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Biodiversity and human well-being trade-offs and synergies in villages

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Europe's rural landscapes, shaped over millennia, support high biodiversity but often have lower living standards than urban areas, potentially leading to social and environmental injustice. Here we studied biodiversity and socioeconomic settings in Central and Eastern European villages across landscape complexity and urbanization gradients. We surveyed the biodiversity of villages by sampling nine taxonomic groups, including plants, arthropods and birds. We found 15% lower multitrophic diversity in villages in agricultural than in forest-dominated landscapes. City vicinity enhanced human well-being (estimated with Better Life Index) but did not affect biodiversity despite a larger human footprint. In agglomerated villages in forest-dominated landscapes, biodiversity was high, with higher Better Life Index and footprint metrics, suggesting associations between biodiversity, socioeconomic status and, thus, environmental injustice. Our results show the high socioecological value of maintaining or restoring landscape complexity around villages and their green infrastructure, requiring top-down incentives and bottom-up initiatives.

The ecological characteristics and biodiversity of rural villages are largely understudied compared with urban and agricultural systems. This is despite the fact that villages may potentially function as biodiversity refuges in human-dominated landscapes[1,2]. A critical question is whether villages situated in simplified landscapes—characterized by a low share of semi-natural habitats[3]—serve as rescue islands and surrogate habitats for biodiversity threatened by agricultural intensification, given their typically large gardens and higher portions of green spaces[4]. Alternatively, is village biodiversity heavily constrained by infiltrating agricultural impacts, such as pesticide use and landscape-scale homogenization, due to the relatively small size of these settlements[5]? For example, the study by Rosin et al.[6] on bird populations in 30 Polish villages revealed that villages support a greater number of bird individuals and species than do forests, agricultural fields or towns. In addition, Hanspach et al.[1] classified 30 Romanian villages on the basis of biophysical and sociodemographic variables and found the highest bird richness in forest-type villages, the highest plant richness in pasture-type villages, and high butterfly richness in arable-dominated and pasture-dominated villages.

While evidence shows that contact with nature positively impacts well-being[7], the specific role of biodiversity itself as a driver remains debated[8]. A closely related question is whether the livelihoods or well-being of village residents is enhanced in complex landscapes with a high share of natural and semi-natural habitats[9] given that such environments may offer cultural ecosystem services (for example, recreational opportunities and experiences of nature)[10] as well as

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Table 1 | Demography, village structure, landscape structure (in 2,000 m buffer) and soil quality and agricultural productivity (in 2,000 m buffer) of villages in agglomeration of mid-sized cities versus far from cities and in agricultural versus forest-dominated landscapes (mean ± 95% confidence interval) (n = 64 villages)

	Agglomeration		Far from city		Estimate ± 95% CI		R^2_m/R^2_c
	Agricultural	Forest-dominated	Agricultural	Forest-dominated	Agglomeration	Landscape simplification	
Demography							
Population size	1,146±359	1,176±472	1,053±359	984±431	–	–	0.00/0.45
Village structure							
Elevation (m)	220±71	278±49	210±46	252±47	–	−0.09±0.04***	0.04/0.89
Village area (km^2)	2.36±1.16	2.39±1.18	2.64±1.29	2.37±1.16	–	–	0.00/0.52
Normalized difference vegetation index	0.51±0.02	0.55±0.02	0.52±0.02	0.56±0.02	–	−0.04±0.02***	0.17/0.60
Sealed area (%)	17.3±3.5	15.2±2.7	13.4±2.4	12.1±2.5	3.48±2.33**	–	0.08/0.38
Edge–centre distance (m)	657±153	615±176	679±131	612±149	–	–	0.00/0.12
Landscape structure							
Agricultural area (%)	73.7±5.8	27.9±8.4	73.1±7.0	32.2±8.8	–	43.40±5.71***	0.65/0.82
Forest area (%)	5.9±3.6	41.4±5.9	7.2±5.4	40.6±6.4	–	−34.51±3.30***	0.71/0.89
Distance to city (km)	9.7±1.3	10.6±2.3	19.9±3.0	20.2±4.2	−9.88±2.29***	–	0.41/0.64
Soil quality and productivity							
Soil organic content (t ha^{-1})	44.4±2.3	44.6±2.7	44.2±2.1	45.2±2.5	–	–	0.00/0.57
Productivity index	6.27±0.51	5.40±0.30	6.21±0.48	5.40±1.19	–	0.84±0.44***	0.17/0.23

