



# Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis

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Managing agricultural landscapes to support biodiversity conservation requires profound structural changes worldwide. Often, discussions are centered on management at the field level. However, a wide and growing body of evidence calls for zooming out and targeting agricultural policies, research, and interventions at the landscape level to halt and reverse the decline in biodiversity, increase biodiversity-mediated ecosystem services in agricultural landscapes, and improve the resilience and adaptability of these ecosystems. We conducted the most comprehensive assessment to date on landscape complexity effects on nondomesticated terrestrial biodiversity through a meta-analysis of 1,134 effect sizes from 157 peer-reviewed articles. Increasing landscape complexity through changes in composition, configuration, or heterogeneity significantly and positively affects biodiversity. More complex landscapes host more biodiversity (richness, abundance, and evenness) with potential benefits to sustainable agricultural production and conservation, and effects are likely underestimated. The few articles that assessed the combined contribution of linear (e.g., hedgerows) and areal (e.g., woodlots) elements resulted in a near-doubling of the effect sizes (i.e., biodiversity level) compared to the dominant number of studies measuring these elements separately. Similarly, positive effects on biodiversity are stronger in articles monitoring biodiversity for at least 2 y compared to the dominant 1-y monitoring efforts. Besides, positive and stronger effects exist when monitoring occurs in nonoverlapping landscapes, highlighting the need for long-term and robustly designed monitoring efforts. Living in harmony with nature will require shifting paradigms toward valuing and promoting multifunctional agriculture at the farm and landscape levels with a research agenda that untangles complex agricultural landscapes' contributions to people and nature under current and future conditions.

landscape configuration | landscape composition | landscape heterogeneity | landscape agronomy | agroecology

Agriculture expansion, intensification, and simplification dramatically contribute to biodiversity collapse (1–3). This is fueled by the acute lack of recognition in development agendas of agriculture's dependence on biodiversity (4) and agriculture's siloed and field-level planning (1, 2, 5–10). Hence, agriculture is underplaying a pivotal role in actively contributing to biodiversity conservation for the ecosystem services it provides, as well as its intrinsic or bequest values (6, 10–16). Many researchers are calling for better consideration of the multifunctional role of agricultural landscapes, including supporting biodiversity (17–19) and improving ecosystem resilience (16) and human well-being (20). The largest managed terrestrial land cover can, as such, be actively managed to offer a high-quality matrix connecting remnant patches of habitat to benefit biodiversity and people (21, 22).

While increasing agriculture's contribution to biodiversity conservation will require field- and landscape-level planning to leverage synergies with production goals (23), cross-sector and multiobjective landscape planning in agriculture policies or interventions remains rare. For example, agrienvironmental schemes, the most common legal mechanism in the European Union to foster sustainable agriculture management, rarely considers interactions and impacts at the landscape level, despite the large body of evidence showing that planning agriculture interventions at the landscape level contributes more efficiently to preserving biodiversity (9, 24–39), including specialist species (40), and even multiple ecosystem services (12, 41). Increasing landscape-level management in agricultural lands requires a science of landscape agronomy yet to be fully developed (23).

Planning and managing agriculture with a landscape perspective acknowledges landscape-level patterns supporting vital ecological processes that enable biodiversity to persist. For example, agricultural landscapes with complex patterns (i.e., complex landscapes) mitigate regional extinctions by providing complementary and accessible resources that enable species survival and interpatch migration (42). Here, we consider landscape

## Significance

Agricultural land, the world's largest human-managed ecosystem, forms the matrix that connects remnant and fragmented patches of natural vegetation where nondomesticated biodiversity struggles to survive. Increasing the resources that this matrix can offer to biodiversity is critical to halting biodiversity loss. Our comprehensive meta-analysis demonstrates the positive and significant effect on biodiversity of increasing landscape complexity in agricultural lands. We found more biodiversity in complex landscapes, potentially contributing to agriculture production, ecosystem resilience, and human well-being. Current biodiversity conservation strategies tend to focus on natural ecosystems, often ignoring opportunities to boost biodiversity in agricultural landscapes. Our findings provide a strong scientific evidence base for synergistically managing agriculture at the landscape level for biodiversity conservation and sustainable production.

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complexity to have three broad dimensions with distinct contributions to ecological processes: composition, configuration, and heterogeneity (*SI Appendix*). Landscape composition (e.g., remnant patches of forest) serves as the pool of biodiversity, landscape heterogeneity (e.g., number of crops) offers year-round resources in dynamic landscapes, whereas landscape configuration (e.g., edge length) enables species movement across the landscape (13, 42, 43). Although these dimensions are clear and well documented, understanding landscape complexity–biodiversity interaction is not straightforward. Landscape complexity and biodiversity are measured through a plethora of methods and metrics which could explain, in some cases, biodiversity’s nonlinear and inconsistent response to landscape complexity across species, taxa, and functional groups (e.g., 2, 29, 44–47).

Despite these methodological challenges, complex landscapes can host larger species diversity, cascading into increased resilience, stability, and capacity to recover from disturbances (16, 40, 48, 49). Similarly, production in complex agricultural landscapes benefits from more diverse (in terms of evolutionary history) pollinator populations, improving ecosystem functioning and services (50, 51), while yields (50, 52–57) and crop products’ market and quality value (56, 58) can improve due to the more diverse pollinators and natural pest control populations.

