	1.47
Annual Mean Temperature	-1.09	0.03	0.39	0.60	1.17	0.45
Annual Precipitation	-3.21	-0.47	0.25	0.69	1.12	0.25
Precipitation Seasonality	-2.64	-0.72	0.07	0.51	2.36	0.08
Seasonality of Vegetation Productivity	-0.15	0.07	0.16	0.28	0.49	0.32

Table S46. Summary of GWR coefficient estimates *(β)* for present distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 =0.35.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.65	0.98	1.19	1.35	1.53	1.47
Annual Mean Temperature	-0.54	-0.02	0.36	0.58	0.72	0.45
Annual Precipitation	-1.02	-0.24	0.23	0.46	0.65	0.25
Precipitation Seasonality	-0.72	-0.50	0.02	0.59	1.08	0.08
Seasonality of Vegetation Productivity	0.04	0.19	0.22	0.27	0.37	0.32

Table S47. Summary of GWR coefficient estimates *(β)* for present distribution of equine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 = 0.30.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	1.09	1.27	1.36	1.41	1.50	1.47
Annual Mean Temperature	-0.13	0.17	0.42	0.56	0.65	0.45
Annual Precipitation	-0.50	0.00	0.25	0.43	0.56	0.25
Precipitation Seasonality	-0.41	-0.22	0.04	0.41	0.78	0.08
Seasonality of Vegetation Productivity	0.19	0.22	0.25	0.31	0.37	0.32

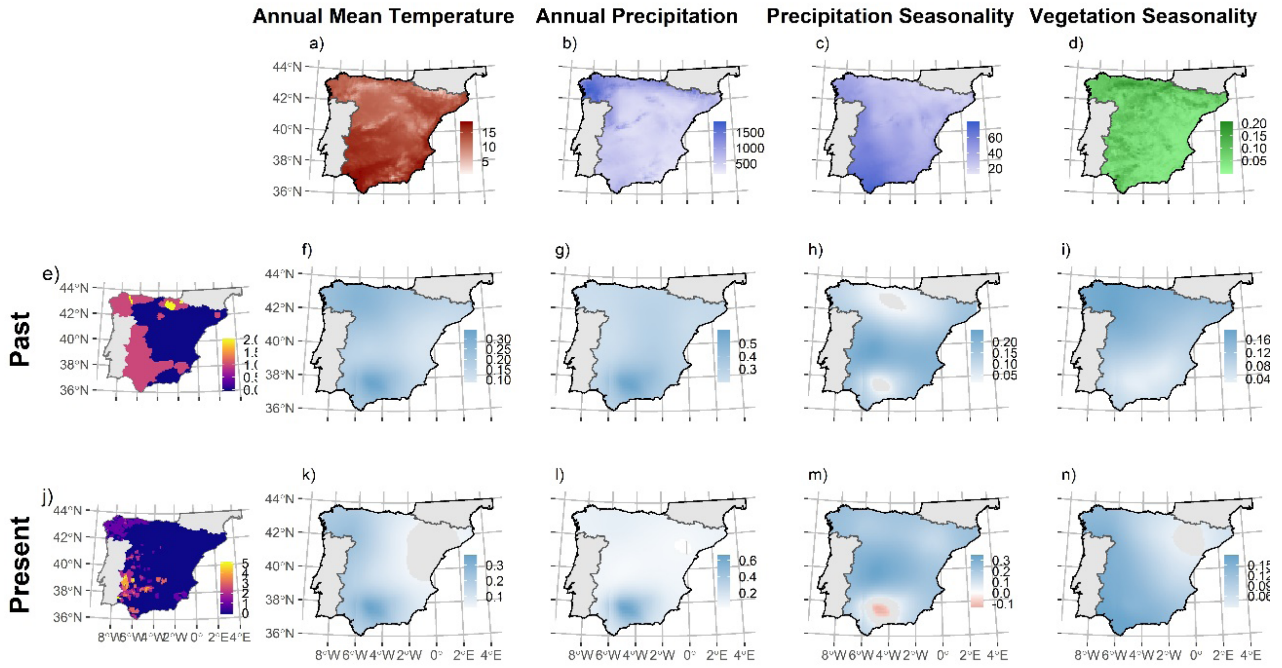

Figure S6: Maps of regression coefficients (surface of predictions) resulting from Geographically Weighted Regression models using 20% of the data as bandwidth, fitting the relationships between porcine local breed richness —sampled at 10×10 km UTM grid cell— for past (e) and present (n) distributions, using as predictors annual mean temperature (a), annual precipitation (b), precipitation seasonality (c) and vegetation productivity seasonality (d). Depicted coefficients are only coloured when statistically significant at [$P = 0$] ≤ 0.05. Blue colour represents positive coefficients and red colour represents negative associations.

Table S48. Summary of GWR coefficient estimates *(β)* for past distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 2,5% of the data as bandwidth. Quasi-Global R^2 = 0.72.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.75	0.12	0.26	0.70	2.43	0.43
Annual Mean Temperature	-0.43	0.03	0.14	0.30	1.20	0.17
Annual Precipitation	-1.48	0.05	0.23	0.40	2.70	0.23
Precipitation Seasonality	-1.42	-0.23	-0.02	0.10	1.04	0.16
Seasonality of Vegetation Productivity	-0.16	0.00	0.03	0.12	0.33	0.14

Table S49. Summary of GWR coefficient estimates *(β)* for past distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 =0.60.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.15	0.31	0.41	0.49	1.06	0.43
Annual Mean Temperature	0.04	0.12	0.20	0.31	0.63	0.17
Annual Precipitation	0.13	0.21	0.29	0.42	1.19	0.23
Precipitation Seasonality	-0.41	-0.06	0.05	0.17	0.39	0.16
Seasonality of Vegetation Productivity	-0.05	0.01	0.09	0.15	0.21	0.14

Table S50. Summary of GWR coefficient estimates *(β)* for past distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 = 0.54.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.32	0.39	0.44	0.45	0.60	0.43
Annual Mean Temperature	0.09	0.15	0.18	0.24	0.34	0.17
Annual Precipitation	0.20	0.24	0.27	0.31	0.60	0.23
Precipitation Seasonality	0.00	0.08	0.13	0.18	0.25	0.16
Seasonality of Vegetation Productivity	0.03	0.07	0.12	0.15	0.19	0.14

Table S51. Summary of GWR coefficient estimates *(β)* for present distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 2.5% of the data as bandwidth. Quasi-Global R^2 =0.43.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.47	0.02	0.12	0.35	4.62	0.31
Annual Mean Temperature	-2.56	-0.02	0.02	0.29	1.89	0.12
Annual Precipitation	-2.46	-0.05	0.03	0.30	4.33	0.10
Precipitation Seasonality	-2.19	-0.27	0.01	0.21	1.80	0.24
Seasonality of Vegetation Productivity	-0.12	0.00	0.02	0.09	0.28	0.11

Table S52. Summary of GWR coefficient estimates *(β)* for present distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 10% of the data as bandwidth. Quasi-Global R^2 = 0.28.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.03	0.17	0.26	0.41	2.02	0.31
Annual Mean Temperature	-0.01	0.02	0.11	0.30	0.83	0.12
Annual Precipitation	-0.21	0.03	0.07	0.24	2.15	0.10
Precipitation Seasonality	-1.05	0.02	0.11	0.18	0.66	0.24
Seasonality of Vegetation Productivity	0.00	0.03	0.08	0.12	0.19	0.11

Table S53. Summary of GWR coefficient estimates *(β)* for present distribution of porcine livestock breed richness sampled at 10 × 10 km UTM cell, using 20% of the data as bandwidth. Quasi-Global R^2 = 0.22.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.15	0.25	0.32	0.36	0.72	0.31
Annual Mean Temperature	0.01	0.05	0.13	0.20	0.36	0.12
Annual Precipitation	0.04	0.06	0.08	0.11	0.65	0.10
Precipitation Seasonality	-0.12	0.17	0.21	0.24	0.34	0.24
Seasonality of Vegetation Productivity	0.02	0.06	0.11	0.15	0.18	0.11

II-3) Sensitivity Analysis

Table S54: Quasi-global R^2 from the Geographically Weighted Regression (analyses extent: 5% of data) fitted models performed at 10% of the total data analysis extent of the local breed richness removing extinct and new recognised breeds (bovine, ovine, caprine, equid —hoses and donkeys—, porcine species and total, sampled at 10×10 km UTM grid cell) for past and present distributions, using as predictors annual mean temperature, annual precipitation, precipitation seasonality and vegetation productivity seasonality.