Effects of agglomeration (reference: far from city) and landscape simplification (reference: forest-dominated) are shown as effect estimates ± 95% CI from general linear mixed-effects models (GLMMs). Population size, village area and edge–centre distance variables were log-transformed before analysis. R^2_m, marginal R^2; R^2_c, conditional R^2; –, effect was discarded from the minimal adequate model during model simplification (interactions between agglomeration and landscape simplification effects were discarded in all models). Significance levels based on GLMM outputs (two-sided t test): **P < 0.01; ***P < 0.001.

improved air quality[11]. For example, a Europe-wide study demonstrated a positive correlation between species diversity and life satisfaction, an effect comparable to that of income, which was attributed to the multisensory experiences provided by birds and the beneficial landscape properties that promote both avian diversity and human well-being[12]. Likewise, the presence of pollinators has been shown to enhance ecosystem health and contribute to human well-being by supporting food production[13] and fostering diverse, thriving and resilient environments that improve overall quality of life[14]. Furthermore, a nationwide study in Germany found a positive association between plant and bird species diversity and mental health, even after accounting for socioeconomic factors[15]. These findings underscore the nuanced connections between nature, biodiversity and human well-being. However, identifying the specific characteristics that drive these benefits—such as the sensory experiences provided by certain species—is essential for understanding how biodiversity influences different aspects of human health and happiness[16].

In addressing challenges related to welfare, quality of life and rural depopulation, the recent Central and Eastern European member states of the European Union (EU) still retain relatively extensive areas of species-rich farmland[17]. Despite these valuable resources, they continue to face socioeconomic difficulties and the ongoing threat of biodiversity loss. After World War II, agricultural intensification was boosted globally due to technological advancements, deforestation and urbanization to support growing human populations[18]. This process resulted in large-scale and widespread landscape homogenization, especially in the Eastern Bloc of Europe, where wetlands and natural grasslands were converted into croplands and small fields were consolidated into larger ones to enhance production efficiency[19]. Consequently, most rural settlements, including villages, became embedded within intensively managed and simplified agricultural landscapes, with largely unexplored implications for both their biodiversity and socioeconomic conditions.

During the communist era in the Eastern Bloc, urban sprawl led to the merging of several villages into nearby cities. Nevertheless, most villages retained their traditional rural character, with semi-subsistence farming practices that included fruit orchards, vegetable gardens and small-scale animal husbandry. However, the collapse of the communist system and the transition to capitalism brought substantial lifestyle changes. Many villagers, particularly those living in city agglomerations, abandoned backyard farming and livestock keeping[20], leading to a notable transformation in the demographic composition of these satellite villages[21]. Therefore, the proximity of villages to cities—which serve as economic, cultural and knowledge hubs—strongly influences the lifestyle of village residents, who benefit from the cultural and financial opportunities provided by nearby cities. This shift may also contribute to growing environmental health inequalities, which are more pronounced in the former Central and Eastern European EU member states compared with their Western counterparts[22]. However, villages near cities may experience reduced wild biodiversity due to increased traffic, intensified land use and higher human activity levels (for example, infrastructure development, increased light and noise pollution, and higher levels of resource consumption). In addition, these peri-urban villages often have higher levels of soil sealing—where impermeable artificial materials such as concrete or asphalt replace natural soil—as well as modern housing development and intensified lawn management, frequently featuring exotic ornamental plant species compared with villages located farther from cities[2,6,23]. For example, a study conducted in Poland found that village modernization dramatically reduces the abundance of birds nesting on buildings[2], highlighting the ecological consequences of these transformations.