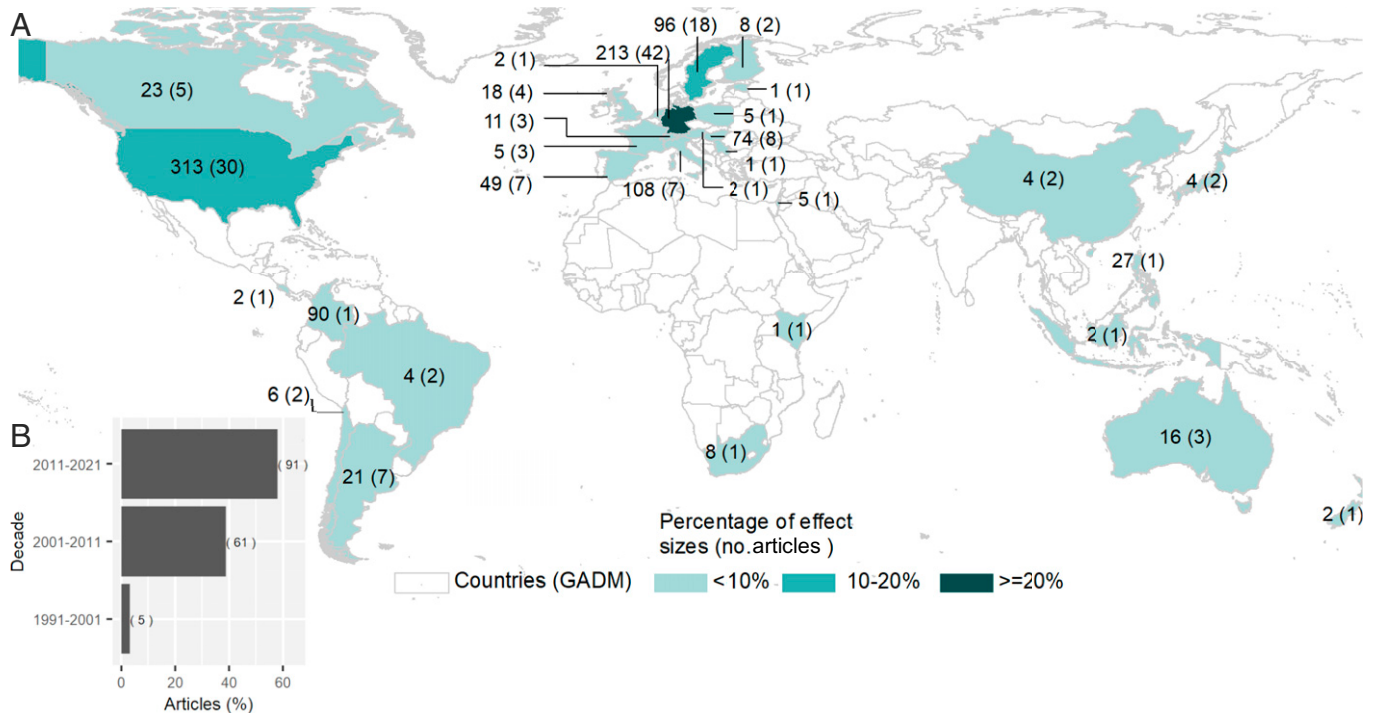
Multiple efforts have synthesized the effect of landscape complexity on biodiversity for specific taxa or functional groups [e.g., arthropods (45, 59) and pollinators (14, 60, 61)] and cropping systems [orchard and vineyards (14)], often using different metrics for biodiversity (e.g., species richness, abundance, or evenness) and landscape complexity dimensions, indicators, or metrics (*SI Appendix*, Table S1). The differences in scope and metrics used in existing reviews hinders consolidating the evidence base to identify consistent versus context-specific results that can then be used for tailoring biodiversity conservation recommendations in agricultural landscapes (60).

We contribute to closing this knowledge gap by creating the most comprehensive global evidence map and meta-analysis to date of field experiments exploring the landscape complexity–biodiversity relationship. We first identify how landscape complexity is currently being measured and assessed in the scientific literature. Then, we use meta-analysis to explore landscape complexity effects on biodiversity in different agronomic and environmental contexts. Finally, we identify critical knowledge gaps that remain (missing crops, biodiversity indicators, and regions). Our comprehensive analysis provides insights and offers tangible next steps to live in harmony with nature by managing and shaping the largest land cover altered by humans.