	Global Quasi-R^2	
	Past	**Present**
Bovine	0.59	0.45
Ovine	0.40	0.20
Caprine	0.40	0.29
Equid	0.73	0.41
Porcine	0.72	0.37
Total	0.62	0.45

Table S55. Summary of GWR coefficient estimates *(β)* for past distribution of total livestock breed richness -removing extinct and new recognised breeds- sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.62.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.48	1.89	2.85	3.93	11.65	4.20
Annual Mean Temperature	-2.84	-1.43	-0.94	-0.63	3.68	-0.90
Annual Precipitation	-3.39	-0.78	-0.01	0.65	8.05	-0.36
Precipitation Seasonality	-3.90	-1.11	0.68	2.32	5.94	1.71
Seasonality of Vegetation Productivity	-0.85	-0.13	0.09	0.34	0.81	0.67

Table S56. Summary of GWR coefficient estimates *(β)* for present distribution of total livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.45.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	1.21	2.54	3.88	5.35	11.21	4.52
Annual Mean Temperature	-1.31	0.03	0.64	1.16	4.09	0.59
Annual Precipitation	-1.45	0.41	1.07	2.17	8.13	0.91
Precipitation Seasonality	-3.97	-1.67	-0.96	1.02	3.22	0.77
Seasonality of Vegetation Productivity	-0.08	0.18	0.53	0.98	1.65	0.94

Table S57. Summary of GWR coefficient estimates *(β)* for past distribution of bovine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.59.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.49	0.34	0.92	1.36	4.39	1.20
Annual Mean Temperature	-1.32	-0.44	-0.24	0.02	2.55	-0.27
Annual Precipitation	-1.75	-0.24	0.20	0.63	3.91	-0.16
Precipitation Seasonality	-2.25	-0.70	0.08	0.75	1.82	0.57
Seasonality of Vegetation Productivity	-0.22	-0.06	0.05	0.16	0.52	0.31

Table S58. Summary of GWR coefficient estimates *(β)* for present distribution of bovine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.45$.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.01	0.94	1.52	2.69	5.31	1.62
Annual Mean Temperature	-0.78	-0.17	0.06	0.63	2.79	0.02
Annual Precipitation	-0.51	0.35	0.69	1.93	5.25	0.48
Precipitation Seasonality	-2.83	-0.64	-0.28	0.43	1.93	0.50
Seasonality of Vegetation Productivity	-0.12	0.04	0.24	0.56	1.00	0.50

Table S59. Summary of GWR coefficient estimates *(β)* for past distribution of ovine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.40$.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.04	1.02	1.32	1.81	4.30	1.34
Annual Mean Temperature	-1.47	-0.60	-0.45	-0.32	1.28	-0.41
Annual Precipitation	-2.60	-0.54	-0.40	-0.16	2.92	-0.39
Precipitation Seasonality	-2.09	-0.05	0.20	0.58	2.13	0.34
Seasonality of Vegetation Productivity	-0.18	-0.09	0.04	0.18	0.45	0.09

Table S60. Summary of GWR coefficient estimates *(β)* for present distribution of ovine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.20.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	0.21	0.57	0.80	1.10	2.90	0.78
Annual Mean Temperature	-0.46	-0.06	0.09	0.27	0.99	0.01
Annual Precipitation	-0.71	-0.20	0.02	0.27	2.55	-0.02
Precipitation Seasonality	-1.55	-0.59	-0.19	0.14	0.54	-0.06
Seasonality of Vegetation Productivity	-0.18	-0.01	0.05	0.14	0.36	0.10

Table S61. Summary of GWR coefficient estimates *(β)* for past distribution of caprine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.40.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.17	0.30	0.60	0.77	1.47	0.56
Annual Mean Temperature	-0.80	-0.45	-0.36	-0.27	0.44	-0.42
Annual Precipitation	-1.08	-0.25	-0.04	0.09	0.91	-0.17
Precipitation Seasonality	-0.44	-0.11	0.10	0.35	1.03	0.25
Seasonality of Vegetation Productivity	-0.33	-0.13	-0.09	0.03	0.18	0.01

Table S62. Summary of GWR coefficient estimates (β) for present distribution of caprine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.29.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.38	0.12	0.21	0.32	1.67	0.47
Annual Mean Temperature	-0.87	-0.26	0.00	0.06	0.44	0.01
Annual Precipitation	-1.75	-0.21	0.16	0.24	1.24	0.06
Precipitation Seasonality	-0.51	-0.12	-0.01	0.42	1.03	0.19
Seasonality of Vegetation Productivity	-0.26	-0.07	-0.02	0.05	0.17	-0.01

Table S63. Summary of GWR coefficient estimates (β) for past distribution of equine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.73.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-2.49	-0.37	0.08	0.18	0.79	0.70
Annual Mean Temperature	-1.12	-0.42	-0.06	0.11	0.25	0.05
Annual Precipitation	-3.26	-1.30	0.13	0.35	0.63	0.13
Precipitation Seasonality	-0.87	-0.48	-0.17	1.48	2.73	0.36
Seasonality of Vegetation Productivity	-0.37	-0.15	0.00	0.09	0.20	0.14

Table S64. Summary of GWR coefficient estimates (β) for present distribution of equine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 =0.41.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	0.03	0.64	1.01	1.29	2.11	1.47
Annual Mean Temperature	-0.77	0.07	0.34	0.58	0.95	0.45
Annual Precipitation	-1.75	-0.47	0.21	0.51	0.87	0.25
Precipitation Seasonality	-1.40	-0.69	0.16	0.62	1.42	0.08
Seasonality of Vegetation Productivity	0.02	0.13	0.21	0.27	0.34	0.32

Table S65. Summary of GWR coefficient estimates (β) for past distribution of porcine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global R^2 = 0.72.

	Min.	1st Q.	Median	3rd Q.	Max.	Global
Intercept	-0.18	0.21	0.33	0.55	1.65	0.404
Annual Mean Temperature	-0.16	0.06	0.17	0.33	0.87	0.1548
Annual Precipitation	-0.55	0.15	0.29	0.45	1.93	0.2281
Precipitation Seasonality	-0.85	-0.11	0.03	0.17	0.64	0.1912
Seasonality of Vegetation Productivity	-0.12	-0.01	0.03	0.11	0.24	0.1117

Table S66. Summary of GWR coefficient estimates *(β)* for present distribution of porcine livestock breed richness —removing extinct and new recognised breeds— sampled at 10 × 10 km UTM cell, using 5% of the data as bandwidth. Quasi-Global $R^2 = 0.37$.

	Min.	**1st Q.**	**Median**	**3rd Q.**	**Max.**	**Global**
Intercept	-0.15	0.06	0.14	0.23	1.27	0.18
Annual Mean Temperature	-0.23	0.01	0.04	0.21	0.40	0.10
Annual Precipitation	-0.41	0.01	0.04	0.26	1.20	0.14
Precipitation Seasonality	-0.61	-0.19	0.03	0.11	0.31	0.07
Seasonality of Vegetation Productivity	-0.02	0.00	0.02	0.06	0.12	0.03

Appendix III Ordination Logistic Regression Models

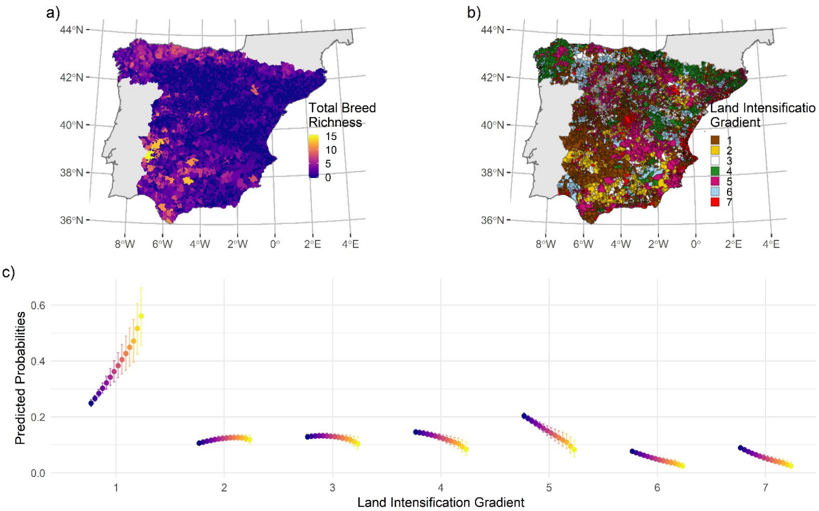

Figure S1. Maps by municipalities of total breed richness distribution (a), and land cover transition (land intensification gradient from 1 to 7) (b). Predicted probabilities of total breed richness (from 0 to 15) in each land intensification gradient class calculated from OLR model (c).