By exploring these dynamics, this study aims to bridge the gap between biodiversity conservation and socioeconomic advancement, addressing pressing challenges such as biodiversity loss, urbanization and the interactions between human well-being and ecological sustainability in Central and Eastern European villages. Understanding these

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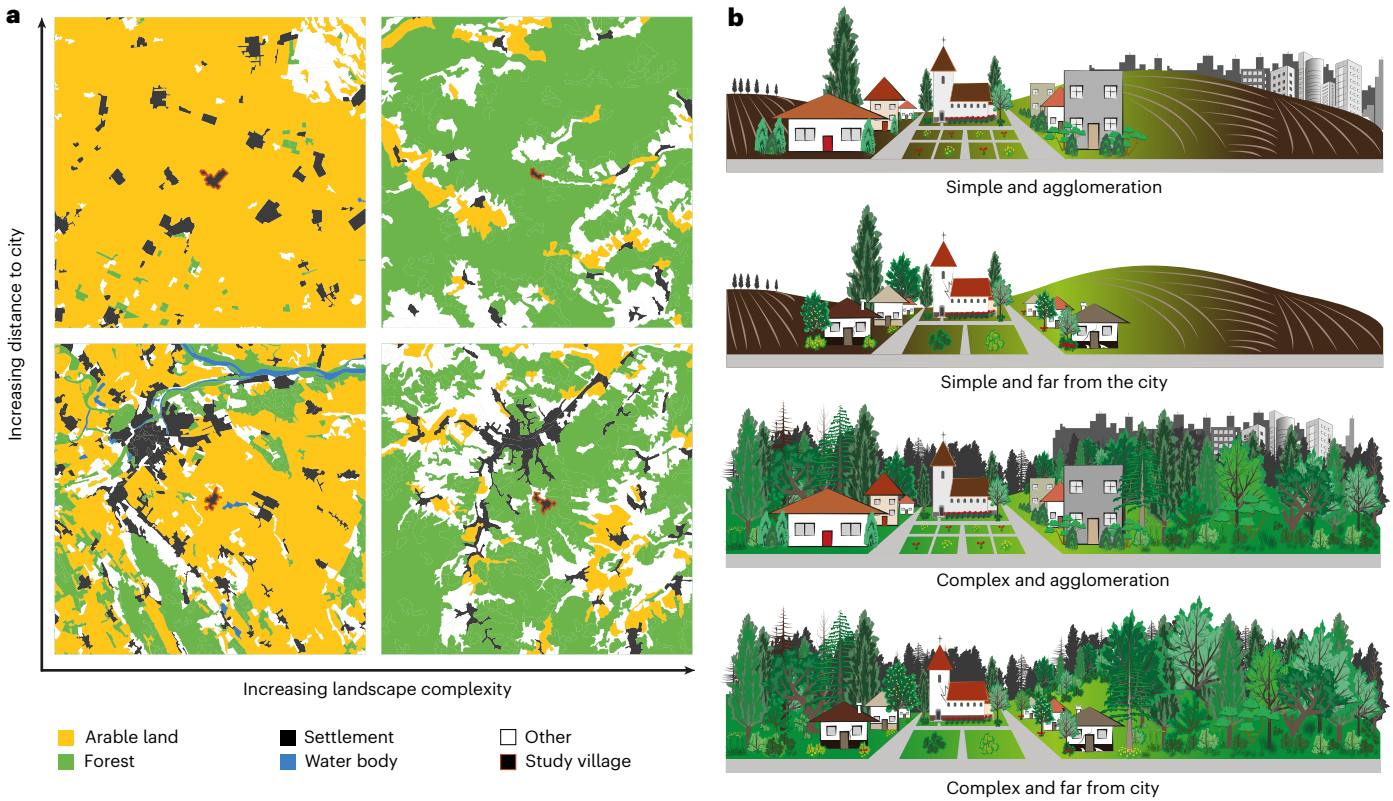

Fig. 1 | Study villages across landscape types and urban proximity gradients. **a**,**b**, Map view (**a**) and schematic view (**b**) of example study villages situated in contrasting landscapes for studying landscape simplification (agricultural versus forest-dominated landscapes) and agglomeration effects (close to a mid-sized city in agglomeration versus far from mid-sized cities), that is, village in agricultural landscape in agglomeration (**a**, bottom left; **b**, top), village in agricultural landscape far from city (**a**, upper left; **b**, second from top), village in forest-dominated landscape in agglomeration (**a**, bottom right; **b**, third from top), village in forest-dominated landscape far from city (**a**, upper right; **b**, bottom). Villages are outlined in red and are in the middle of each map. Other, mainly grassland and wetland. Map in **a** based on the CORINE Land Cover 2018[55].