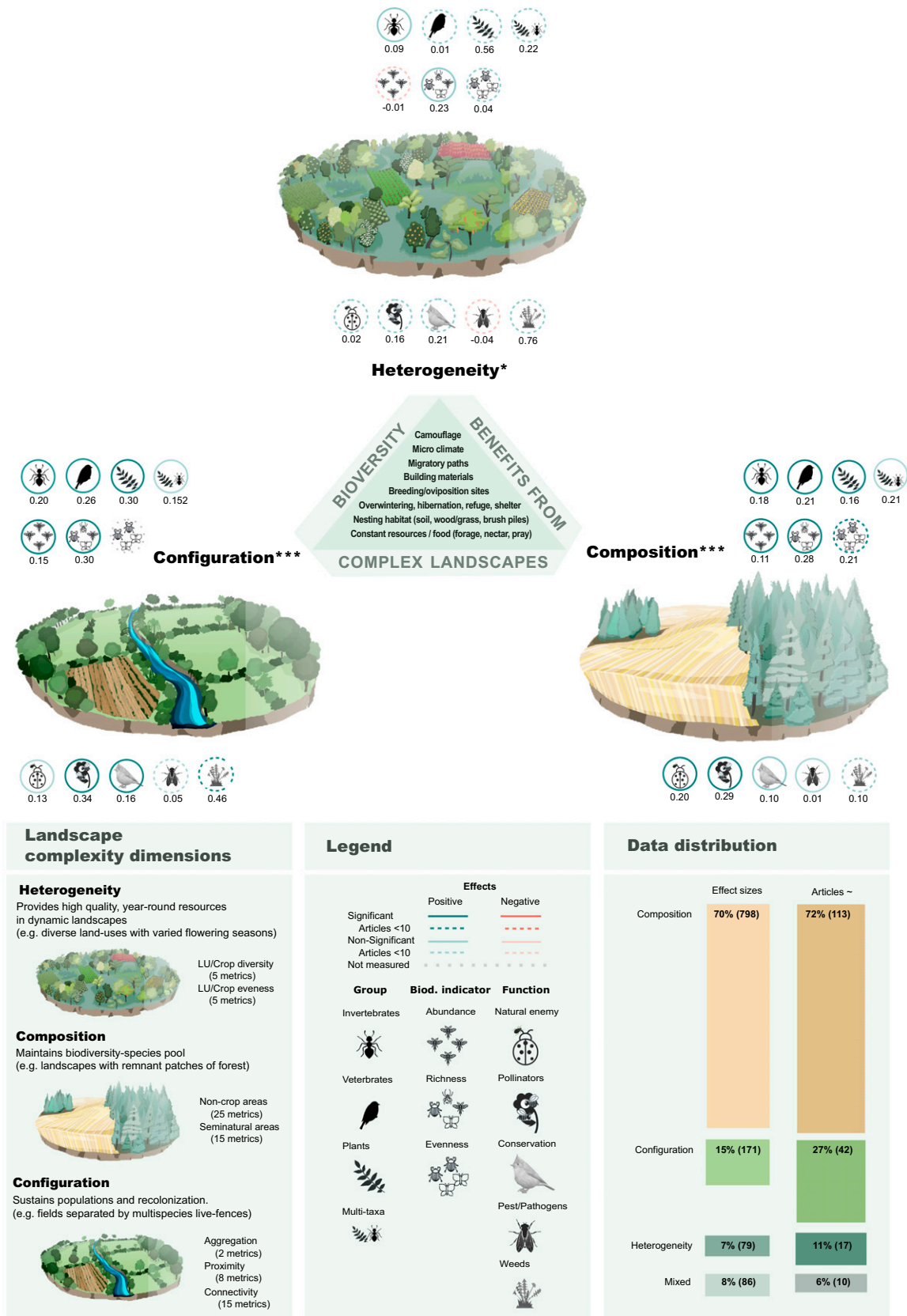
## Results and Discussion

**Regions Other Than Europe and the United States Are Heavily Understudied.** The metadataset included 1,134 effect sizes from 157 primary peer-reviewed articles collected from field experiments in 29 countries. The majority of effect sizes were from Europe (53% effect sizes) and North America (30%), followed by Central and South America (11%). Asia, Africa, and Oceania were less well-represented (<4% effect sizes each) (Fig. 1*A*). Most of the included articles were published in the last decade (2011 to 2021 = 58% articles) (Fig. 1*B*).

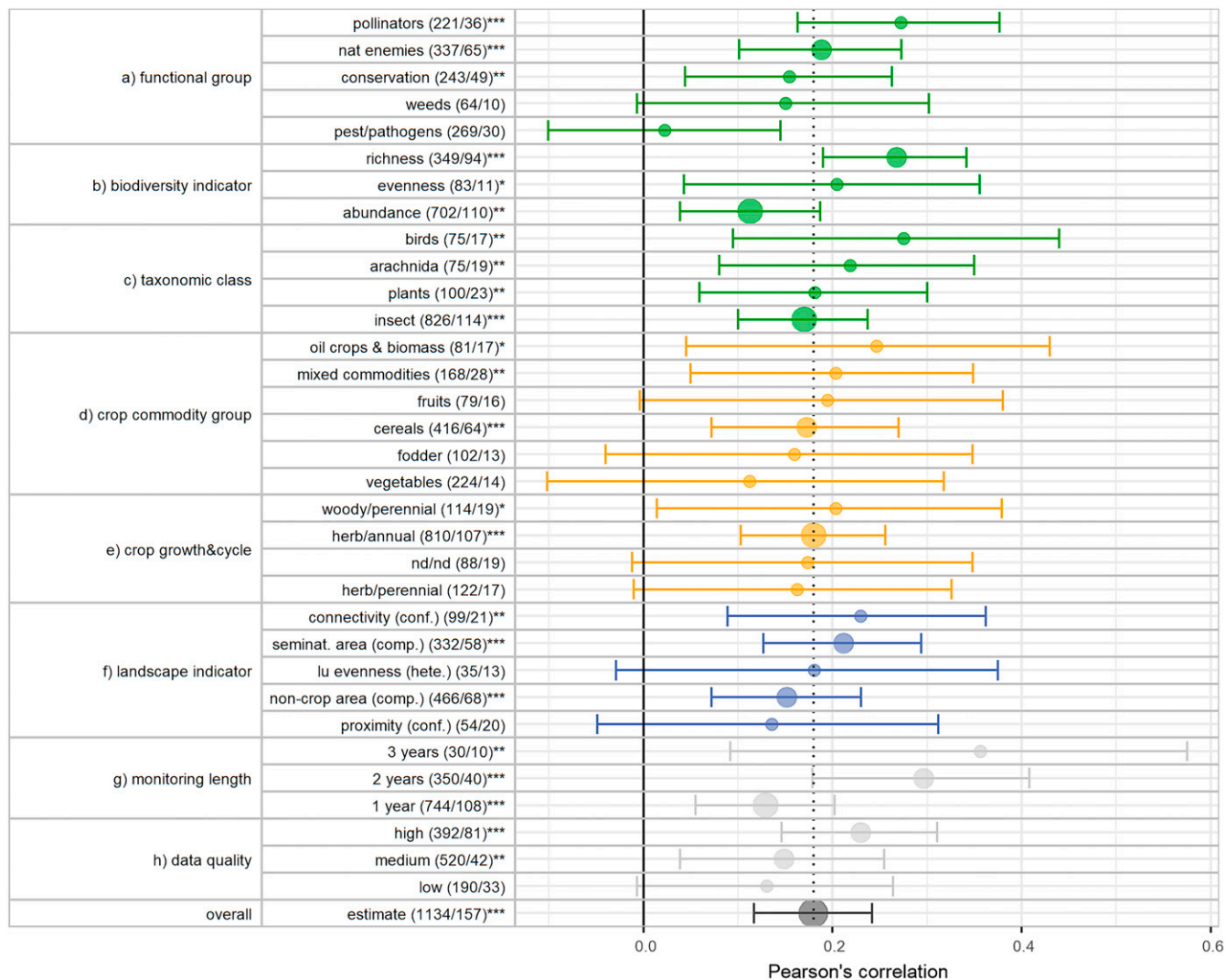
**Three Landscape Complexity Dimensions Contribute Distinctly to Biodiversity with Contrasting Levels of Evidence.** We found that articles used metrics covering the three dimensions of landscape complexity (*SI Appendix*, Figs. S2 and S3), where each landscape complexity dimension positively and significantly affects biodiversity (composition:  $r = 0.18$ ,  $P < 0.001$ , effect sizes = 798, articles = 113; configuration:  $r = 0.20$ ,  $P = 0.001$ , effect sizes = 171, articles = 42; heterogeneity:  $r = 0.17$ ,  $P = 0.050$ , effect sizes = 79, articles = 17) (Figs. 2 and 3 and