Land intensification gradient classes definition:

1. Abandonment: those municipalities where afforestation dominates, related to agricultural abandonment in tension with conversion to agriculture.
2. Extensification: agriculture extensification.
3. Stability: municipalities where stability along the 22 years period dominates.
4. Forest Changes: afforestation and changes on forest composition.
5. Intensification: agricultural intensification.
6. Deforestation: deforestation.
7. Artificialization: increase of urban areas.

Tables S1. Summary of OLR relating contemporary total livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Total Breed Richness	-0.09	0.01	-6.73	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.10	0.03	-39.14
2|3	-0.60	0.03	-22.91
3|4	-0.06	0.03	-2.53
4|5	0.53	0.03	20.42
5|6	1.61	0.03	49.41
6|7	2.32	0.04	55.67

Tables S2. Summary of OLR relating contemporary bovine livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Bovine Richness	-0.25	0.027	-9.33	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.10	0.03	-41.08
2|3	-0.59	0.02	-24.19
3|4	-0.06	0.02	-2.43
4|5	0.54	0.03	22.04
5|6	1.62	0.03	51.51
6|7	2.33	0.04	57.09

Tables S3. Summary of OLR relating contemporary ovine livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Ovine Richness	-0.14	0.05	-3.05	0.00	**

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.04	0.03	-39.50
2|3	-0.54	0.02	-22.23
3|4	-0.01	0.02	-0.36
4|5	0.59	0.02	23.88
5|6	1.66	0.03	52.74
6|7	2.37	0.04	58.07

Tables S4. Summary of OLR relating contemporary caprine livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Caprine Richness	-0.29	0.07	-4.05	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.04	0.03	-40.31
2|3	-0.54	0.02	-22.76
3|4	-0.01	0.02	-0.26
4|5	0.59	0.02	24.67
5|6	1.66	0.03	53.66
6|7	2.38	0.04	58.63

Tables S5. Summary of OLR relating contemporary equine livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Equine Richness	0.03	0.03	0.80	0.43	

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.01	0.03	-37.35
2|3	-0.51	0.03	-20.35
3|4	0.02	0.02	0.94
4|5	0.62	0.03	24.35
5|6	1.69	0.03	52.48
6|7	2.40	0.04	57.89

Tables S6. Summary of OLR relating contemporary porcine livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Porcine Richness	-0.32	0.083	-3.86	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.03	0.03	-40.55
2|3	-0.52	0.02	-22.72
3|4	0.01	0.02	0.22
4|5	0.60	0.02	25.53
5|6	1.68	0.03	54.42
6|7	2.39	0.04	59.13

Tables S7. Summary of OLR relating contemporary increasing in number (see Appendix I, Table S1) livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Increasing Number Breed Richness	-0.36	0.04	-9.97	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.10	0.03	-41.30
2|3	-0.59	0.02	-24.34
3|4	-0.06	0.02	-2.39
4|5	0.54	0.02	22.28
5|6	1.62	0.03	51.73
6|7	2.33	0.04	57.22

Tables S8. Summary of OLR relating contemporary in danger of extinction (see Appendix I, Table S1) livestock breed richness distribution and land cover transition.

	Estimate	Std. Error	z value	Pr(>|z|)	Signif.
Increasing Number Breed Richness	-0.10	0.02	-4.70	0.00	***

Threshold coefficients:			
	Estimate	**Std. Error**	**z value**
1|2	-1.07	0.03	-39.36
2|3	-0.56	0.03	-22.53
3|4	-0.03	0.02	-1.24
4|5	0.56	0.03	22.42
5|6	1.64	0.03	51.40
6|7	2.35	0.04	57.10

Lit. de L. Péant é hijos. M

DIRECCIÓN GENERAL DE AGRICULTURA INDUSTRIA Y COMERCIO

MAPA PECUARIO

formado por la

JUNTA CONSULTIVA AGRONÓMICA

con arreglo á la Memoria reglamentaria redactada en 1891
por los Ingenieros del servicio agronómico.

GANADO CABRIO

EXPLICACIÓN

▨	De	0	á	1.000	Cabezas
▨	De	1.000	á	10.000	id.
▨	De	10.000	á	20.000	id.
▨	De	20.000	á	40.000	id.
▨	De	40.000	á	60.117	id.

Escala de 1: por 2000000

50 40 30 20 10 0 50 100 150 Kilómetros.

é hijos. Madrid

SECCIÓN C

DISCUSIÓN GENERAL

C.1. LA DISTRIBUCIÓN DE LA DIVERSIDAD GANADERA

En este trabajo de tesis doctoral, se han estudiado las razas ganaderas autóctonas del territorio peninsular de España desde una perspectiva ecológica y biogeográfica. Sus resultados pueden contribuir a establecer las bases científicas sobre las que apoyar una gestión integradora y sostenible de la ganadería extensiva, compatible con la conservación de la biodiversidad silvestre. Para ello, en los distintos trabajos de investigación que se presentan en esta memoria, se han considerado tanto factores ambientales de expresión territorial amplia (Capítulos 1 y 3), como factores relacionados con los usos humanos (Capítulos 2 y 3), así como la distribución en el territorio de la diversidad de algunos grupos faunísticos representativos (Capítulo 2).

Inicialmente, en el capítulo uno se estudió la distribución de las razas pertenecientes a distintas especies domésticas (bovina, ovina, caprina, asinina y equina) para analizar cómo las razas ganaderas autóctonas responden a la heterogeneidad ambiental. Ello permitió reconocer las diferencias existentes entre los distintos patrones de expresión territorial de la diversidad de razas. Como resultado se establecieron ecorregiones pecuarias que relacionan la diversidad de razas con el conjunto de variables eco-geográficas que delimitan su área de distribución potencial. Posteriormente, en el capítulo dos, se analizó la relación entre las dos expresiones relevantes de la biodiversidad. Por una parte, la diversidad de ciertas especies nativas de vertebrados terrestres y por otra, la diversidad de razas ganaderas autóctonas. Este análisis, con perspectiva territorial amplia, ecológica y biogeográfica, permite apreciar la influencia de factores ambientales o humanos en dicha relación. Por último, en el capítulo tres, se cuantificó el efecto de algunos factores ambientales, seleccionados por su mayor influencia sobre la distribución de las razas (esencialmente de tipo climático). Asimismo, considerando la importancia de la transformación que se ha producido en la ocupación del territorio durante las últimas décadas en España, se estudió la relación de la distribución contemporánea de la diversidad de razas autóctonas con las principales tendencias de cambio en los usos del suelo identificadas para el territorio estudiado.

La evolución histórica de la actividad ganadera en la España peninsular, adaptándose a las condiciones físicas y ecológicas del territorio, y respondiendo a los distintos objetivos de los sistemas de producción, ha dado origen a una notable diversidad de razas autóctonas. La complejidad y variedad del territorio ha tenido un papel fundamental en el origen de esta diversidad ganadera. Las distintas especies domésticas analizadas responden de manera distinta a esta heterogeneidad ambiental. La diversidad de estas razas ha estado ligada históricamente al aprovechamiento de espacios de productividad limitada. Los resultados muestran que, a la escala territorial amplia adoptada en este trabajo, aquellas zonas que albergan mayor diversidad de especies silvestres también sostienen una mayor diversidad de razas ganaderas autóctonas. De este modo, existe una relación positiva en la mayor parte de la España peninsular entre la distribución de especies nativas de vertebrados terrestres y las razas autóctonas, estando mediada de forma indirecta por factores climáticos, que condicionan la productividad. Estas relaciones positivas en la distribución son más marcadas en el caso de los mamíferos y las aves, que en el de los anfibios y los reptiles. Sin embargo, estas relaciones varían cuando se considera la relación de grupos determinados de vertebrados nativos —con distintos requerimientos y preferencias de hábitat— y distintas especies ganaderas.

El efecto del ambiente ha disminuido su importancia entre los dos periodos de tiempo estudiados (la agricultura tradicional y la actualidad). Esto se asocia a los cambios en la distribución de las razas autóctonas en el presente, como consecuencia de la intensificación ganadera. Asimismo, está ligado con una tendencia en la actualidad a ocupar lugares más productivos por parte de las razas estudiadas. Además, los resultados muestran que la distribución de razas autóctonas está concentrada mayoritariamente en áreas en las que los procesos de abandono agrario son comunes. Todo ello parece indicar que la gestión sostenible de la ganadería y la conservación de las razas autóctonas pueden verse comprometidas por dos de los principales procesos del Cambio Global: el cambio climático y los cambios de uso del suelo. Las ecorregiones pecuarias propuestas en este trabajo reconocen la variedad de posibilidades ecogeográficas en las que se distribuye la diversidad de razas autóctonas. Por ello, estas pueden ser una herramienta útil para organizar la gestión integrada de la ganadería extensiva y la conservación de la diversidad.