interactions is vital for informing policy decisions and promoting sustainable development in these often-overlooked yet ecologically and socially important rural landscapes. The historically divergent trajectory of these villages provides an opportunity to investigate the interactive effects of landscape simplification and proximity to cities (hereafter referred to as the agglomeration effect) on both biodiversity of villages and the socioeconomic conditions of village residents. To achieve this, we selected sets of four villages in Hungary and Romania, situated around 16 mid-sized cities. Within each set, two villages were located within city agglomerations, and two were located farther from cities, and were further categorized on the basis of landscape complexity: two being in agricultural landscapes while the other two were in forest-dominated landscapes (that is, 16 cities × 4 villages = 64 villages in total; Table 1, Fig. 1, Extended Data Fig. 1 and Methods). All selected villages have historical roots dating back to the medieval period or even earlier to the Roman era, making them representative of small settlements in these former Eastern Bloc countries. Notably, these still have a relatively high share of rural populations compared with older EU member states and the United Kingdom (2022 data: Hungary 27%; Romania 46%; EU15, including the United Kingdom, 20% (https://www.macrotrends.net/)), indicating the continued importance of rural communities in these regions.

In 2022, we measured the multitrophic diversity by sampling vascular plants, seven arthropod groups (carabids, isopods, spiders, true bugs, and cavity-nesting bees, wasps and their parasitoids) and birds in public grassy green spaces at village edges and centres (Methods). We hypothesized that multitrophic diversity would be (1) lower in villages embedded within agricultural landscapes compared with those in forest-dominated landscapes and (2) lower in villages situated within city agglomerations compared with those farther from cities. In the studied villages, we also aimed to explore how biodiversity patterns change from village edges to village centres, hypothesizing (3) stronger edge effects (that is, higher multitrophic diversity at village edges) in forest-dominated versus agricultural landscapes due to spillover from the surrounding landscape, and in villages farther from cities compared with those in city agglomerations due to the weaker urbanization pressures.

To ensure comparability across our study sites, we confirmed that villages within each of the two landscape-scale design categories (agricultural versus forest-dominated landscapes; agglomeration versus far from city) did not differ significantly in terms of human population size, village area, soil organic content or the distance of biodiversity survey transects from the village edge to the centre (Methods and Table 1). However, key landscape characteristics varied: villages in agricultural landscapes had more than twice the proportion of agricultural land and approximately four times less semi-natural forest cover in the surrounding landscapes than villages in forest-dominated landscapes (Table 1). They also had 7% less green space, as indicated by the normalized difference vegetation index (Table 1). Villages in complex landscapes were situated at slightly higher elevations, between 200 and 300 m above sea level, and had a lower agricultural productivity index than villages in simple landscapes (Table 1). Villages outside city agglomerations were on average twice as far from the nearest focal city as those within city agglomerations (Table 1). By contrast, agglomerated villages had over 25% more sealed surfaces, such as buildings and asphalt roads, than villages farther from cities (Table 1).

To complement our biodiversity assessment, we collected socioeconomic data (only for Hungarian villages, $n = 44$, due to data