**Fig. 1.** (A) Data distribution across countries indicating effect sizes (number of articles). Effect sizes from multicountry articles are excluded from the figure (12 from four articles). (B) Percentage of articles assessing the landscape complexity effect on biodiversity during the last three decades. Country boundaries are from the Database of Global Administrative Areas (GADM) version 3.6.



**Fig. 2.** Direction and strength of the effect on biodiversity of each landscape complexity dimension.  $*P \leq 0.05$ ,  $***P < 0.001$ . The triangle in the center lists the different mechanisms or processes reported in the literature explaining the use of biodiversity's natural and cultivated elements embedded in agricultural landscapes. The total percentage for articles is above 100% since one article can measure more than one dimension. Values next to icons indicate Pearson's correlation estimated mean value. Linear elements are represented in configuration (e.g., live fences), whereas areal elements are represented in composition (e.g., patches of habitat). comp: composition, conf: configuration, herb: herbaceous, hete: heterogeneity, lu: land use, nat: natural, nd: no data, semin: seminatural.



**Fig. 3.** Landscape complexity effect (estimated mean and 95% confidence intervals) on biodiversity across the significant moderators with the most studied and strongest evidence ( $\geq 10$  articles). Moderators (a to h) and their respective levels (nested labels) are grouped by theme: green, biodiversity; orange, cropping system; blue, landscape; gray, study design. Effects sizes are calculated as Pearson correlations; hence, values  $> 0$  indicate larger biodiversity outcomes in complex than in simple landscapes, and confidence interval values overlapping zero indicates no significant difference between complex and simple landscapes. Numbers in parentheses indicate the number of effect sizes/number of articles with a significance level of  $***P < 0.001$ ,  $**P < 0.01$ , and  $*P < 0.05$ . The dotted line shows the mean overall estimate, and the size of the circles corresponds to the number of effect sizes. comp: composition, conf: configuration, herb: herbaceous, hete: heterogeneity, lu: land use, nat: natural, nd: no data, seminatal: seminatal.

*SI Appendix, Fig. S4*). The importance of the three dimensions is often recognized in the scientific literature when discussing the hypothesis mediating the interaction between landscape complexity and biodiversity (6, 11, 40, 48). Yet landscape complexity is dominantly measured as landscape composition (70% effect sizes and 72% articles; Fig. 2), followed by landscape configuration (15% effect sizes and 27% articles) and landscape heterogeneity (7% effect sizes and 11% articles), a dimension given little focus (62).

The more complex configurations and compositions of agricultural landscapes resulted in significantly higher species richness and abundance for vertebrates, invertebrates, and plants compared to simpler landscapes (Fig. 2). Within these overall trends, our data indicates that pest and pathogen diversity tends to remain statistically similar in complex and simple landscapes (Fig. 2 and *SI Appendix, Fig. S4*). However, both composition complexity and configuration complexity particularly favor pollinators, whereas composition favors natural enemies and configuration favors species of conservation concern and weeds (Fig. 2). Heterogenous landscapes also tend to host more biodiversity than

their simpler counterparts except for pests, pathogens, and abundance; however, evidence remains weak due to the small sample sizes (i.e.,  $< 10$  articles) (Fig. 2).

#### Landscape Complexity Benefits Biodiversity despite Intricate Interactions.

Overall, complex agricultural landscapes host significantly more biodiversity than simpler ones regardless of the dimension (Fig. 3; Pearson's correlation = 0.18,  $P < 0.0001$ ). In our assessment, we tested 16 variables affecting the direction and intensity of the landscape complexity–biodiversity relationship (i.e., moderating effect) through two complementary methods (*SI Appendix*). Half of these variables have a significant moderating effect, including landscape indicator, biodiversity functional group, and biodiversity indicator, which is coherent with previous assessments (45, 63). Biodiversity functional group was the only variable consistently identified as a significant moderator across methods (*SI Appendix, Table S5*), suggesting a very strong moderating effect. Other moderators identified as significant include monitoring length, data quality, taxonomic class, crop commodity group, and crop growth form

and life cycle (*SI Appendix*, Table S5). Despite the many tested moderators, a large portion of the effect sizes variability remains unexplained (>26%, *SI Appendix*).

Other moderators, namely, landscape complexity dimensions, location of biodiversity (above or below ground), measured extent ( $\leq 1$  or  $>1$  km), and management system (high versus low intensity) seem to have a null moderating effect due to the positive, significant, and overlapping intervals across levels (*SI Appendix*, Fig. S8). This suggests that species with both contrasting life histories and foraging ranges benefit from complex landscapes through multiple ecological processes (40, 57, 64).

