Contributions of Hedgerows to People: A Global Meta-Analysis

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Hedgerows are linear landscape features of woody vegetation usually located around agricultural fields. An increasing number of studies have addressed the effects of hedgerows on biodiversity and ecosystem services. This study is aimed to synthesize these effects and compare the levels of biodiversity and ecosystem services in farmland with hedgerows and (1) farmland without hedgerows and (2) nearby natural habitat at the global scale. We hypothesized that farmland with hedgerows (1) enhances biodiversity and ecosystem services as compared to farmland without hedgerows but (2) supports lower levels of biodiversity and ecosystem services than natural habitat. Our systematic literature review retained 835 observations from 170 primary studies, which were analyzed following the standard methodology in meta-analyses. Our results partially support both hypotheses. Farmland with hedgerows exhibited higher levels of biodiversity and provisioning services than farmland without hedgerows (H1). Farmland with hedgerows provided similar levels of biodiversity (edge effects) but lower levels of ecosystem services than natural habitat (H2). The effects of hedgerows on biodiversity and ecosystem services depended on control ecosystem type (grassland/meadow or forest/woodland) but were largely independent of climate type (temperate or tropical) and the focus of spatial scale (field or landscape). In conclusion, conservation and restoration of hedgerows contribute to people in several ways by enhancing biodiversity and multifunctionality in agricultural landscapes.

Keywords: biodiversity, ecosystem services, farmland, multi-functionality, natural habitat

INTRODUCTION

Agricultural production must be more sustainable if the society wants to redress the major source of direct and indirect environmental impacts on the planet, particularly biodiversity loss and climate change (IPBES, 2017, 2019; IPBES and IPCC, 2021). To achieve this goal, the EU Biodiversity Strategy for 2030 aims to convert 10% of farmland into high-diversity landscape features (European Commission, 2020), as species-rich semi-natural habitat and natural habitat remnants play a key role in maintaining biodiversity and a range of ecosystem services in agricultural landscapes (Jahnová et al., 2016; Dainese et al., 2017). High-diversity features in agricultural landscapes include a wide range of non-cropped habitats such as ponds, herbaceous and woody buffer strips, forest patches, and hedgerows (Rey Benayas and Bullock, 2012).

Hedgerows are linear landscape features of woody vegetation usually located around agricultural fields (Lajos et al., 2020). They can be either spontaneous (naturally grown) or planted. Spontaneous hedgerows reflect, to some extent, the woody community composition of remnant forests in a

particular region (Rey Benayas et al., 2020). Hedgerows harbor a high diversity of plants (Freemark et al., 2002; Aavik et al., 2008) in terms of both plant abundance (Aavik et al., 2008) and richness (Evans et al., 2011). They can function as plant colonization sources (Endels et al., 2004; Rey Benayas and Bullock, 2015) and modulate plant community composition, which benefit native plants against exotic plants (Freemark et al., 2002).

Other species benefit from hedgerows, including small mammals such as mice (Fialho et al., 2019) and bats (Vandevelde et al., 2014; Heim et al., 2018). Large mammals such as the roe deer (*Capreolus capreolus*) and the Iberian wolf (*Canis lupus*) find hedgerows a substitutable habitat for woodland (Rodríguez-Freire and Crecente-Maseda, 2008; Morellet et al., 2011). They provide nest sites (Hotaling et al., 2018), food (Evans et al., 2003; Barbaro et al., 2008), or shelter (Ceresa et al., 2012) for many bird species (Burgess et al., 2015). Invertebrates such as less-common species of insects (Morandin and Kremen, 2013; Ponisio et al., 2016) and spiders find hedgerows a valuable habitat as well (Wu et al., 2009; Mestre et al., 2018), as they provide relatively stable microenvironmental conditions that allow them to overcome adverse changes in humidity, temperature, or wind, and recolonize other habitats when favorable conditions return. Butterflies and moths are subjected to complex effects of hedgerows (Berwaerts et al., 1998; Feber et al., 2007) as crops with hedgerows might or might not exhibit richer and more abundant communities of these taxa than crops without hedgerows; however, forests clearly benefit these taxa (Ouin and Burel, 2002). Also, Dainese et al. (2015) concluded that hedgerows result in higher species richness of both butterflies and parasitoid flies, with butterflies showing a significantly higher species richness in complex hedgerows.

Hedgerows provide multiple ecosystem services, some of which may directly enhance food and forage production through shelter (Hauser, 2008), pest regulation (Koellner and Scholz, 2008; Pfister et al., 2017), pollination (Sardiñas and Kremen, 2015; Byrne and Del Barco-Trillo, 2019), soil water content (Luptáčik et al., 2012; Wolka et al., 2018; Holden et al., 2019), and soil quality (Monokrousos et al., 2006). For instance, Van Vooren et al. (2017) found that hedgerows in temperate areas intercepted nitrogen from the surface and subsurface flow and phosphorus and soil sediment from the surface flow that increased the crop yield.

It has been proposed that hedgerows are an intermediate habitat between crops and forests in terms of biodiversity and provision of ecosystem services (Slade et al., 2013) and that a well-developed hedgerow network may be seen as a form of forest in agricultural landscapes (Rey Benayas and Bullock, 2015). Despite their numerous advantages, hedgerows also portrait some drawbacks (Capotorti et al., 2019). They occupy some land, make machinery mobility more difficult, and may spread some pests (Barr et al., 1995). Hedgerows by roadside margins may increase the mortality of some species such as mammals and birds (Orłowski, 2010). Recent review studies that have addressed the overall effect of hedgerows on biodiversity and ecosystem services have found contrasting results for individual taxa or ecosystem services (Van Vooren et al., 2017; Montgomery et al., 2020; Albrecht et al., 2021). For instance, the increase of

ecosystem services such as pest regulation provided by hedgerows seems to be, overall, nonsignificant (Montgomery et al., 2020); however, Van Vooren et al. (2017) found an increase in natural enemy species richness. On the other hand, there is a lack of primary studies on individual ecosystem services other than pest regulation, pollination, and water regulation (Albrecht et al., 2021).