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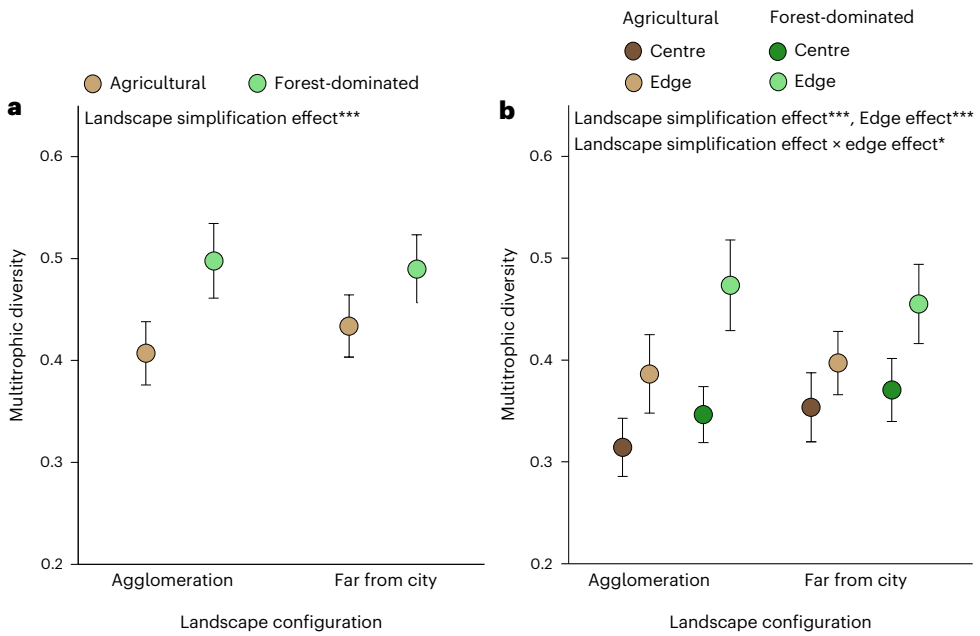

Fig. 2 | Effects of agglomeration and landscape simplification on multitrophic diversity. a, In villages. **b**, At transect level, including edge effects. Error bars represent mean ± 95% CI ($n = 64$ villages for **a**; $n = 128$ transects for **b**). Edge effect, village centre versus village edge; landscape simplification effect, agricultural versus forest-dominated landscapes; agglomeration effect, agglomerations versus far from cities (not shown as it was discarded from the models). Significance levels (two-sided t test): $^{*}P < 0.05$; $^{***}P < 0.001$.

deficiency in Romania) to calculate the Better Life Index (BLI) following the approach developed by the Organisation for Economic Co-operation and Development (OECD[24]; Methods). This composite index captures the multidimensional nature of human well-being, incorporating both material conditions and quality-of-life indicators[25]. In addition, for all study villages ($n = 64$), we calculated the Human Footprint Index (HFI[26]), which quantifies human pressures, including land transformation, population density, human access by transportation, and infrastructure. We tested the hypotheses (4) that the BLI would be higher in villages within agglomerations due to better access to social infrastructure (for example, schools, health-care facilities, recreation amenities, and administrative and commercial services) and in forest-dominated landscapes due to a healthier environment (for example, lower pollution levels and better access to green spaces). We also hypothesized that (5) the HFI would be higher in agglomerated villages, especially those embedded in agricultural landscapes, due to the more extensive urban and agricultural development. Finally, on the basis of our data, we examined the relationship between biodiversity and socioeconomic factors, hypothesizing that (6) higher BLI would be associated with higher HFI, reflecting stronger village development but potentially leading to lower multitrophic diversity.

Results

Biodiversity patterns in villages

The multitrophic diversity, based on 1,164 species of the 9 studied taxonomic groups—including plants (406 species), arthropods (676 species from 72,639 sampled individuals of carabids, isopods, spiders, true bugs, and cavity-nesting bees, wasps and their parasitoids) and birds (82 species)—exhibited clear effects of landscape simplification, with an average of 15% lower diversity in villages within agricultural compared with forest-dominated landscapes (marginal and conditional R^2 values: $R^2_m = 0.20$; $R^2_c = 0.51$; Fig. 2a and Extended Data Table 1). When analysing the species richness of individual taxonomic groups, a positive agglomeration effect was observed only for plants, due to the presence of more ruderal species (that is, plants that thrive in disturbed environments, such as roadsides, construction sites or abandoned fields; Extended Data Fig. 2). By contrast, the agglomeration effect was negative for isopods in agricultural landscapes but positive in forest-dominated landscapes. Landscape simplification significantly decreased the species richness of plants and spiders. This negative effect was also marginally significant for the richness of cavity-nesting bees, wasps and their parasitoids, and birds.