C.2. LOS FACTORES AMBIENTALES

El interés por conocer cuál es el origen de la variación de los animales domésticos viene de lejos. Darwin (1868) utilizó estos animales como modelo de estudio a través del cual comprender la variación de los organismos en la naturaleza. En su estudio llegó a la conclusión de que el clima y la topografía debían estar actuando sobre la variedad de animales domésticos, pero siempre en menor medida que la acción directa del ser humano (Darwin, 1868). Desde entonces, la literatura ha considerado que tanto la selección artificial como la selección natural han actuado en la promoción de la diversidad de los animales domésticos, con una preeminencia de la primera sobre la segunda (Hall, 2004). De este modo se ha asumido que las diferencias morfológicas en las especies domésticas son debidas a la selección humana, las diferencias fisiológicas son debidas a la selección natural y las diferencias en su distribución son consecuencia de las migraciones humanas más que de factores ecológicos (Mason, 1973).

Nuestros resultados muestran un papel fundamental del ambiente en la distribución de las razas ganaderas autóctonas en la España peninsular, matizando o contextualizando, de acuerdo con la escala espacial, dichas asunciones, que no han sido cuestionadas con anterioridad. Hay que tener en cuenta que los procesos de selección han estado mediados por numerosos factores naturales y humanos interconectados a lo largo del tiempo (Hall, 2004), donde la acción humana se ha ido intensificando paulatinamente (Zeder, 2015). Sin embargo, no ha sido hasta periodos recientes (más o menos contemporáneos al inicio de la industrialización) cuando la selección humana comenzó a realizarse de manera sistemática, orientada a la mejora de caracteres (y solo sobre ciertos grupos poblacionales —aquellas razas en proceso de industrialización—) (Wood & Orel, 2001). La selección natural ha tenido, por tanto, un importante papel en las razas ganaderas autóctonas a lo largo del tiempo, dado que estas han sido desarrolladas en sistemas ligados a la tierra y han permanecido expuestas a los factores ambientales (Kim et al., 2016). En el caso de las razas españolas, su diversidad ya aparece documentada en el s. XIX por la Junta General Estadística (1868).

Los resultados evidencian un uso diferencial del espacio geográfico por parte de las distintas especies domésticas estudiadas, respondiendo a los gradientes ambientales a lo largo del territorio peninsular español. Ello concuerda con la literatura, que refiere numerosos procesos determinados por la geografía como influyentes en la diversificación de las subpoblaciones domésticas, por ejemplo, el efecto fundador, el aislamiento genético, el entrecruzamiento con animales silvestres y poblaciones locales (Larson & Fuller, 2014). Así, la selección no intencionada, la adaptación a nuevas condiciones ambientales y el desarrollo de aptitudes dentro de ambientes específicos han determinado —y durante algunas épocas predominado en— el desarrollo de la diversidad doméstica (Mignon-Grasteau et al., 2005; Zeder, 2012). Los factores ambientales limitan la distribución de las especies a través de su influencia en la distribución de los recursos (Hawkins et al., 2003), y del mismo modo influyen en la distribución de las especies domésticas. En este caso según sus necesidades fisiológicas y la disponibilidad de recursos naturales, interactuando con las decisiones humanas.

Las especies domésticas han sido dispersadas más allá las áreas de domesticación inicial (Zeder, 2017b) y de lo que permitirían sus adaptaciones naturales (Ethier et al., 2017), rebasando las área de distribución potencial. Para ello, ha sido necesaria una plasticidad adaptativa por parte de estas especies (Zeder, 2017a), que no solo permitió la colonización de nuevos ambientes, sino que ha favorecido la diferenciación de razas. A nivel genético se aprecian también señales geográficas en la diversidad de las especies y razas domésticas (Ajmone-Marsan et al., 2014; Colli et al., 2013; Gibbs et al., 2009; Lawson Handley et al., 2007), y se han encontrado asociaciones significativas entre el genotipo y variables ambientales, fruto de la selección y la adaptación (Bertolini et al., 2018). Por ejemplo, se han encontrado señales de selección asociadas al ambiente en un amplio número de caracteres morfológicos y otros asociados con la termorregulación, la hipoxia, la resistencia a la sequía, o del sistema inmune, impulsados por procesos de regulación metabólicos y endocrinos, entre otros (Bertolini et al., 2018; Colli et al., 2018; Lv et al., 2014; Witt & Huerta-Sánchez, 2019; Xu et al., 2015; Yang et al., 2016). Esta flexibilidad adaptativa aparece en nuestros resultados a través de la distinta respuesta de la diversidad de razas de las especies ganaderas estudiadas respecto a los gradientes ambientales.

Nuestros resultados también muestran una preeminencia del papel del ambiente en la distribución de la riqueza de razas autóctonas. Sin embargo, las tendencias son contrarias a las encontradas con mayor frecuencia en las distribuciones de animales silvestres (Field et al., 2009; Hawkins et al., 2003; Stein, Gerstner, & Kreft, 2014; Willig, Kaufman, & Stevens, 2003; Wright, 1993), con predomino de la estacionalidad y el efecto limitante de la productividad primaria. Los estudios sobre patrones filogenéticos de especies domésticas muestran que los mamíferos pertenecen a clados adaptados a ambientes moderadamente productivos, contrariamente a las plantas que presentan rasgos ventajosos para hábitats ricos en recursos (Milla et al., 2018). Asimismo, las razas ganaderas locales son reconocidas y valoradas por su adaptación a ambientes extremos (Hoffmann, 2013). Por ello, cabría esperar que los mecanismos subyacentes en el caso de la diversidad ganadera estén mediados por la domesticación, la historia de cría y manejo de las razas, algo que no ocurre en los animales silvestres. De este modo, parece que la diversidad intraespecífica de las especies domésticas y por tanto la diferenciación de razas estaría impulsada por la adaptación y diferenciación en zonas poco favorables.

Es bien conocido que el ambiente determina el desempeño del ganado, afectando al rendimiento productivo y reproductivo, así como al sistema inmune y estado general de los animales (Nardone, Ronchi, Lacetera, Ranieri, & Bernabucci, 2010). Sin embargo, pese al importante papel del ambiente en la adaptación y rendimiento de las razas autóctonas, apenas se conocen los mecanismos subyacentes en la adaptación local de las mismas (Hoffmann, 2013). El estudio genético de la diversidad animal se ha centrado en la heredabilidad, muy importante para la cría y mejora animal, dejando de lado la variabilidad debida al ambiente y el papel de la correlación e interacción genotipo-ambiente en las especies domésticas (Hall, 2004). No obstante, estos últimos puntos son imprescindibles para una gestión integrada y sostenible de los sistemas ganaderos, y la conservación de la diversidad de razas. De hecho, en la literatura sobre ganadería se ha planteado recientemente la pregunta de si son necesarios genotipos óptimos adaptados a los diferentes ambientes para mantener la producción en el contexto actual de cambio climático (Mulder, Veerkamp, Ducro, Van Arendonk, & Bijma, 2006). Nuestros resultados evidencian la importancia del ambiente para la diversidad de razas y subrayan la oportunidad que representa para una gestión ganadera más vinculada al medio.

C.3. LOS FACTORES HUMANOS

Es evidente que los seres humanos han sido los responsables esenciales de la formación y distribución de la diversidad ganadera global. Como se ha explicado anteriormente, han sido los responsables de la domesticación, dispersión, diversificación y creación de las razas, han dirigido la selección artificial y modulado la adaptación de las especies domésticas. Todo ello ha ido asociado a la capacidad humana de transformación de la naturaleza. Creando agroecosistemas y paisajes ganaderos, han relajado los efectos de la selección natural sobre animales domésticos y alterado las interacciones con otras especies —como por ejemplo en la competencia, la depredación o el parasitismo—, han retroalimentado procesos evolutivos entre humanos y especies domésticas, modelando la capacidad evolutiva de estas, con un peso importante de la herencia eco-cultural (Hall, 2004; Zeder, 2015, 2017a).