It is likely that pastures, herbaceous crops, woody crops, grasslands, and meadows without hedgerows would behave differently if hedgerows were planted around them (Jahnová et al., 2016; Timberlake et al., 2019). For instance, crop type seems to be a significant predictor of native species richness (Boutin et al., 2008). In addition, different climate types (Pinkus-Rendón et al., 2006) and focus of the spatial scale (e.g., field vs. landscape scale) might potentially have contrasting benefits by the presence of hedgerows as well (Freemark et al., 2002; Aavik et al., 2008).

This study is aimed to synthesize the published scientific evidence on the effects of hedgerows on local biodiversity and provision of ecosystem services and compare the levels of such biodiversity and ecosystem services provided by hedgerows and nearby natural habitats (mostly forest and grassland) at the global scale. We hypothesized that hedgerows (1) enhance contributions of nature to people in agricultural landscapes but (2) support lower levels of biodiversity and ecosystem services than natural habitat. We expect that this study provides further support for the need for widespread hedgerow restoration and more wildlife-friendly farming and multifunctional landscapes.

MATERIALS AND METHODS

Database

On July 25, 2019, we performed a scientific literature search on Web of Science for years 1969 to 2019 with the following combination of keywords in the title or the abstract: [(hedgerow* OR "living fence*" OR "woody field margin" OR "woody edge" OR "woody buffer strip") AND (benefit* OR *diversity OR function* OR service*)] and these words in Spanish, namely, [("cerca* viva*" OR seto* OR "borde leñoso" OR "margen leñoso" OR "franja leñosa") AND (beneficio* OR *diversidad OR funcion* OR servicio*)]. This search identified 985 studies that might report quantitative evidence of levels of biodiversity and/or ecosystem services rendered by hedgerows.

One co-author read the abstracts of all 985 studies. After reading these abstracts, 294, 314, and 377 articles were deemed as useful, possibly useful, or non-useful, respectively, in terms of including quantitative information related to biodiversity or ecosystem services in hedgerows and paired control ecosystems. The 608 useful and possibly useful studies were carefully revised to identify and extract relevant data; this task was performed by the same author in the interest of consistency for data gathering. We finally extracted data from 294 studies (detailed PRISMA flow diagram in **Supplementary Figure 1**).

A database was built to systematize the extracted information of the following variables for each article: article's identifier, reference of the study, response variables (indicators), units of response variables, effect sign (direct or inverse), taxa

(see below), type of ecosystem service (see below), sample size, response value at farmland with hedgerows and control ecosystems (namely, farmland without hedgerows or nearby natural habitat), variation and type of variation (variance, standard deviation (SD), standard error, interquartile range, confidence interval) of the response value, farmland type (crop or pasture), crop type (herbaceous or woody), natural habitat type (forest/woodland or grassland/meadow), country, climate type (tropical or temperate), focus of the spatial scale (field or landscape), overall effect of hedgerows on biodiversity and ecosystem services (positive, neutral, or negative), and type of inference for this overall effect.

Once completed, another coauthor independently revised the database to double-check the procedure and detect possible inconsistencies, errors, and noticeable weird information. This revision corrected the signs of many relationships and excluded 124 studies: 81 of them because they did not report the variability of response variables (i.e., a robust effect size measure could not be used with these articles) and 43 because they referred to non-woody margins. **Appendix 1** lists the 170 primary studies that provided data that were finally analyzed. The response variables were linked to the taxonomic groups (biodiversity) plants, invertebrates, and vertebrates, and one of the four categories of ecosystem services according to the Millennium Ecosystem Assessment (MEA, 2005), namely, supporting, regulating, provisioning, and cultural ecosystem services. Farmland type, crop type, natural habitat type, climate type, and focus of the spatial scale were used as context factors (moderators) of hedgerow effects.

Data Analysis

We analyzed the database following standard methodologies in meta-analyses (Koricheva et al., 2013). We split the database into four datasets for further analyses. The first and second datasets allowed to compare the biodiversity levels between farmland with hedgerows and farmland without hedgerows (**Data File 1**; R script BioHEFA) and between farmland with hedgerows and natural habitat (**Data File 2**; R script BioHENH). The third and fourth datasets allowed to compare the ecosystem services between farmland with hedgerows and farmland without hedgerows (**Data File 3**; R script ESHEFA) and between farmland with hedgerows and natural habitat (**Data File 4**; R script ESHENH). As using the broad ecosystem-service categories might result in lumping together cases that clearly have opposite signs, which will level out the overall response and reduce the likelihood of significant findings, we performed supplementary analyses on the ecosystem services with, at least, three primary studies and ten observations (**Table 1**; **Data Files 5**, **6**; R scripts ESHEFA_specific, ESHENH_specific).

Standardized mean difference (SMD) was computed as a robust estimate of effect size of farmland with hedgerows vs. control ecosystems using the *escalc* function in metafor R package (Viechtbauer, 2010). The sign of SMD was changed if an effect in each observation was based on an inverse relationship (e.g., invasive species and di-services). The SMD is commonly used to estimate the magnitude of the effect by comparing an experimental group and a control group (Hedges and Olkin, 1986; Gurevitch et al., 2001).

A null mixed model adjusted for meta-analysis was fit (Borenstein et al., 2009) to assess whether farmland with hedgerows showed different biodiversity or ecosystem services levels from either farmland without hedgerows or natural habitat. By using a mixed model, we assumed that each case study was a random sample of a larger overall population and considered the primary study (article) as a nesting factor to avoid violating the assumption that effect sizes are independent from each other. We evaluated the extent of heterogeneity by using the statistic I^2 (Higgins and Thompson, 2002), which estimates the percentage of variability due to heterogeneity rather than due to the sampling error.