The significant interaction between edge effect and landscape simplification effect on multitrophic diversity showed that the edge effect was more pronounced in forest-dominated landscapes, with a 20% decline of multitrophic diversity from edges to centres, compared with a 15% decline in agricultural landscapes ($R^2_m = 0.29$; $R^2_c = 0.49$; Fig. 2b and Extended Data Table 2). Further analysis of the individual taxonomic groups indicated significant edge effects, with higher species richness in edges than in centres, particularly for plants, carabids, spiders, true bugs and wasps; these edge effects were more substantial in forest-dominated landscapes for plants and wasps (Extended Data Fig. 3). In addition, we found an interaction between agglomeration and edge effects for true bugs and birds, indicating more pronounced edge effects in the agglomerated villages, where species richness was generally lower in village centres.

Linking human well-being and multitrophic diversity

Our analysis revealed that the BLI was 27% higher in villages located in city agglomerations compared with those farther from cities, and 14% higher in villages situated in forest-dominated landscapes than in villages in agricultural landscapes ($R^2_m = 0.27$; $R^2_c = 0.60$; Fig. 3a; Extended Data Table 1). Analysing the individual components of the BLI, we found that residents of villages in agglomerations (versus residents in villages farther from cities) had higher per capita income, better-equipped homes, a higher proportion of secondary and higher education, and a higher level of civic engagement, as measured by voting in elections (Extended Data Table 3). Moreover, village residents in forest-dominated versus agricultural landscapes had better-equipped houses and enjoyed cleaner air quality, as indicated by lower levels of inhalable particulate matter and nitrogen dioxide.

The HFI was similarly high in agglomerated villages regardless of whether they were located in agricultural or forest-dominated landscapes. However, a significant interaction between agglomeration and

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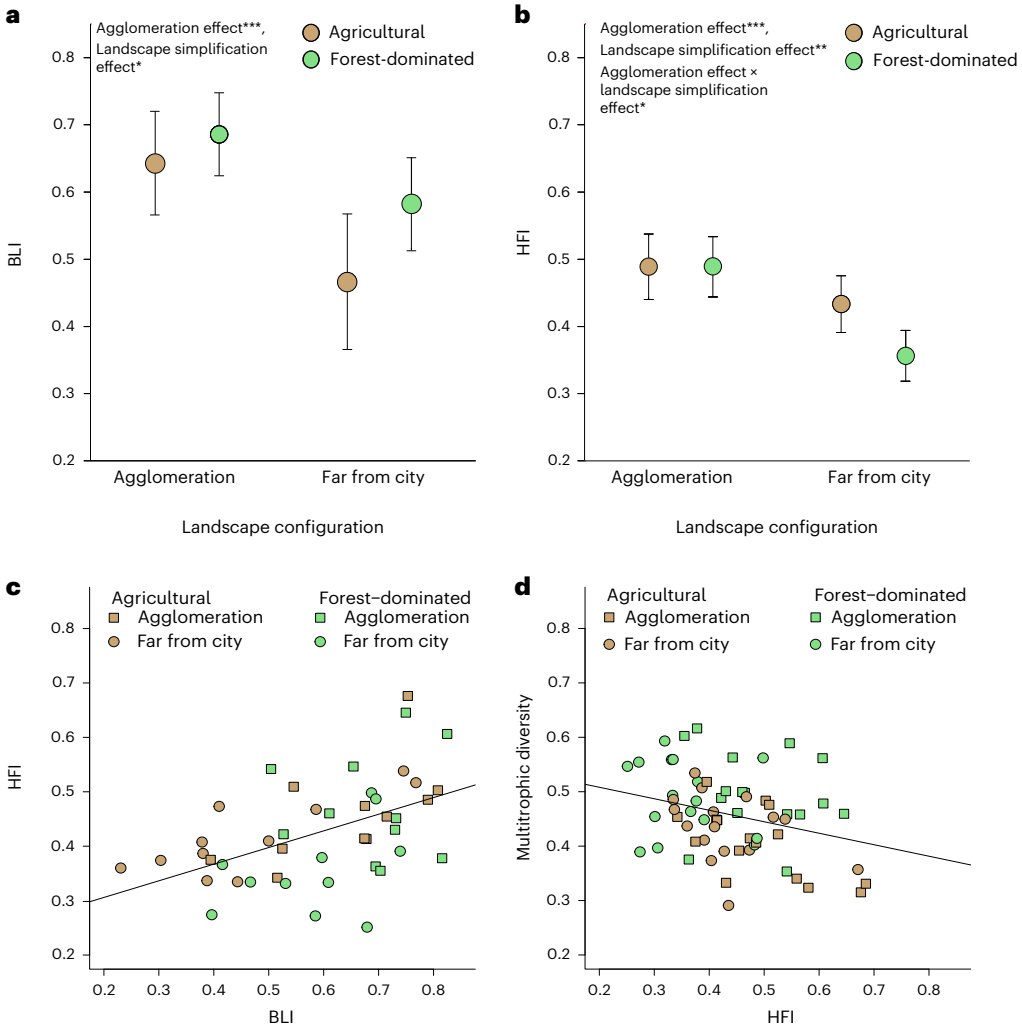