**Complex Landscapes Host More Beneficial Species for Agriculture and Biodiversity Conservation, yet the Magnitude of the Response Is Taxa Dependent.** Overall, we found that landscape complexity has a large and significant positive effect on functional groups beneficial for agriculture (i.e., pollinators and natural enemies) and species of conservation concern (Fig. 3A). In contrast, the diversity of nonbeneficial species (i.e., pests, pathogens, and weeds) remained nonstatistically different in complex and simple landscapes (Fig. 3A). Complex landscapes significantly increase species richness, abundance, and evenness (Fig. 3B), where abundance is the most assessed biodiversity indicator. Our data show how biodiversity indicators are used differently. For example, articles measuring species abundance often assessed landscape complexity effect on pests and pathogens (21% effect sizes), natural enemies of pests (19% effect sizes), or pollinators (13% effect sizes). On the other hand, species richness was often used to assess the contribution to species conservation (13% effect sizes), which is in line with other studies (65). Finally, measures of evenness (4% effect sizes) were more commonly used to assess natural enemy dynamics (e.g., 41, 62) (*SI Appendix*, Fig. S6). The magnitude of the positive and significant effect across biodiversity indicators, however, varies among the most studied taxa (Fig. 3C). The diversity of taxa with weaker evidence (i.e., <10 articles), such as mammals, amphibians, clitellate, and microorganisms, on the other hand, is statistically similar between complex and simple landscapes (*SI Appendix*, Fig. S8).

In general, maintaining high diversity of beneficial species is central for ecosystem service provisioning, including yield production (52, 66–68). Yet in some cases, larger species diversity might not translate into ecosystem services beneficial for agriculture, such as biological control and pollination (69). Recent research suggests that the understanding of biodiversity-mediated ecosystem services and their interactions is limited, resulting in underestimated and undervalued contributions (70). Regardless of the status of scientific understanding, taking only an ecosystem service-centered approach to managing agricultural landscapes for biodiversity conservation is a slippery and risky path. Often, ecosystem services (e.g., pollination) are provided by extremely few common species responding better to biodiversity-friendly practices (71). Hence, increasing landscape complexity in agricultural lands would most likely improve certain ecosystem services, but most importantly, it can also contribute to conserving threatened or vulnerable species while improving overall system performance through enhanced ecosystem function, resilience, and adaptability under current and future conditions (71).

**Commodity Group and Landscape Context Influence Biodiversity Response.** Biodiversity response to landscape complexity varies across the monitored commodity crop groups, growth form, and life cycle (Fig. 3D and E). The largest positive and significant effects of landscape complexity on biodiversity exist in oil

crops (e.g., canola, cup plant, oilseed rape, olive, and sunflower), mixed commodities (e.g., annual crops and pastures), and cereals (e.g., maize, wheat, and barley) (Fig. 3D). Interestingly, effects are positive and significant in oil crops and biomass, despite the varying pollination requirements. Similarly, we found strong and positive effects on woody/perennial and herbaceous/annual crops (Fig. 3E). These results show that the quality of the resources offered by the crop (e.g., mass flowering or perennial crops) (57, 72–74), the biodiversity pool, and the history in these landscapes (e.g., oil crops occurred in simpler landscapes) (75) jointly influence biodiversity response. For example, landscapes with large seminatural habitats may result in a weak biodiversity response, particularly if those habitats are impoverished or monospecific (e.g., as depicted in Fig. 2, composition) (76). Among the less studied commodities, with landscape complexity effects on biodiversity similar in simple and complex landscapes, we find underconsumed crops vital for human nutrition and high dependency on pollination (e.g., fruits and vegetables) (Fig. 3D and *SI Appendix*, Fig. S8) (77, 78). Further analysis to assess the effect of crop traits (i.e., pollination dependency) was hindered by the often limited and poor description of crop species (*SI Appendix*, Fig. S5). However, a functional analysis could better explain biodiversity's response to landscape complexity (41, 74).

**Biodiversity Positively Responds to Multiple Landscape Dimension Indicators and to Both Linear and Areal Elements.**

We found that each landscape complexity dimension contributes to biodiversity, but when dimensions are combined, effects can be contrasting (*SI Appendix*, Fig. S8). Few effect sizes and articles (i.e., three articles) measured the combined effect of configuration and heterogeneity, resulting in a negative but not significantly different effect (*SI Appendix*, Fig. S8). Slightly more articles (i.e., seven articles) assessed the combined effect of composition and configuration (5% effect sizes, 5% articles), resulting in the largest, positive, and significant effect on biodiversity, although evidence remains weak (*SI Appendix*, Fig. S8).

Overall, we found strong evidence indicating that biodiversity positively and significantly responds to the various landscape indicators used across dimensions (e.g., connectivity, seminatural area, and noncrop area) (Fig. 3F). Still, the differences for land-use evenness and proximity remained statistically similar between complex and simple landscapes, suggesting these are potentially weak indicators to capture effects on biodiversity (Fig. 3F). Among the less studied indicators (<10 articles), we found land-use richness and abundance, as well as aggregation (*SI Appendix*, Fig. S8), as promising indicators for capturing the effect on biodiversity that need further evidence (79, 80); however, some exceptions to the universality of aggregation (i.e., field size) exist (81).