We also evaluated if moderators explained a significant part of the heterogeneity in the true effect by using simple meta-regressions. Moderators were farmland type (crop or pasture), crop type (herbaceous or woody), natural habitat type (forest/woodland or grassland/meadow), climate type (tropical or temperate), and focus of the spatial scale (field or landscape). Finally, we evaluated if the difference between the effect sizes of factor levels was significantly different from zero by conducting an omnibus test based on a chi-square distribution with the number of coefficients tested as degrees of freedom and following default settings. All statistical analyses were performed in *metafor* R package (R Core Team, 2021).

RESULTS
Database Description
Data filtering retained 835 case studies from 170 primary studies conducted in 39 countries of all continents but Antarctica (**Figure 1**; **Data File 7**; script **Figure 1**). Most records (70% of observations and 74% of primary studies) were related to biodiversity (abundance = 38 and 41%; diversity = 31 and 32%; plants = 35 and 25%; invertebrates = 21 and 23%; vertebrates = 14 and 16%), followed by supporting services (16%, 20%), regulating services (13%, 26%), provisioning services (5%, 15%), and cultural services (<1%, excluded for further analyses due to low sample size). The number of observations and primary studies was as follows: crop = 64 and 56%, pasture = 4 and 7%, herbaceous crop = 54 and 42%, woody crop = 17 and 16%, forest/woodland habitat = 29 and 24%, grassland/meadow habitat = 3 and 5%, tropical climate = 22 and 21%, temperate climate = 78 and 72%, field scale = 67 and 49%, and landscape scale = 33 and 29% (see **Table 2** for absolute numbers).

Contributions to Biodiversity as Compared to Farmland Without Hedgerows
The effect of farmland with hedgerows as compared to farmland without hedgerows on biodiversity was positive, negative, and neutral in 243, 107, and 13 observations, respectively (N = 363 observations from 72 primary studies). Meta-analysis showed significantly higher biodiversity levels in farmland with hedgerows than in farmland without hedgerows (**Figure 2**; estimated effect size = 0.64 ± 0.18, p < 0.01). Heterogeneity was very high (I^2 95% CI: 99.6–99.8%), suggesting that most heterogeneity not explained by sampling error and thus justifying the inclusion of moderators in the model.

TABLE 1 | Number of primary studies and observations providing data for specific ecosystem services.

Ecosystem service	Category	FwH vs. FwoH		FwH vs. NH	
		Number of studies	Number of observations	Number of studies	Number of observations
SoilF	**Supporting**	**10**	**21**	**4**	**19**
Nitrogen	**Supporting**	**12**	**49**	**3**	**8**
Phosphorus	**Supporting**	**6**	**10**	1	2
Others	Supporting	2	7	0	0
Habitat	Supporting	2	5	0	0
Water	**Regulating**	**8**	**13**	2	2
SoilR	**Regulating**	**6**	**11**	0	0
Pests	**Regulating**	**10**	**17**	**3**	**11**
Climate	**Regulating**	**9**	**34**	2	3
Pollination	Regulating	1	1	2	6
Food	**Provisioning**	**14**	36	0	0

SoilF, Soil formation; Nitrogen, Nitrogen cycling; Phosphorus, Phosphorus cycling; Others, other supporting ecosystem services (e.g., minor nutrients' cycling); Habitat, creation and maintenance of habitats; Water, water regulation; SoilR, soil regulation; Pests, Pest regulation; Climate, climate regulation; Pollination, pollination services; Food, food production; FwH, Farmland with hedgerows; FwoH, Farmland without hedgerows; NH, Natural habitats. Ecosystem services that were analyzed individually are highlighted in bold.

FIGURE 1 | World map showing the countries where the selected primary studies were run.
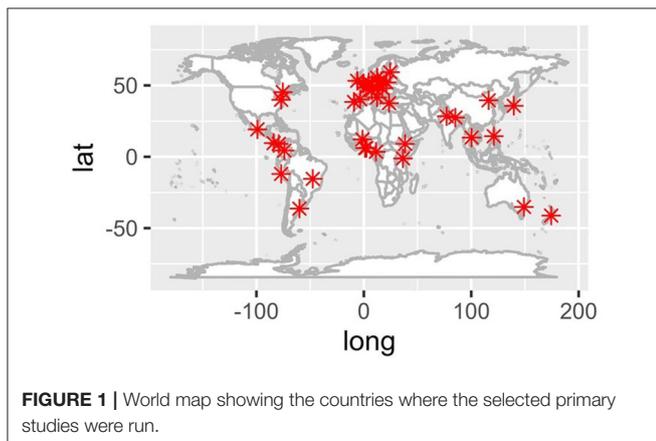
Farmland with hedgerows was equally beneficial for both abundance and diversity metrics (**Figure 2**; $Q_M = 3.24$, $p = 0.07$). Type of organism explained a significant part of the heterogeneity of effect sizes (**Figure 2**); while plants were more positively affected by hedgerows than invertebrates ($Q_M = 7.69$, $p = 0.01$), enhancement of vertebrate biodiversity was similar to that of plants ($Q_M = 0.96$, $p = 0.33$) and invertebrates ($Q_M = 3.19$, $p = 0.07$).

Hedgerows enhanced biodiversity levels in both cropped farmland and pastures, with no significant differences between these two farmland types (**Figure 2**; $Q_M = 0.13$, $p = 0.72$). However, hedgerows did not show a positive effect on biodiversity for crop types; hedgerows enhanced biodiversity on herbaceous crops, but the biodiversity of woody crops was higher without hedgerows (**Figure 2**; $Q_M = 186.88$, $p < 0.01$). Farmland with hedgerows supported higher biodiversity than farmland without hedgerows in temperate regions only (**Figure 2**; estimated effect size: temperate $= 0.78 \pm 0.20$, $p < 0.01$; tropical $= -0.02 \pm 0.42$, $p = 0.97$), and the difference

between tropical and temperate regions was not significant (**Figure 2**; $Q_M = 2.91$, $p = 0.09$). Likewise, both field and landscape studies were equally positively benefitted by hedgerows (**Figure 2**; $Q_M = 0.61$, $p = 0.43$), but hedgerows effects at the landscape scale were barely significant.