De este modo, la diversidad ganadera ha estado potenciada por la actividad humana y ello ha ido asociado a la provisión de diversos servicios de los ecosistemas (Leroy et al., 2018). Así, las especies ganaderas, han influido en los procesos ecológicos de los agroecosistemas (Gliessman, 2014) determinando la diversidad de plantas y animales en los mismos (Hendershot et al., 2020; Tóth et al., 2018), especialmente en áreas antropizadas desde hace largo tiempo, como en el caso de España. Nuestros resultados muestran la existencia de relaciones positivas en la distribución entre la riqueza de especies de vertebrados nativos y de razas autóctonas en la mayor parte del territorio peninsular español. Ello concuerda con estudios previos que indican que los factores históricos y la diversidad de usos del suelo son determinantes en el mantenimiento y distribución de los vertebrados terrestres en la Península Ibérica (Moreno-Rueda & Pizarro, 2007; Nogués-Bravo & Martínez-Rica, 2004).

No obstante, las relaciones encontradas en la presente tesis van más allá, mostrando por primera vez relaciones positivas entre la distribución de la diversidad silvestre y la agrobiodiversidad ganadera. La distribución de animales silvestres en la región Mediterránea europea (en realidad el conjunto de la cuenca mediterránea y áreas limítrofes) está determinada por procesos ecológicos naturales, la biogeografía, el paisaje y la historia humana (Blondel, Aronson, Bodiou, & Boeuf, 2010). Los usos ganaderos históricos han influido y determinado estos factores en el caso de España (Gómez-Sal, 2001, 2017; Montserrat, 2009), fomentando no solo la diversidad ganadera, sino promovido la heterogeneidad ambiental favoreciendo indirectamente la riqueza de especies silvestres. En el caso de aves y mamíferos, probablemente ello ha estado favorecido por los efectos directos del pastoreo del ganado sobre los hábitats que utilizan las especies silvestres. Podemos decir que son hábitats compartidos por especies domésticas y silvestres. Mientras que, en el caso de anfibios y reptiles, la influencia habría sido indirecta a través de la heterogeneidad que provoca la actividad ganadera, creando hábitats favorables para otras especies (caso de los puntos de agua) o bien hábitats refugio (caso de los lugares pedregosos o roquedos, no frecuentados por el ganado).

La actividad ganadera, sin embargo, ha sufrido una gran transformación durante las últimas décadas, impulsada por la “revolución ganadera” que ha fomentado la expansión de sistemas de producción industriales basados en unas pocas razas cosmopolitas altamente productivas (FAO, 2015; Steinfeld, 2004). Esta transformación ha afectado a la distribución de las razas ganaderas autóctonas en España y su estado de conservación

(MAPA, 2019). Fruto de ello, se observa en nuestros resultados una relajación en la interacción de la diversidad de razas y el ambiente, y una tendencia a ocupar ambientes más productivos que los que ocupaban en el pasado. Asimismo, los resultados muestran que los cambios de uso del suelo están influyendo en la distribución contemporánea de las razas, especialmente los procesos de abandono agrícola.

C.4. IMPLICACIONES

Como ya hemos indicado, los cambios de uso del suelo y seguramente el cambio climático, están teniendo efectos sobre la diversidad de razas ganaderas autóctonas. Ello supone una amenaza para la gestión sostenible e integradora de las razas ganaderas autóctonas y la conservación de la naturaleza, como sugieren nuestros resultados. Por un lado, la intensificación de los sistemas de producción ganadera, la expansión de sistemas de manejo uniformes, la separación de las razas de sus áreas de origen y de los ambientes en los que se han desarrollado, podría disminuir su capacidad adaptativa a condiciones locales, así como las condiciones conductuales y fisiológicas necesarias para ocupar ambientes extremos. Por otro lado, ello podría tener efectos negativos en la conservación de algunas especies silvestres, tal como sugieren los resultados obtenidos.

Las ecorregiones pecuarias propuestas en este trabajo han permitido identificar un conjunto de posibilidades de expresión de la diversidad de razas autóctonas en el territorio estudiado. Estas ecorregiones están caracterizadas por valores específicos de un conjunto de factores ambientales asociados a la distribución tradicional de las razas ganaderas autóctonas. Por ello, suponen una herramienta para apoyar la gestión ganadera integrando la diversidad de razas y la heterogeneidad ambiental. Podrían también utilizarse como base para una caracterización de los sistemas ganaderos extensivos y como herramienta a la hora de adaptar las políticas agroambientales a escalas regionales o locales.

Considerando el papel fundamental del ambiente en la diversidad de razas ganaderas autóctonas españolas, sería muy aconsejable su inclusión como condición importante en las estrategias y planes de conservación de estas. Los efectos de los cambios en el sector ganadero durante las últimas décadas estudiados en este trabajo deberían hacer reflexionar sobre la gestión del ganado autóctono, con la adopción de perspectivas más holísticas de manejo y conservación. Éstas no deberían centrarse solo en aspectos genéticos y productivos, sino que deberían también incluir perspectivas ecológicas y socioculturales. Asimismo, las relaciones observadas entre la diversidad silvestre y ganadera suponen una nueva oportunidad para apoyar la conservación de la biodiversidad en los agroecosistemas, más allá de los espacios naturales protegidos. Por otra parte, en estos espacios, en particular en aquellas categorías que permiten los usos humanos, como por ejemplo Parques Naturales, Reservas de la Biosfera, debería incluirse la diversidad de razas autóctonas en sus planes de conservación.

En general, existe un escaso conocimiento sobre la diversidad intraespecífica en las especies ganaderas, su significado, funciones y distribución. Este trabajo supone un primer paso para el estudio de la distribución y funciones de diversidad las razas ganaderas autóctonas y su interacción con el ambiente y las especies silvestres. Entre las perspectivas que sería de interés desarrollar, queremos mencionar las siguientes. En primer lugar, es necesario integrar en un esfuerzo de interpretación común, los conocimientos sobre los procesos de adaptación de las especies domésticas, generados desde distintas disciplinas —genética, ecológica, evolución—, y a distintas escalas geográficas y ámbitos culturales. Ello haría posible comprender los mecanismos que determinan la diversidad de las razas autóctonas, apoyar su conservación como legado y ser utilizadas en los retos futuros. De este modo, se fomentaría una gestión extensiva, que interprete y aproveche las condiciones locales, preparada para afrontar los distintos retos del cambio global. En segundo lugar, sería necesario analizar el legado y efecto histórico de los factores, tanto naturales como humanos, en la distribución de la diversidad doméstica en los distintos territorios y países, dado que ayudaría a comprender mejor cómo dichos efectos han modulado la diversidad ganadera globalmente. Asimismo, sería de gran interés analizar el efecto ambiental en los rasgos morfológicos, productivos y reproductivos, y su papel en la heredabilidad, para expandir los campos de la cría y mejora animal, fomentando una producción más sostenible, contemplando un uso racional de los recursos locales y la adaptación al cambio global. Igualmente, examinar a distintas escalas los impulsores, mecanismos y consecuencias de la interacción entre las diversidades silvestre y doméstica, abriría nuevas perspectivas y aportaría bases científicas para la conservación de la biodiversidad en el contexto de la biosfera humanizada. Confiamos por último en que los resultados de este trabajo permitan mejorar la gestión de la ganadería extensiva, con un enfoque integrador y comprometido con la conservación de la biodiversidad.

CONCLUSIONES

1. Existen muy pocos estudios centrados en la ecología de las razas ganaderas autóctonas. Apenas se conocen los determinantes de la distribución y funciones de la diversidad ganadera, lo que limita la gestión y conservación de esta. Existe, por tanto, un vacío en el conocimiento que abre una nueva línea de investigación.

2. La actividad ganadera, combinando factores naturales y humanos y adaptándose a la variedad de condiciones ambientales, ha favorecido la diversidad intraespecífica de las especies domésticas. El ambiente ha tenido un papel fundamental en el origen y distribución de la diversidad ganadera.

3. Las distintas especies estudiadas responden de manera diferente a los gradientes ambientales y a la heterogeneidad territorial. En la España peninsular, el ganado bovino se ve favorecido por la influencia atemperante del océano Atlántico y su diversidad responde a gradientes de altitud y precipitación, mientras que el ganado ovino está más relacionado con los climas continentales del ámbito mediterráneo. El ganado caprino en contraste se asocia a áreas más templadas del ámbito mediterráneo, montaña mediterránea y zonas con estacionalidad muy marcada. El ganado equino y asinino muestra una mayor diversidad en el ámbito atlántico, aunque su distribución ocupa asimismo zonas situadas en los extremos ambientales.