We documented around 90 simple and composed landscape metrics measuring complexity (*SI Appendix*, Fig. S2). However, a large proportion of effect sizes (38%) are measured with metrics capturing composition-related indicators such as percentage of agriculture, percentage of seminatural land, and percentage of arable land (*SI Appendix*, Fig. S3). Connectivity (elements that enable species mobility) and proximity (neighboring measurements from biodiversity-high areas) are both the most measured indicators in the configuration dimension (Fig. 3 and *SI Appendix*, Fig. S3). Regarding metrics, edge length, distance from forest, and percentage hedgerow are the most used (*SI Appendix*, Fig. S3). Landscape heterogeneity is also measured in various ways (*SI Appendix*, Fig. S2). Thirteen articles measured heterogeneity as habitat, land cover, land use, or crop

evenness, whereas only four measured it as land use or crop richness or abundance (*SI Appendix, Fig. S3*). In both cases, differences in biodiversity between simple and complex landscapes are nonstatistically significant, potentially driven by the small sample (*Fig. 3F*). However, field data suggest that crop-type richness plays a more prominent role in positively contributing to biodiversity (74, 80). Heterogeneity at the management system level, such as crop-livestock integration, contributed positively to native species (i.e., birds), although only one study measured this type of heterogeneity (82). Likewise, the role of intraspecific heterogeneity at the landscape level is understudied, with only one study assessing field varietal diversity-pest incidence, suggesting regulation effects (e.g., 83). Despite the large landscape indicators and metric diversity used in the scientific literature, connected landscapes with more seminatural habitats (or less crop area) and varying land use/land cover significantly and consistently benefit biodiversity, although the evidence for heterogeneity at multiple levels (management, land cover, crop, and varieties) remains weak (*Figs. 2 and 3*).

Studies assessing landscape elements separately potentially underestimate landscape complexity effects on biodiversity. Our results indicate that studies considering the effect of both elements, linear and areal, resulted in effect sizes almost double than when measured separately, although only eight articles assessed the combined effect (*SI Appendix, Fig. S8*). Restoring, diversifying, and protecting linear elements (i.e., configuration) in agricultural landscapes could be the most straightforward strategy to foster biodiversity worldwide across production systems, given the small farmland area occupied by linear elements and their positive contributions to production and conservation objectives (84). In tandem, ensuring the quality and maintenance of remanent patches of seminatural habitat, regardless of their size, is also a central strategy to guarantee biodiversity pools to enable species' recolonization, which is, in turn, critical for ecosystem functioning (85).

**Stronger Effects on Biodiversity with Long-Term and High-Quality Data.** The longer the study and the better the quality of the data (i.e., nonoverlapping landscapes), the larger the positive effect of landscape complexity on biodiversity. Longer studies report stronger positive effects (*Fig. 3G*), indicating the potential increase over time of these effects and the importance of including study length as a moderator. In our dataset, 66% of the effect sizes from 108 articles monitored biodiversity for <1 y, 31% effect sizes from 40 articles monitored biodiversity for between 1–2 y, and only 3% effect sizes from 10 articles monitored biodiversity for over 3 y. Thus, landscape complexity effects on biodiversity are grounded in short-span monitoring efforts, hindering the understanding of temporal dynamics in agricultural landscapes and the importance of continued resource availability to satisfy nondomesticated species' needs across their life cycle stages and generations (86).

**Changing Narratives: Attaining Agriculture and Conservation Goals Synergistically.** Our results confirm that agricultural landscapes can host more diversity if year-round, high-quality habitat and resources exist to enable wild biodiversity persistence and mobility across remaining patches of habitat (13, 87, 88). In the megadiverse tropics, campesinos and smallholder-dominated landscapes often produce and maintain landscape complexity with high levels of agricultural and wild diversity (75, 89–91). Yet these farmers and their mixed farming systems, with critical contributions to regional and global nutrition security (3, 75), are often put under pressure by socio-economic drivers (22) and are

being replaced by conventional, high-input monocultures (91). Hence, we consider that at least two paradigm shifts are necessary to achieve the Convention on Biological Diversity (CBD) vision of living in harmony with nature by 2050. First, it is necessary to enhance and value farms and landscapes' multifunctionality and actively manage these for production, biodiversity, human well-being, and overall ecosystem resilience (9, 20, 92). Second, national and international efforts must be better aligned to repurpose perverse incentives or policies supporting unsustainable agriculture (93, 94) and trade currently driving biodiversity loss and land-use change in the tropics (95, 96).

**Time to Act: Complex Agricultural Landscapes for Biodiversity and People.** Although gaining a better understanding of the relationship between landscape complexity and biodiversity is essential (*Table 1*), current scientific evidence is more than enough to act. Three main pragmatic biodiversity-friendly practices have already been put forward for biodiversity conservation in agricultural landscapes: diversifying cropland (heterogeneity), reducing field sizes (configuration), and retaining at least 20% of seminatural habitat per landscape (composition) (19, 97). Some prior assessments identified that biodiversity responds to landscape complexity inconsistently (e.g., 2, 29, 44–47). However, our global and extensive synthesized evidence demonstrates a clear overall pattern: complex landscapes host more biodiversity. This result holds for most taxa, in most environmental contexts, and effects become increasingly positive over time, although key knowledge gaps persist for certain specific taxa, cropping systems, and geographies.

Complexifying agricultural landscapes will demand cross-collaborative efforts at multiple levels (e.g., from local to global), where the roles and voices of farmers already producing in complex landscapes are recognized, valued, and supported. Likewise, a multidisciplinary, collaborative, well-designed, and long-term research agenda for multifunctional agricultural landscapes is urgently needed (e.g., *Table 1*). A fit-to-purpose agenda will enable understanding of the effects of landscape complexity on production (12, 60, 98), the landscape's overall performance (e.g., resilience through phylogenetic diversity and ecosystem services and functions) (50, 99), and the landscape inhabitants' multiple dimensions of human well-being (quality of life, material and relational) (20, 100). More than one decade ago, the need for systemic biodiversity assessments, landscape agronomy, and orchestrated work by agriculture and conservation sectors was already raised (11, 47, 60, 101–104).