Contributions to Biodiversity as Compared to Natural Habitat

The effect of farmland with hedgerows as compared to natural habitat on biodiversity was negative, positive, and neutral in 116, 92, and 9 observations, respectively ($N = 217$ observations from 43 primary studies). Consequently, meta-analysis revealed no significant differences between farmland with hedgerows and natural habitat in terms of biodiversity (**Figure 3**; estimated effect size $= 0.11 \pm 0.14$, $p = 0.43$; I^2 95% CI: 87.70–95.16%).

There were significant differences in the effect of hedgerows between biodiversity metrics, organism types, and natural habitat type (**Figure 3**). Abundance of organisms did not differ between farmland with hedgerows and natural habitat, but diversity was higher in farmland with hedgerows (**Figure 3**; $Q_M = 128.78$, $p < 0.01$). Only invertebrates exhibited higher biodiversity levels in farmland with hedgerows than in natural habitat (**Figure 3**; estimated effect size $= 0.39 \pm 0.17$, $p = 0.02$). Biodiversity differed between natural habitat types; farmland with hedgerows had a higher level than grasslands/meadows but similar to forest/woodlands (**Figure 3**; $Q_M = 5.39$, $p = 0.02$). Neither climate type ($Q_M = 3.38$, $p = 0.07$) nor focus of spatial scale ($Q_M = 0.66$, $p = 0.41$) influenced the magnitude of effect size (**Figure 3**).

Contributions to Ecosystem Services as Compared to Farmland Without Hedgerows

The effect on ecosystem services of farmland with hedgerows as compared to farmland without hedgerows was positive, negative, and neutral in 127, 65, and 12 observations, respectively

TABLE 2 | Number of studies and observations per level of each moderator and context factor.

| Moderator	Level	Number of studies	Number of observations
Type of organism	Plants	43	289
Type of organism	Invertebrates	39	175
Type of organism	Vertebrates	28	116
Ecosystem service	Supporting	23	121
Ecosystem service	Regulating	32	98
Ecosystem service	Provisioning	14	36
Farmland type	Crop	95	535
Farmland type	Pasture	12	32
Crop type	Herbaceous	71	424
Crop type	Woody	27	114
Natural habitat type	Forest/Woodland	41	244
Natural habitat type	Grasslands/Meadow	9	24
Climate type	Tropical	35	184
Climate type	Temperate	97	651
Focus of the spatial scale	Field	84	560
Focus of the spatial scale	Landscape	50	275
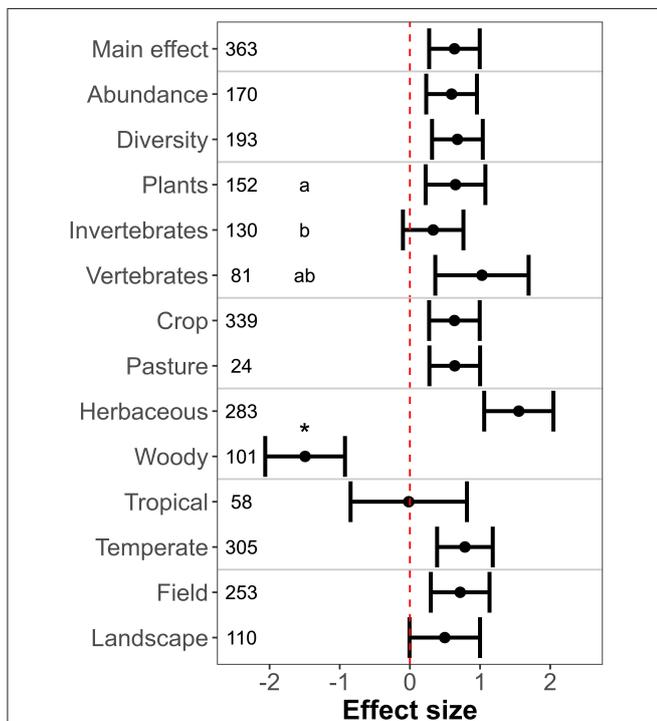
FIGURE 2 | Biodiversity levels in farmland with hedgerows as compared to farmland without hedgerows. X-axis indicates the mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant. Significant differences between levels of moderators are indicated by asterisks (two levels) and different letters (three levels), respectively.
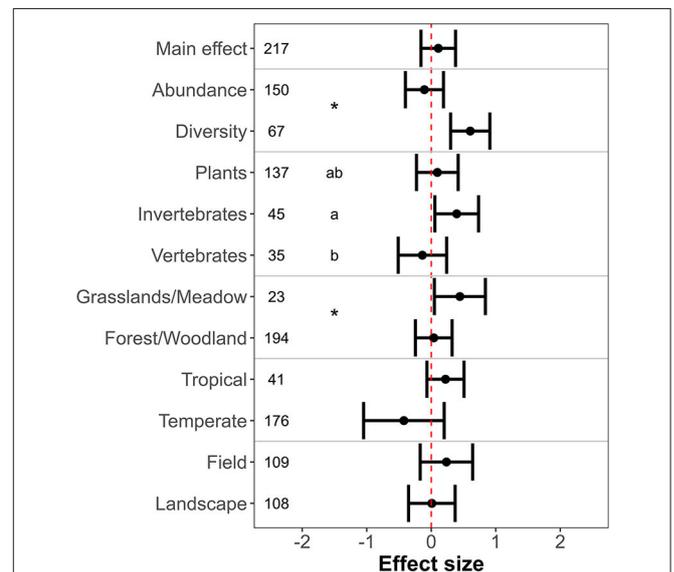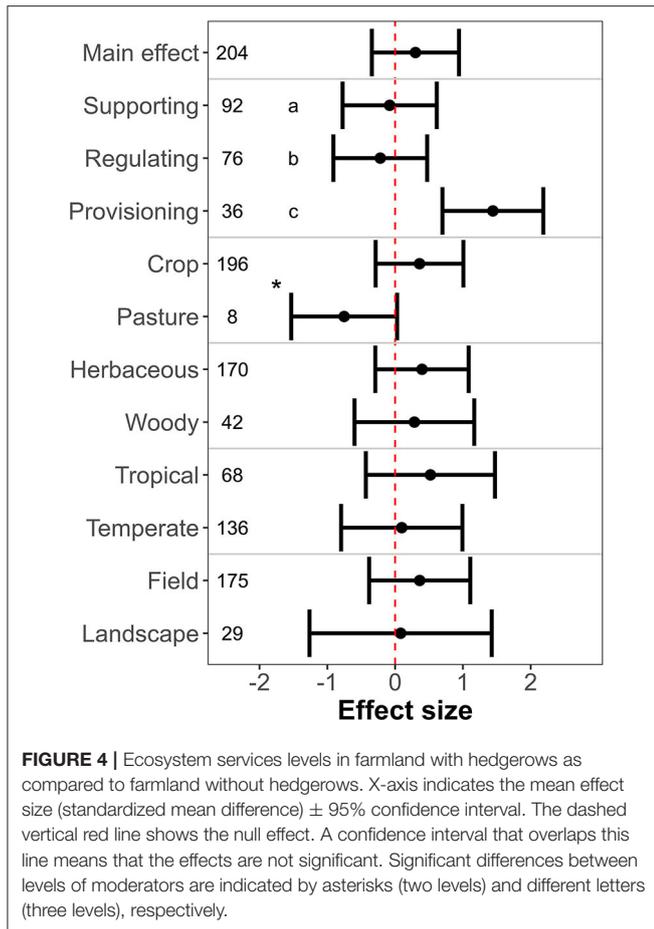