4. En general, aquellas zonas que han albergado una mayor diversidad de razas también han sostenido una mayor diversidad silvestre de vertebrados en la España peninsular. La distribución de las especies de vertebrados silvestres estudiadas en este trabajo se relaciona de manera positiva con la riqueza de razas en la mayor parte del territorio estudiado. La relación es mayor en el caso de los mamíferos y las aves que en el de los anfibios y los reptiles. No obstante, dichas relaciones varían cuando se consideran determinados grupos de vertebrados y especies ganaderas concretas. Estos resultados sugieren la posibilidad de plantear de forma conjunta la gestión de la biodiversidad natural y doméstica en el territorio estudiado.

5. El efecto de los factores ambientales en la distribución de la diversidad de razas ganaderas autóctonas ha disminuido con el paso del tiempo y su naturaleza ha cambiado. De este modo, la riqueza de razas autóctonas antes de la intensificación agrícola tendía a ocupar lugares de productividad limitada, mientras que en la actualidad ocupa áreas potencialmente más productivas.

6. La distribución contemporánea de las razas autóctonas está ligada a los procesos de transformación del sector ganadero en España y se relaciona con las extensas áreas afectadas por el abandono agrícola y rural en las últimas décadas.

7. La gestión y conservación de las razas ganaderas autóctonas se enfrenta por tanto a un doble reto en el mundo cambiante actual según los resultados obtenidos: el cambio climático y el cambio de usos del suelo. Es necesario por tanto adoptar una perspectiva más holística, que incluya dimensiones no solo técnicas, productivas y económicas, sino también ecológicas, sociales y culturales. Dicho enfoque tendría efectos positivos sobre los dos componentes de la biodiversidad (doméstica y silvestre) que han sido estudiados en este trabajo.

8. Las ecorregiones pecuarias propuestas sintetizan la variedad de posibilidades ecológicas y geográficas en las que se distribuye la diversidad ganadera. Pueden ser consideradas como una herramienta útil para avanzar hacia una gestión ganadera más racional, basada en la interpretación y aprovechamiento de la heterogeneidad ambiental.

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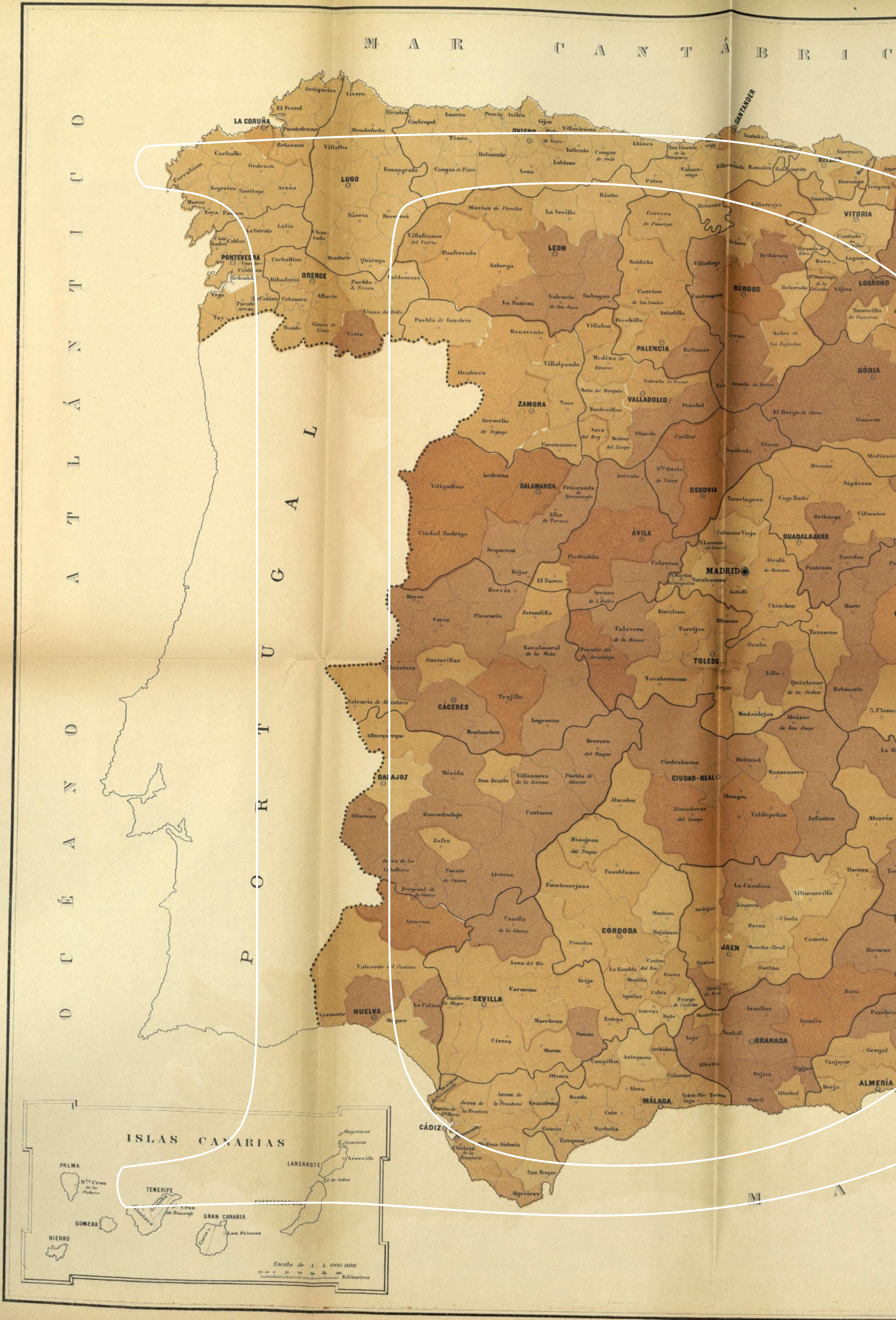
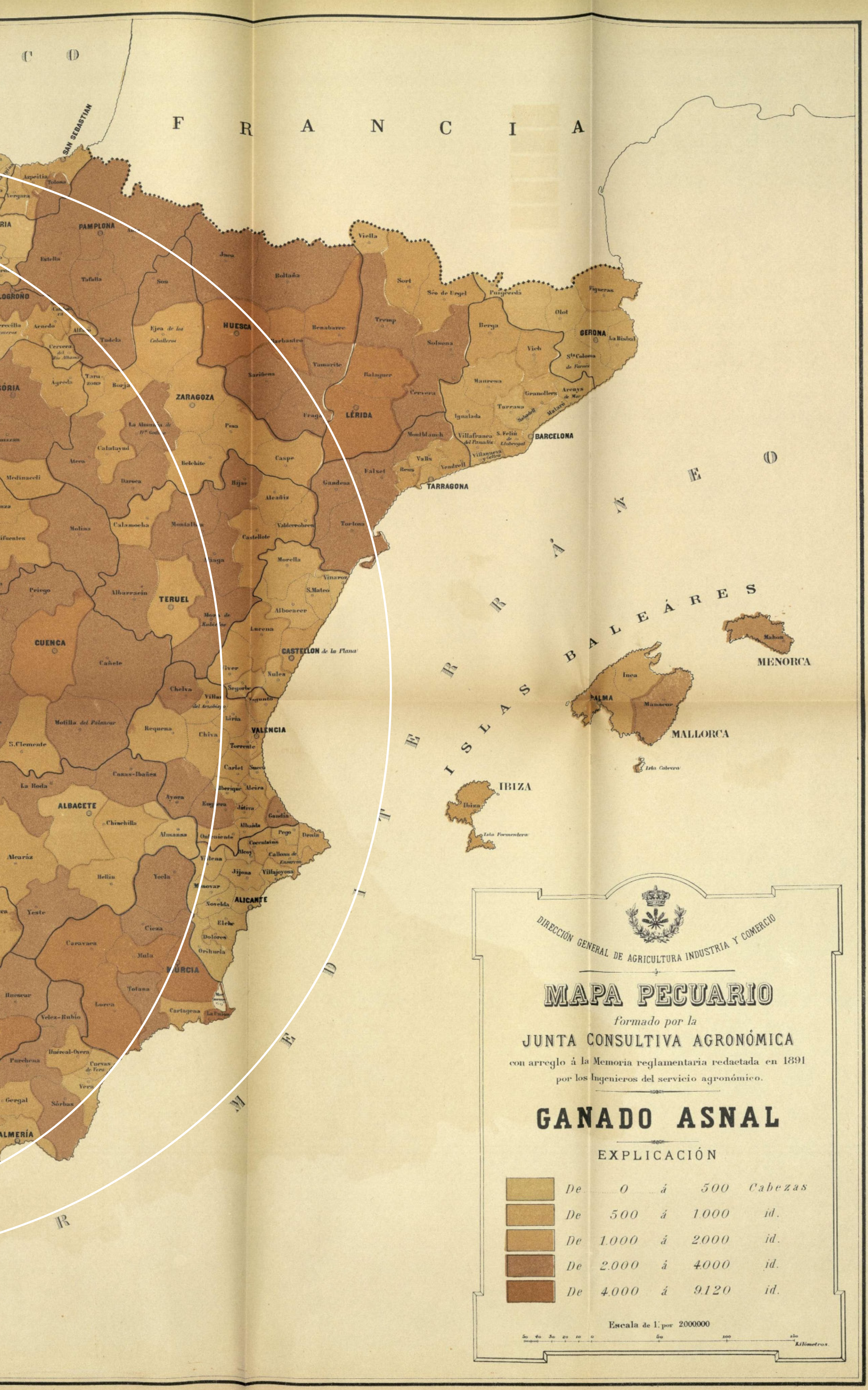