## Conclusion

Our study demonstrates that if properly managed, current agricultural landscapes are far from being a vast, empty, and hostile environment for biodiversity. As it stands, agricultural land, the matrix connecting what is left of seminatural habitat, is underplaying a pivotal role in active contribution toward biodiversity conservation objectives. Compared to simplified landscapes, complex agricultural landscapes host significantly more diversity across taxa and functional groups, including beneficial species for agriculture production, ecosystem functioning, resilience, and human well-being. Landscape complexity contributes to complementary ecological processes through three dimensions, namely, composition, configuration, and heterogeneity—and increases in any of these dimensions positively and significantly impact biodiversity. Maintaining and increasing landscape complexity in agricultural landscapes will be central to achieving the CBD 2050 vision of living in harmony with nature. This

**Table 1. Mind the gap: Understanding landscape patterns, biodiversity, and their interactions in agricultural landscapes is also complex**

Systemic	Scope	Quality
<p>Where are the agroecologists? The landscape complexity–biodiversity relationship is dominantly understood from an ecological perspective. This leaves critical knowledge gaps from the production perspective, resulting in the following:</p> <ul style="list-style-type: none"> <li>• Few articles measuring yield or productivity</li> <li>• Half of the effect sizes with unspecified use of inputs (e.g., pesticide, fertilizer, insecticide)</li> <li>• 9% of the articles with unspecified management type (e.g., organic, low intensity)</li> <li>• Rare documentation on complexifying agricultural landscapes' costs, labor requirements or constraints on mechanization, and farm production</li> <li>• General and poor crop descriptions, including their vegetational complexity</li> </ul> <p>The effects of time? The moderating effect of monitoring length is rarely discussed in the literature, yet it seems critical. The overdominance of 1-y studies limits our long-term understanding of biodiversity dynamics in agricultural landscapes.</p> <p>Locally or globally relevant agricultural landscape complexification? Each landscape will have different starting points, thresholds, and a plethora of options for designing or improving landscape complexity levels. For this reason, engaging landscape inhabitants to mobilize their knowledge/desires is vital for identifying viable and durable interventions that will benefit people and biodiversity.</p>	<p>Crops other than cereals? 41% of the articles assessed cereals, whereas critical knowledge gaps on other commodities vital for human health remain understudied.</p> <p>Regions other than high-income countries? 85% of the studies are from research conducted in North America (United States and Canada) and Europe (including England). Megadiverse areas remain heavily understudied.</p> <p>Species other than insects? 73% of the studies are on insects, leaving critical knowledge gaps in other groups (e.g., fungi are absent in the landscape complexity–biodiversity research) and even multitaxa response.</p> <p>A multidimensional reality? Our data and previous studies show that landscape complexity is multidimensional. However, heterogeneity (62) and the overall multidimensional effect remain poorly understood.</p> <p>Biodiversity as a hypervolume? Species richness and abundance (and most likely evenness, but less discussed in the literature) respond differently to environmental variation (52, 120). Systemic collection of biodiversity indicators will help better understand biodiversity's response to complex landscapes and the ecological drivers behind these responses.</p> <p>More is better? Landscape complexification can also result in conflicts with wildlife in certain contexts (121, 122). Hence, each landscape should consider the specific trade-offs, along with thresholds, and identify viable mitigation strategies to increase synergies among objectives.</p>	<p>To overlap or not? Data autocorrelation from overlapping landscapes is contested (123); however, articles with nonoverlapping landscapes moderate biodiversity responses to landscape complexity. Details matter? Often, species, crop, and landscape metric classification into functional groups was hindered by vague and general descriptions, such as arthropods, agroforestry, and percentage of open space.</p> <p>Superfluous and disparate metrics? We found around 90 distinct metrics; hence, testing and using strong, consistent, universal metrics (124) will improve scientific evidence.</p> <p>Fuzzy or accurate patterns? Landscape complexity assessments depend on the quality of the maps used (i.e., accuracy on the spatial, temporal, and thematic resolutions). Although it was out of the scope of our study to analyze the robustness of the maps, wide ranges of methods, resolutions, and accuracies are being used. Hence, evidence may gain from a more systematic land-use/land cover classification (125–127).</p>

Current scientific evidence is enough to act. However, designing and fostering multifunctional and resilient agricultural landscapes for people and nature will need a research agenda with a systemic approach, a broader scope, and better quality. Here we offer a selection of critical points to move landscape complexity–biodiversity research forward; however, this is by no means a comprehensive list.

challenge will require shifting narratives to recognize, value, and foster agriculture multifunctionality and those already contributing to production–conservation objectives, all while supporting an integrative, multidisciplinary, well-designed, system-based, and long-term research agenda to quantify complex agricultural landscape contributions to nature and people.

## Materials and Methods

We searched for peer-reviewed scientific articles estimating the effect of landscape complexity on nondomesticated terrestrial biodiversity. We searched

for relevant articles on Web of Science, Scopus, and Google Scholar between 10 April and 21 July 2021. We searched peer-reviewed articles in English with the following search string combination among terms related to agriculture ("agricultur\*" OR "mosaic landscapes" OR "agro?ecosystem\*" OR "landscape matrix" OR "cultivat\*" OR "farm\*" OR "arable land" OR "mixed landscape\*"), landscape complexity ("landscape complexity" OR "complex landscape" OR "simplif\* landscape" OR "landscape simplify\*"), and biodiversity ("richness" OR "abundance" OR "evenness" OR "densities" OR "species diversity" OR "functional diversity" OR "index" OR "population\*" OR "community" OR "diversity"). We searched the terms in the articles' title, keywords, and abstract. When searching in Google Scholar (21 July 2021), we screened the first 20 pages that the search returned. Additionally, we screened the primary articles included in other

meta-analyses (2, 14, 47, 60, 61, 105) assessing biodiversity-landscape complexity and added these. Some other meta-analyses were excluded since landscape complexity was not mentioned or it was calculated a posteriori (e.g., based on the site location) (e.g., 45, 87) (*SI Appendix, Table S1*).