FIGURE 3 | Biodiversity levels in farmland with hedgerows as compared to natural habitat. X-axis indicates the mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant. Significant differences between levels of moderators are indicated by asterisks (two levels) and different letters (three levels), respectively.

($N = 204$ observations from 43 primary studies). Hedgerows did not enhance overall ecosystem service levels (**Figure 4**; estimated effect size = 0.30 ± 0.33, p = 0.36; I^2 95% CI: 95.75–98.63%). However, meta-analysis revealed significant differences when comparing ecosystem services and farmland types (**Figure 4**). Farmland with hedgerows showed positive effects on provisioning services (estimated effect size: 1.44 ± 0.38, p <0.01), but not on regulating (estimated effect size: -0.22 ± 0.35, p = 0.54) or supporting services (estimated effect size: -0.08 ± 0.35, p = 0.82). In addition, farmland with

FIGURE 4 | Ecosystem services levels in farmland with hedgerows as compared to farmland without hedgerows. X-axis indicates the mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant. Significant differences between levels of moderators are indicated by asterisks (two levels) and different letters (three levels), respectively.

FIGURE 5 | Ecosystem services levels in farmland with hedgerows as compared to natural habitat. X-axis indicates the mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant.

hedgerows provided more supporting than regulating services ($Q_M = 5.61$, $p = 0.02$). Crops showed higher ecosystem service levels than pastures (**Figure 4**; $Q_M = 22.06$, $p < 0.01$). The magnitude of effect size did not vary between crop types (**Figure 4**; $Q_M = 0.09$, $p = 0.76$), climate type (**Figure 4**; $Q_M = 0.40$, $p = 0.53$), and the spatial scale (**Figure 4**; $Q_M = 0.13$, $p = 0.72$). The complementary analyses on specific ecosystem services confirmed the pattern observed for the broad ecosystem-service categories (**Supplementary Figure 2**; **Data File 5**; R script ESHEFA_specific).

Contributions to Ecosystem Services as Compared to Natural Habitat

The effect of farmland with hedgerows on ecosystem services as compared to natural habitat was negative, neutral, and positive in 32, 11, and 8 observations, respectively ($N = 51$ observations from 11 primary studies). Meta-analysis showed that natural habitat provided higher levels of ecosystem services than farmland with hedgerows (**Figure 5**; estimated effect size: -0.49 ± 0.20, $p = 0.02$; I^2 95% CI: 58.20–94.84%).

The magnitude of the effect size was similar between regulating and supporting services (**Figure 5**; $Q_M = 0.21$, $p = 0.64$), tropical and temperate climates (**Figure 5**; $Q_M = 0.36$, $p = 0.55$) and field and landscape scales (**Figure 5**; $Q_M = 1.39$, $p = 0.24$). There was insufficient statistical power to test the
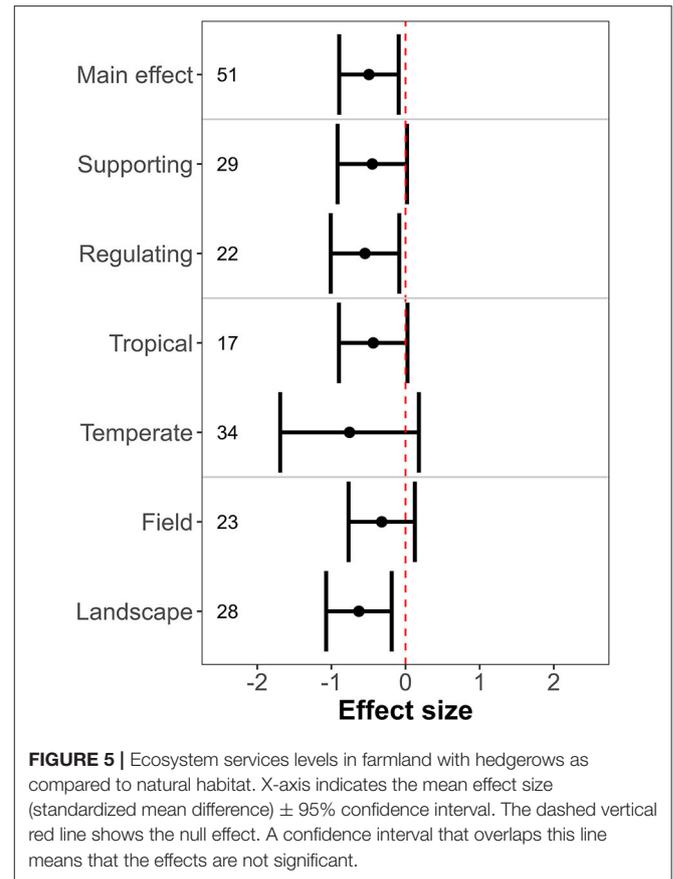
differences in effects size related to natural habitat types and provisioning services.