Lit. de L. Péant é hijos. Madrid



DIRECCIÓN GENERAL DE AGRICULTURA INDUSTRIA Y COMERCIO

MAPA PECUARIO

formado por la

JUNTA CONSULTIVA AGRONÓMICA

con arreglo á la Memoria reglamentaria redactada en 1891
por los Ingenieros del servicio agronómico.

GANADO ASNAL

EXPLICACIÓN

▨	*De*	*0*	*á*	*500*	*Cabezas*
▨	*De*	*500*	*á*	*1.000*	*id.*
▨	*De*	*1.000*	*á*	*2.000*	*id.*
▨	*De*	*2.000*	*á*	*4.000*	*id.*
▨	*De*	*4.000*	*á*	*9.120*	*id.*

Escala de 1. por 2000000

Kilómetros

...hijos. Madrid

D

SECCIÓN D

GUÍA VISUAL

Bovino - Fomento


Asturiana de los Valles


Avileña Negra Ibérica


Lidia


Morucha


Parda de montaña


Pirenaica


Retinta


Rubia Gallega

BOVINO - PELIGRO DE EXTINCIÓN


Albera


Alistano-Sanabresa


Asturiana de Montaña


Avileña Negra Ibérica


Avileña Negra Ibérica Bociblanca


Berrenda en Colorado


Berrenda en Negro


Betizu

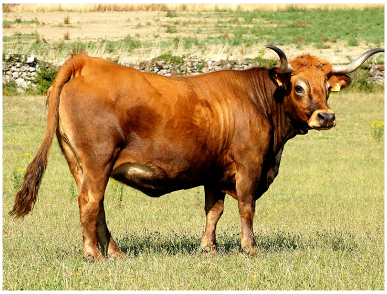
Blanca Cacereña

Bruna de los Pirineos

Cachena

Caldelá

Cárdena Andaluza



Frieiresa

Limia

Marismeña

Monchina

Morucha Negra

Murciano-Levantina

Negra Andaluza

Pajuna

Pallaresa

Pasiega

Sayaguesa

Serrana de Teruel

Serrana Negra

Terreña

Tudanca

Vianesa

CAPRINO - FOMENTO

Florida

Malagueña

Murciano-Granadina

Caprino - Peligro de Extinción

(Cabra del) Guadarrama

Agrupación de las Mesetas

Azpi Gorri

Bermeya

Blanca Andaluza

Blanca Celtibérica

Blanca de Rasquera

Galega

Moncaina

Negra Serrana

Payoya

Pirenaica

Retinta

Verata

EQUINO - FOMENTO

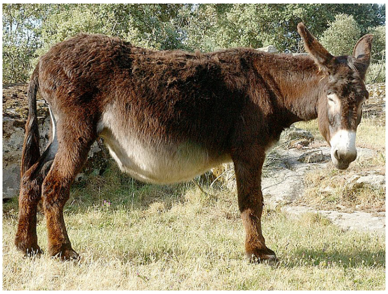
Español

EQUINO - PELIGRO DE EXTINCIÓN

Asno Andaluz

Asno Catalán

Asno de las Encartaciones



Asno Zamorano-Leonés

Caballo Asturcón

Caballo de Burguete

Caballo de las Retuertas

Caballo de Monte del País Vasco

Caballo Hispano Bretón

Caballo Hispano-Árabe

Caballo Losino

Caballo Marismeño

Caballo Monchino

Cabalo Pura Raza Galega

Cavall del PirInenc Català

Jaca Navarra

Pottoka

Ovino - Fomento

Castellana

Churra

Latxa

Manchega

Merino

Navarra

Ojinegra de Teruel

Rasa Aragonesa

Ovino - Peligro de Extinción


Alcarreña


Ansotana


Aranesa

Carranzana


Carranzana Negra


Cartera


Castellana


Castellana Negra

Chamarita

Churra Lebrijana

Churra Tensina

Colmenareña

Galega

Guirra

Lojeña

Maellana


Manchega Negra


Merina Negra


Merinno de los Montes Universales


Merino de Grazalema


Montesina


Ojalada


Ripollesa


Roya Bilbilitana

Rubia del Molar

Sasi Ardi

Segureña

Talaverana

Xalda

Xisqueta

PORCINO - FOMENTO

Ibérico

Ibérico Entrepelado

Ibérico Retinto

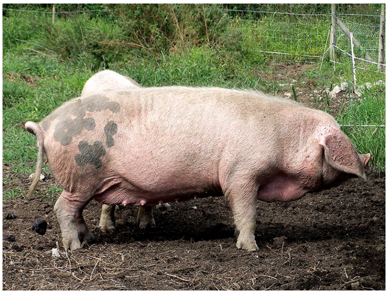
PORCINO - PELIGRO DE EXTINCIÓN

Ibérico Torbiscal

Celta

Chato Murciano

Euskal Txerria



Gochu Asturcelta

Ibérico Lampiño

Ibérico Manchado de Jabugo

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Antes que nada, quiero agradecer a la Fundación Tatiana Pérez de Guzmán el Bueno el haber depositado su confianza en este proyecto, en un tema tan poco estudiado, y haber sido flexibles con todas las contingencias que han ido sucediendo a lo largo del camino. Desde el inicio la Fundación y su personal no solo nos han prestado su apoyo económico, sino que han sido comprensivos y mostrado, en la medida de sus posibilidades, su ayuda para que el proyecto avanzase. Espero que la presente memoria esté a la altura de las expectativas de la Fundación. También quiero tener unas palabras de agradecimiento para todas las personas e instituciones que han prestado su colaboración para poder desarrollar los distintos capítulos de investigación, en cada uno de ellos -a lo largo de la sección B- aparecen adecuadamente mencionados.

Conocí a Antonio Gómez Sal, director de esta tesis, en Baeza, hablando sobre trashumancia. De su mano me he adentrado en el apasionante mundo de la Ecología y he conseguido acabar esta tesis sobre razas ganaderas autóctonas. Quiero agradecerle las oportunidades que me ha brindado en esta importante etapa de mi formación. También, el haberme imbuido en su visión de España y el haber compartido conmigo su vasto conocimiento sobre los sistemas ganaderos de nuestro país. Gracias Antonio por haberme dado esta importante oportunidad y haberme enseñado tanto.

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Supongo que si Homero viviera en nuestros días sería escritor freelance y le costaría escoger una aventura épica en la cotidianeidad de nuestra vida apresurada en esta sociedad líquida. Yo considero que lo vivido durante estos años para cerrar la tesis se podría utilizar para escribir una *Odisea* moderna, no por la proeza de los hechos, sino por la inmensidad de sus personajes. El laberinto de la academia nos enfrenta a numerosos monstruos: la precariedad y la incertidumbre de contratos temporales y una carrera altamente competitiva, el estrés crónico de la exigencia constante y a largo plazo, el gran esfuerzo y la falta de reconocimiento, el síndrome del impostor, etc. En mi caso, tal vez en demasiadas ocasiones, estos monstruos han hecho aflorar en mí sentimientos como la frustración, la tristeza, el enfado y el miedo. Sin embargo, si les he plantado cara y he conseguido avanzar para llevar a buen puerto esta tesis y crecer como persona ha sido por la gran calidad de la comunidad que me ha rodeado.