The search resulted in 614 unique primary peer-reviewed articles. All articles were fully screened and selected if they satisfied our PICOC criteria (106): Our population (P) is any nondomesticated plant or animal in terrestrial ecosystems; our interventions (I) and comparators (C), also referred to as the treatment and control, respectively, include biodiversity indicators in complex and simple landscapes, respectively; outcome (O) measures include biodiversity levels measured as richness, abundance, or other biodiversity indicators (e.g., often evenness or Shannon indicators); and our context (C) includes articles in mixed or mosaic agricultural landscapes and primary articles with observational data from the field. We excluded articles with missing biodiversity information (i.e.,  $R^2$ , mean, standard deviation [SD], standard error [SE], and interquartile range [IQR]), articles using landscape complexity indicators with unclear directionality for biodiversity (e.g., slope steepness), and articles measuring landscape complexity on a radius below 100 m. In total, we entered information from 157 articles that fully satisfied our selection criteria, resulting in 1,134 effect sizes (*SI Appendix* gives meta-analysis workflow and details).

Article screening and data entry followed a systematic and interactive process for consistently applying the inclusion criteria at the article and effect size level, always verified by at least two coauthors. We further classified these effect sizes as high quality if the information was complete and came from nonoverlapping landscapes, medium quality if at least one of the landscapes overlapped, low quality if information on the minimum distance between landscapes was lacking, and extremely low quality if sample sizes were below four landscapes or if the year of data collection was missing. Landscape metrics, main studied crops, and biodiversity species were also further classified. Landscape metrics were grouped into indicators and dimensions borrowing from landscape ecology research. We grouped crops into commodity crops and further reclassified these, when information was available, into crop growth form and life cycle (perennial/annual and herbaceous/woody). We retrieved from the original research the functional group of the studied species and assigned, when possible, the taxonomic class and order (*SI Appendix* gives reclassification details).

We included biodiversity indicators that took place in predefined landscapes (e.g., simple or complex) or in a gradient of landscape complexity (e.g., distance to seminatural habitat). For predefined landscape data, we calculated the standardized mean difference or Hedges'  $g$  (107) by pairing the mean, variance values, and sample sizes between study control (i.e., simple landscapes) and treatment (i.e., complex landscapes); then, we converted Hedges'  $g$  to Fisher's  $z$  values (107). For the data in a gradient of landscape complexity, we converted linear Pearson product-moment correlation coefficient  $r$  values from landscape complexity and biodiversity associations to the effect measure Fisher's  $z$  values (ZCOR escalc function metaphor R package) (108). In both cases, positive Fisher's  $z$  values indicate higher biodiversity in complex over simple landscapes, whereas negative values indicate the opposite (*SI Appendix, Table S3*).

We used the metafor R package and a three-level meta-analytic random-effects model for dealing with effect size dependency since multiple effect sizes can come from the same article (108–111). Confidence intervals for the overall mean effects in each model uses the  $t$  distribution, and model fitting was through the restricted maximum-likelihood method (108). To calculate the statistics of individual levels of moderators mediating landscape complexity effects on biodiversity, we used an F-distribution omnibus test that adjusts degrees of freedom based on the total number of moderators' levels (i.e., coefficients) (109). We pursue single and multiple mixed-effects metaregression models due to the low effect size variability, explained by a

random model in the first level—sampling variance of 11.96% against other levels (second level within-article variance of 51.91%, and the third level between-article variance of 36.13%) (107, 109, 112). We tried to explain variance through moderators potentially having strong effects across articles, such as crop commodity group, crop growth form and life cycle, biodiversity functional group, biodiversity indicator, biodiversity groups (e.g., arthropods or vertebrates), biodiversity taxonomic class, landscape complexity indicators, continent, extent of analysis (e.g., <1 km), measured landscape element (e.g., linear or areal), crop management, and data quality. The true effect of each moderator on the association between landscape complexity and biodiversity was tested through single and multiple-moderator meta-analytical models, which test linear relationships (109). We then extended the meta-analytical model to include all significant moderators and further assess the existence of confounding effects (*SI Appendix, Table S5*).

Determining which moderators are the most important is not straightforward and is an error-prone task (109). Hence, we also conducted a global sensitivity analysis to test moderators' nonlinear relationships (e.g., combined contribution), explaining effect size variability (113, 114). A global sensitivity analysis (GSA) was used to rank moderator importance with randomForest (115) and then visualize higher-level interactions that result in larger or smaller effect size values through a classification and regression tree (116). GSA is grounded in bootstrapping algorithms that split data into training and test groups and iteratively and randomly test the importance of each moderator when growing the multiple trees. Both analyses (i.e., testing linear and nonlinear relationships) indicate that a great proportion of the variance remains unexplained with the tested moderators (*SI Appendix*).

We tested the effect of outliers or low-quality effect sizes on our results by running the meta-analytical model without these (*SI Appendix, Table S6*). We identified and removed outliers, such as those with Cook's distance values greater than the  $\chi^2$  distribution with  $df = (k + 1)$  and at  $\alpha = 0.005$  (108), resulting in persisting statistical significance and similar estimates. Similarly, meta-analysis results were not affected when removing extremely low- and low-quality data (*SI Appendix, Table S6*).

Additionally, we tested for publication bias. Although solid methods for assessing publication bias on continuous data are still under development, traditional methods such as the Fail Safe number are heavily criticized (117, 118). Therefore, we explored three alternative methods: funnel plots, Eggers linear regression test adapted method using the squared root of effect sizes' SE as the moderator (119), and the inverse of sample size as a predictor (118) in a mixed-effects metaregression model (*SI Appendix, Fig. S9*). Across the three methods, we found no evidence of publication bias.

**Data, Materials, and Software Availability.** Data are available for download from the Harvard Dataverse (128). All other details and analyses are included in the article and/or *SI Appendix*.

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