The complementary analyses for specific ecosystem services (soil formation, nitrogen cycling, and pest regulation) showed that natural habitats exhibited greater pest regulation services than farmland with hedgerows (**Supplementary Figure 3**; **Data File 6**; R script ESHENH_specific). These ecosystem services depended on climate type (hedgerows were more beneficial in temperate than in tropical regions; estimated effect size: temperate $= -0.29 \pm 0.06$, $p < 0.01$; tropical $= -1.00 \pm 1.13$, $p < 0.01$; $Q_M = 23.37$, $p < 0.01$).

DISCUSSION

Our results support the starting hypothesis (H1) of higher levels of biodiversity and provisioning ecosystem services in farmland with hedgerows as compared to farmland without hedgerows. However, despite farmland with hedgerows harbored as much biodiversity levels as natural habitat, natural habitat provided higher levels of ecosystem services than farmland with hedgerows (H2). Overall, the current meta-analysis agrees with a previous one (Van Vooren et al., 2017) conducted on arable crops in temperate regions. By broadening the scope to tropical regions and pastureland, we provide new insights on the contribution of hedgerows to people. In addition, the comparison of farmland with hedgerows and natural habitat supports the idea that

farmland with hedgerows is an "intermediate," more wildlife and ecosystem service friendly habitat than farmland without hedgerows (Rey Benayas and Bullock, 2012). The recent review by Albrecht et al. (2021) found that plant-species identity is crucial to optimize the contributions of hedgerows to ecosystem service delivery and ecological intensification of agriculture in the future. **Table 3** synthesizes the results and hypotheses of this study that are discussed in the following paragraphs.

Hedgerows Enhanced the Farmland Habitat

Hedgerows enhanced the biodiversity levels in farmland, and both metrics (abundance and diversity) and farmland types (cropland and pastureland) studied here were similarly benefitted (**Figure 2**). Plants were the most positively affected taxa by hedgerows in agreement with previous studies. For instance, Aavik et al. (2008) found that semi-natural elements in the landscape enhanced plant species richness both at the field and at the landscape scales, and Evans et al. (2011) showed that uncultivated semi-natural habitats such as mature hedgerows are more species rich and have higher biomass than cropped habitat.

Hedgerows around herbaceous crops provide woody habitat otherwise absent or very scarce in agricultural landscapes. However, woody crops contain part of the hedgerows' functional diversity (i.e., the cultivated shrubs or trees) that may explain why herbaceous crops are more positively affected in terms of biodiversity than woody crops. For instance, the cultivated shrubs and trees facilitate the establishment of non-cropped perennial plants and other species (Oliveira et al., 2015). Castro-Caro et al. (2015) also reported that hedges, and ground covers to a lesser extent, efficiently increased the abundance and richness of passerine communities in olive groves, particularly of insectivorous birds. Other vertebrate species benefit from the presence of hedgerows. For instance, Verboom and Huitema (1997) suggested that landscapes with a high density of linear elements have a surplus value for serotine bats because bats use hedgerows as orientation clues, foraging habitat, and shelter from wind and predators.

The plant species that are found only in non-cropped habitat are primarily native and perennials, whereas a high proportion of the species found only in cultivated fields are annual and introduced species (Jobin et al., 1996). More exotic plants in farmland without hedgerows than in farmland with hedgerows have also been reported by Boutin et al. (2008). Plant species richness and composition varied substantially among the five landscapes studied by Freemark et al. (2002), ranging from a row-crop monoculture landscape to a diverse mosaic of cropped and non-cropped habitat landscape. The more complex the hedgerows, the species-richer farmland is (Klimek et al., 2014). Established shrubs may attract seed-dispersing wildlife and create proper environments for plant recruitment, generating reforestation feedback (Suárez-Esteban et al., 2013). In addition, trees planted into living fences generally have greater survival, relative growth, and height compared to those planted in open pasture (Love et al., 2009).

The difference in biodiversity levels between farmland with hedgerows and farmland without hedgerows was maximum in temperate regions (**Figure 2**). Such an extra benefit of hedgerows in temperate regions with respect to the tropics may be due to more ameliorated microclimate conditions for plant recruitment and wildlife animals (Ceresa et al., 2012; Burgess et al., 2015). For instance, the spider *Nephila clavipes* persists in highly fragmented tropical farmland landscapes thanks to the prevalence of relatively stable conditions (Pinkus-Rendón et al., 2006), whereas butterflies have been found to be favored by intermediate levels of landscape complexity (Dainese et al., 2015). The influence of drivers other than climate (e.g., hedgerow complexity) may explain why our analysis exhibited non-significant effects of hedgerows on invertebrate biodiversity (**Figure 2**).

Hedgerows were more beneficial at the field than at the landscape scale (**Figure 2**) since there is often some natural habitat other than hedgerows to support biodiversity at the landscape scale. The landscape context is important to the delivery of ecosystem services (Dainese et al., 2017). For instance, Fritz and Merriam (1996) concluded that habitat qualities that result from the architectural differences between hedgerows and forest may constrain plant movement. In landscapes of fragmented forest, hedgerows may provide corridors for woodland plants (Fritz and Merriam, 1996). However, non-fragmented (i.e., well-connected) forests do not need hedgerows for connectivity.