Nuestro microcosmos tesista tiene un epicentro claro, el Gabinete Forestal, que decidimos renombrar como el Despacho Guay. En él he tenido la suerte de coincidir en tiempo y espacio con Verito (Verónica Cruz) y Zowi (Zoë Rohrer), mis dos hermanas mayores durante el doctorado, que iban abriendo camino en este laberinto. Con ellas he compartido un número infinito de horas, en los que hemos aprendido juntas, trabajado concentradas, desconcentradas, hemos reído y llorado, hemos enfrentado dificultades y hemos discurrido genialidades. Sin vosotras, amigas, el proceso tesis hubiera sido completamente distinto. Habéis sido un ejemplo en el que me he ido fijando estos años. Sois unas mujeres inteligentes y trabajadoras, que habéis mostrado una fortaleza excepcional ante las adversidades del doctorado. Gracias por haberme ayudado siempre, por haber apoyado los mil proyectos dentro y fuera del departamento, por haber confiado en mí, incluso cuando yo no lo hago. Por todos los buenos momentos que hemos pasados juntas y los que aún nos quedan por vivir.

Nuestra generación de doctorado espero que pase a la historia del departamento, por la alta implicación y el dinamismo que ha tenido. Quiero tener unas palabras especiales también para las Quasi-Doctoras de Alcalá (ahora muchas de ellas ya Doctoras), que han constituido la red de apoyo mutuo académico y emocional, base de una larga amistad. Loreto, que es la previsión en persona, que siempre ha sabido escuchar los lamentos y trasmitir calma incluso en los momentos de más desasosiego, Laura Marqués, que fue la mejor compañera de piso, aunque fuera por unos meses, siempre ha tenido soluciones ante cualquier problema, Navila, que se incorporó más tarde, pero que desde el principio se ha preocupado e implicado, junto con Verónica y Zoë, representan las mejores cualidades de un doctorando, siempre dispuestas a aprender, siempre dispuestas a compartir en lo bueno y en lo malo, y con una tremenda disposición a pasarlo bien.

En el Despacho Guay muchos han sido víctimas de nuestras idas y venidas, y en ocasiones guirigáis, Enrique el primero. Henry, fuiste la primera persona que conocí en Alcalá, nos has visto crecer a todas, nos has enseñado y siempre has estado dispuesto a celebrar. Espero que cuando esta situación mejore, sigamos conquistando juntos ferias por Andalucía. Marga, que compartiste tu maternidad con nosotras y siempre has tenido palabras positivas para levantar mi autoestima y Elena Granda que, aunque fuiste la última incorporación, has sido la postdoc de nuestros sueños. Gracias por el apoyo, el güertix y unirte a la vida garrapiñada. También a Asun que, aunque te mudaste pronto, hemos seguido compartiendo en la distancia la aventura del doctorado. A David, gran víctima de nuestras charlas y a Alex y Cristina con presencia esporádica. En ese despacho, pese a todo, siempre se ha mantenido la alegría y el compás como reza en la puerta.

Mi comunidad como doctoranda se extiende además a un grupo excepcional, conocido como los Ecofísicos; compuesto por doctorandos de generaciones anteriores con los que hemos celebrado como terminaban, Silvia, que me animaste y cuidaste en el inicio, Joaquín, siempre aportando ideas, Andrei, y sus idas y venidas por EE. UU., Laura, Patri. También el resto de doctorandos y técnicos: Julen, gracias por tu colaboración en Gestiones y ser la punta de lanza en los últimos paquetes de R, Marta, siempre dispuesta a ser una compañera en el crimen, Andrea, Denis, Pablo, Dani, Sonia, Luciano, Indra, Julián, y a la larga lista de postdoc: Judith, Paloma, Jaime, Antonio, Lupe, Germán, Rafa, Rafa Barrientos, Sara, Guida, Merche, Asier. Todos vosotros habéis estado presentes en este viaje hacia Ítaca que es la tesis, de vosotros he aprendido y espero que podamos más pronto que tarde celebrar con alegría el haber llegado al final de este proceso. Todos habéis cuidado de la comunidad, dado consejos, aportado nuevas visiones y estado dispuestos a celebrar con poco. Muchas gracias. Quiero mencionar además la Beca Barrientos-Cantalapiedra-Malo (y a sus responsables Rafa, Juan y Aurelio), que pagó nuestra subscripción para seguir aprendiendo a programar. También agradecer a todas las mujeres del departamento que colaboraron en las distintas actividades de divulgación sobre la mujer en la ciencia de la OTRI. Habéis conseguido que esta haya sido una divertida aventura.

No puedo olvidarme tampoco de María Fernandez-Gimenez y su grupo de investigación, que me acogió con cariño durante la estancia en Colorado. Los meses que pasé en EE. UU. me han abierto horizontes y supusieron una gran aventura académica y personal. Ariana, Jasmine, Kevin, gracias por vuestro apoyo. Katie, Kuhm y Arian, gracias por haber hecho más amenas las largas jornadas de escritura de tesis y no haber renegado de las zucchini party. Chelsea y Brielle, por haber sido unas grandes compañeras de piso. Gracias a todos por haber sido una puerta de entrada a la cultura americana.

No puedo cerrar el capítulo académico sin mencionar a cuatro grandes mujeres. Ana Guerrero, para mí una madre académica, fue la que se preocupó inicialmente por que me matriculase en el doctorado y ha sido mi madrina por excelencia en Alcalá. Rosi, junto con Ana, son la parte invisible del funcionamiento del departamento, y siempre nos ayudan diligentemente ante los vericuetos de la burocracia universitaria. Nuria, del gabinete psicopedagógico, que me ha ayudado a comprender y gestionar todas las malas emociones que me han acompañado en este proceso. Por último, a Mika, que siempre está atenta a todo lo que nos pasa y nos cuida desde el otro lado de la barra en la cafetería. Muchas gracias por todo el cariño que ponéis en vuestro trabajo.

Aunque estos agradecimientos son muy extensos no puedo dejar de tener unas palabras para toda esa gente que ha estado y está fuera de la Universidad. Durante estos años me he hecho Alcalína Garrapiñada. Por un lado, Ribera, 4 (y ahora Calderón, 5) ha sido un hogar donde sentirse acogida y protegida. También capital de nuestro microcosmos tesista. Borja, Denis, Asier, Héctor, y ahora también Radi, habéis sido unos grandes compañeros, facilitando la convivencia al máximo. Héctor merece un reconocimiento especial, pues no solo ha visto doctorarse y conoce la historia de la gran mayoría de becarios Ecofísicos de la UAH, sino que ha compartido los meses de encierro y cuarentena en los que he acabado de escribir esta tesis.

Por otro lado, familia extendida en la que os habéis convertido mis buenos amigos alcalaínos. Manuel, Ana y ahora también Sofía, gracias por todo vuestro cariño y por imponer la coherencia. Irene, Miguel y David, os conocí en un momento muy duro de mi vida, y en seguida me acogisteis. La terapia de miércoles de vinos en el Tempranillo debería ser reconocida con el Nobel de Medicina. Sois unas personas excepcionales, inteligentes, divertidas y trabajadoras, conoceros abrió un nuevo universo para mí en Alcalá. También a los compañeros de swing, Fer, gracias por haber creado ese espacio para el apoyo y la diversión, Alba, compañera y confidente, Sara, todas esas conversaciones sobre el porvenir y la vida, Elena Tirado, tu animosidad por hacer este un mundo mejor, las hermanas leonesas Cati y Nuria, y el resto de compañeros bailarines, no hay mejor manera de olvidar las penas y preocupaciones que bailando con vosotros. También a los Mayéuticos del Val, Sara, Carlos, Joseba, Luis, Miguel C, María, y resto de tropa, estoy convencida de que si vosotros pararais, Alcalá se convertiría en un no-lugar. Nunca dudéis de vuestra creatividad, sois geniales. Todos habéis sido espectadores de este proceso, sin vuestras palabras de ánimo, el tirar la toalla hubiera sido una opción mucho más presente, gracias.

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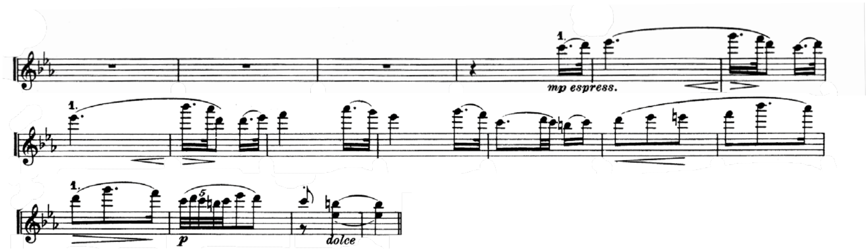

El hombre puede actuar sobre la naturaleza y apoderarse de sus fuerzas para utilizarlas solo si comprende sus leyes

Cosmos, Alexander von Humboldt

Universidad
de Alcalá