Ecosystem service levels in farmland with hedgerows were higher, albeit statistically insignificant, than in farmland without hedgerows. Our synthesis failed to highlight that hedgerows, in general, increased supporting or regulating services; however, hedgerows resulted in a higher amount of provisioning services – the ones that are sought in farmland habitat (**Figure 4**).

The complementary analyses confirmed the lack of significant differences for individual supporting and regulation services between farmland with hedgerows and farmland without hedgerows. This finding agrees with Albrecht et al. (2021) who concluded inconsistent and highly variable effects of hedgerows on crop pollination and yield and non-significant effects on pest control. Many agricultural systems use hedgerows as a supplementary source for cropping (for instance, intercropping of annual crops between *Inga edulis* contour hedgerows; Alegre and Rao, 1996). Hauser (2008) found that hedgerows dominated by cassava *Manihot esculenta* increased groundnut and maize production. In their meta-analysis, Van Vooren et al. (2017) reported that, up to 20 times the hedgerow height, yield is increased by an average of 6% as compared with farmland without hedgerows.

Conserving and restoring hedgerows may enhance some supporting services such as habitat creation (linked to biodiversity levels) and a range of regulating services. Shrubs and trees of hedgerows usually have well-developed root systems compared to herbaceous crops, which increases soil organic matter and sequesters carbon. Boutin's (2006) analyses of soil properties showed that organic matter and nutrient levels are often higher in hedgerows than in open fields. A hedgerow network protects landscapes from soil organic carbon erosion

TABLE 3 | Summary of comparisons of biodiversity (Bio) and ecosystem service (ES) levels between farmland with hedgerows (FwH) and farmland without hedgerows (FwoH), and between farmland with hedgerows (FwH) and natural habitat (NH).

	Contributions to people	H1: FwH > FwoH	Farmland with hedgeows vs. FwoH	vs. NH	H2: FwH < NH
	Biodiversity	✅	>	=	❌
Metrics	Abundance	✅	>	=	❌
	Diversity	✅	>	<	✅
Type of organism	Plants	✅	>	=	❌
	Invertebrates	❌	=	<	✅
	Vertebrates	✅	>	=	❌
	Ecosytem services	❌	=	<	✅
	Supporting	❌	=	=	✅
	Regulating	❌	=	<	❌
	Provisioning	✅	>	No data	No data

	Context factors	H1: FwH > FwoH Bio	ES	FwH vs FwoH Bio	ES	FwH vs NH Bio	ES	H2: FwH < NH Bio	ES
Farmland type	Crop	✅	❌	>	=				
	Pasture	✅	❌	>	=				
Crop type	Herbaceous	✅	❌	>	=				
	Woody	❌	❌	<	=				
Natural habitat type	Grassland/Meadow					<	No data	✅	No data
	Forest/Woodland					<	No data	✅	No data
Climate type	Tropical	❌	❌	=	=	=	=	❌	❌
	Temperate	✅	❌	>	=	=	=	❌	❌
Focus of spatial scale	Field	✅	❌	>	=	=	=	❌	❌
	Landscape	✅	❌	=	=	=	<	❌	✅

">," "<," and "=" indicate that a given factor level is higher, lower, or similar, respectively, in that scenario than in its paired scenario. H1 and H2 are the tested hypotheses in this study; a green tick and a red cross indicate that a given hypothesis was supported or not, respectively, by the results.

by runoff (Lacoste et al., 2016). Legume shrubs, which naturally fertilize soils, are common in hedgerow composition (Lemage et al., 2021). The architecture of some species such as the broom *Retama sphaerocarpa* provides shelter for many species (Matías et al., 2011). Franco (1998) and Van Vooren et al. (2017) reported that hedgerows retain 85 and 90% of suspended solids, 73 and 67% of total nitrogen, and 70 and 73% of total phosphorus in runoff, respectively.

Pastures were less benefitted by hedgerows than crop fields in terms of ecosystem services (**Figure 4**). Crop fields usually support a more intensive management scheme (tillage, fertilization, pesticide application) than pastures, where livestock fertilize the soil on crop fields. Heavy machinery compact soils and reduce supporting and regulating services (Power, 2010; The Research Council of Norway, 2011). Thus, hedgerows (i.e., unploughed, unfertilized features) around crop fields

may become a reservoir for ecosystem services on top of biodiversity (Speir, 2015). In short, hedgerows play a relevant role in biodiversity conservation and climate change mitigation (Montgomery et al., 2020).

Farmland With Hedgerows Supports Similar Biodiversity Levels but Provides Lower Ecosystem Service Levels Than Natural Habitat

In farmland with hedgerows, abundance and diversity levels were similar and higher, respectively, than in natural habitat (**Figure 3**). At the population level, seedlings and juveniles are, usually, proportionally less abundant in hedgerows than in forests (Wehling and Diekmann, 2010), and the establishment of new populations of forest species in hedgerows is lower than in forests (Schmucki and De Blois, 2009). However, hedgerows represent a strong edge effect (forest and open fields) that may favor diversity (Litza and Diekmann, 2019).

We found a higher diversity of invertebrates in farmland with hedgerows than in natural habitat, particularly in grasslands and meadows. While these herbaceous habitats have seasonal food availability and fluctuant microclimate conditions, farmland with hedgerows can feed invertebrates along the year with complementary food resources and offer overwintering refuges. Thus, Jahnová et al. (2016) recorded more diverse ground-dwelling beetle communities in meadow margins than inside the meadows. Hedgerows help in ensuring a continuous supply of nectar on farmland; for instance, Timberlake et al. (2019) suggested that semi-natural habitat maintains complementary flowering phenology. The higher diversity of invertebrates in farmland with hedgerows than in natural habitat might be taxon specific. The finding of this study contrasts with Berwaerts et al. (1998) who found that the genetic diversity of speckled wood butterflies (*Pararge aegeria* L.) of large continuous woodland was significantly higher than in a highly fragmented area with very small woodland fragments and hedgerows scattered in an intensive agricultural landscape. Similarly, Buddle and Higgins (2020) suggested that lower spider diversity in hedgerows than in riparian forests may be due in part to the invasive honeysuckle shrub *Lonicera maackii*, which reduces hedgerow complexity on the ground layer.

Farmland with hedgerows provided higher amounts of ecosystem services than farmland without hedgerows, but lower amounts than natural habitat (**Figure 5**), thus supporting our H2 as other studies did. Hannon and Sisk (2009) found that hedgerow herbaceous flora is intermediate to that of crop fields and woodlands; consequently, regulating services such as pollination provided by natural habitat were higher than those provided by farmland with hedgerows. Byrne and Del Barco-Trillo (2019) found greater densities of bumblebees in unmanaged grasslands than in farmland with hedgerows. In this study, regulating services were particularly greater in natural habitat than in farmland with hedgerows at the landscape scale, whereas this effect is diluted at the field scale. However, we were unable to disentangle what moderators drove such a scale effect due to shortage of data.

CONCLUSION

The presence of hedgerows enhances the contributions of nature to people in agricultural landscapes (first hypothesis supported), including provisioning services. Farmland with hedgerows provides similar levels of biodiversity (an unexpected result mostly due to invertebrates) but lower levels of ecosystem services than natural habitat (second hypothesis partially supported). It is justified to recommend practitioners and policy makers conserving hedgerow networks and planting new hedgerows where they are absent or scarce to reach the goals of the EU Biodiversity Strategy for 2030 and maximize biodiversity and ecosystem services globally.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JR conceived and designed the study. DG collected data and wrote first draft of the manuscript. DG and JR built the database. DG and EA analyzed the data. All authors contributed to revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.789612/full#supplementary-material

Supplementary Figure 1 | PRISMA flow diagram showing the process of study selection and exclusion criteria (adapted from Page et al., 2021).

Supplementary Figure 2 | Levels of specific ecosystem services in farmland with hedgerows as compared to farmland without hedgerows. X-axis indicates the mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant. The significance of differences between specific ecosystem services are indicated in R script ESHEFA_specific.

Supplementary Figure 3 | Levels of specific ecosystem services levels in farmland with hedgerows as compared to natural habitats. X-axis indicates the

mean effect size (standardized mean difference) ± 95% confidence interval. The dashed vertical red line shows the null effect. A confidence interval that overlaps this line means that the effects are not significant. The significance of differences between specific ecosystem services are indicated in R script ESHENH_specific.

Data File 1 | Contains the data used for comparing biodiversity of farmland with hedgerows and farmland without hedgerows; Identifier: it codes the primary study (**Appendix 1**); New.sign: it informs whether a given relationship is direct (+) or inverse (–); New.Response: it codes all response variables; New.Taxa: it categorizes all possible taxa into Plants, Invertebrates and Vertebrates; nHedgerow: The number of observations in farmland with hedgerows; nControl: The number of observations in farmland without hedgerows; Hedgerow.Value: The average value of the response variable in farmland with hedgerows; Hedgerow.SD: The standard deviation of the response variable in farmland with hedgerows; Farmland.Value: The average value of the response variable in farmland without hedgerows; Farmland.SD: The standard deviation of the response variable in farmland without hedgerows; Farmland.type: it indicates either crop or pasture; Crop.type: it indicates either herbaceous or woody; Climate.type: it indicates temperate or tropical; Spatial.Scale.Focus: it indicates field or landscape.

Data File 2 | Contains the data used for comparing the biodiversity of farmland with hedgerows and natural habitats: nControl: The number of observations in natural habitats; Natural.habitat.Value: it provides the average of response variable at natural habitats; Natural.habitat.SD: The standard deviation of the response variable in the natural habitat; Natural.habitat.type; it indicates whether the control is a forest/woodland or a grassland/meadow; for other variables, see description in **Data File 2**.

Data File 3 | Contains the data used for comparing the ecosystem services levels of farmland with hedgerows and farmland without hedgerows; Ecosystem.Service: it categorizes New.Response into Provisioning, Regulating, and Supporting; for other variables, see description in **Data File 2**.

Data File 4 | Contains the data used for comparing the ecosystem services levels of farmland with hedgerows and natural habitats. Response: it indicates the

ecosystem service involved in a given observation; Natural.habitat.type was excluded from these analyses due to a lack of power from grasslands/meadow level of factor; for other variables, please see description at **Data File 3**.

Data File 5 | Contains the data used for comparing the levels of specific ecosystem services of farmland with hedgerows and farmland without hedgerows. The levels of New.Response are: SoilF: soil formation, Nitrogen: nitrogen cycling, Phosphorus: phosphorus cycling, Water: water regulation, SoilR: soil regulation, Climate: climate regulation, Food: food production; for other variables, see description of variables in **Data File 3**.

Data File 6 | Contains the data used for comparing the levels of specific ecosystem services of farmland with hedgerows and natural habitats. See description of variables in **Data Files 4**, **5**.

Data File 7 | Contains the data needed to build **Figure 1**.
R scripts | Figure_1a.docx contains the code applied on **Data File 1** for building **Figure 1**; BioHEFA.docx contains the statistical analyses performed on **Data File 2**; BioHENH.docx contains the statistical analyses performed on **Data File 3**; ESHEFA.docx contains the statistical analyses performed on **Data File 4**; ESHENH.docx contains the statistical analyses performed on **Data File 5**; ESHEFA_specific.docx contains the statistical analyses performed on **Data File 5**; ESHENH_specific.docx contains the statistical analyses performed on **Data File 6**.

Appendix 1 | List of studies used for each comparison, including the full reference and the identifier. This list eases the reproduction of meta-analyses with the provided data (**Data Files 1–6**). Specifically, section (a) includes the studies used for comparing biodiversity between farmland with hedgerows and farmland without hedgerows; section (b) the studies used for comparing biodiversity between farmland with hedgerows and natural habitats; section (c) the studies used for comparing ecosystem services provided by farmland with hedgerows and farmland without hedgerows; and section (d) the studies used for comparing the ecosystem services provided by farmland with hedgerows and natural habitat.

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