Fig. 3 | Impact of agglomeration and landscape on well-being, footprint and diversity. a,**b**, Effects of agglomeration and landscape simplification on BLI (**a**) and HFI (**b**) in villages. **c**,**d**, Relationships between BLI and HFI (**c**) and between HFI and multitrophic diversity (**d**) in villages. Bars represent mean ± 95% CI (n = 44 villages for **a**; n = 64 villages for **b**). Lines represent significant fitted regression lines (n = 44 villages for **c**; n = 64 villages for **d**). Significance levels (two-sided t test): *P < 0.05; **P < 0.01; ***P < 0.001.

landscape simplification emerged: in agricultural landscapes, villages farther from cities exhibited an HFI that was 11% lower than in agglomerated villages, whereas in forest-dominated landscapes, this difference was 27% (R^2_m = 0.27; R^2_c = 0.49; Fig. 3b; Extended Data Table 1).

Further analysis of the relationship between BLI and HFI revealed that doubling the BLI from 0.4 to 0.8 resulted in a 33% increase in HFI (effect size mean ± 95% CI 0.30 ± 0.16; P < 0.001; R^2_m = 0.24; R^2_c = 0.53; Fig. 3c). By investigating the relationship between HFI and multitrophic diversity, we found evidence of a trade-off: doubling the HFI from 0.3 to 0.6 resulted in a 13% decline in multitrophic diversity (effect size mean ± 95% CI −0.19 ± 0.16; P = 0.025; R^2_m = 0.06; R^2_c = 0.50; Fig. 3d). However, there was no significant direct effect of BLI on multitrophic diversity (effect size mean ± 95% CI −0.04 ± 0.12; P = 0.519; R^2_m = 0.01; R^2_c = 0.44; Extended Data Fig. 4). When we included the two main design variables—landscape simplification and agglomeration effect—as fixed instead of random factors, while considering all two-way interactions, we found that HFI continued to increase significantly with BLI, maintaining a similar effect size after model simplification (Extended Data Table 4). The interaction effect between landscape simplification and agglomeration on HFI was also consistent with the model excluding BLI, as illustrated in Fig. 3b. Furthermore, our analysis revealed that multitrophic diversity significantly decreased with increasing HFI, indicating a persistent trade-off independent of the effects of landscape simplification. Notably, villages in forest-dominated landscapes consistently supported significantly higher multitrophic diversity than those with agricultural landscapes (Extended Data Table 4), as shown in Fig. 2a.

Discussion

Biodiversity patterns in villages

While it is widely recognized that land-use and land-cover changes diminish and homogenize biodiversity, research specifically focusing on villages at the urban–rural interface remains limited. Our study conducted a multitaxa biodiversity analysis across 64 villages, structured according to two key landscape variables: landscape composition (agricultural landscapes versus forest-dominated landscapes) and landscape configuration (agglomerated villages versus those located farther from cities). Although responses varied among taxa, our findings indicate that multitrophic biodiversity was significantly influenced by landscape complexity, with higher biodiversity levels observed in forest-dominated landscapes. This suggests that the landscape-wide species pool plays a crucial role in shaping village biodiversity[27]. By contrast, the proximity to cities did not significantly determine the species numbers of most individual taxa, nor did it affect multitrophic diversity, suggesting that factors other than city proximity play a greater role in shaping the biodiversity of villages.

Overall, biodiversity was higher at village edges and declined towards village centres, with this reduction being more pronounced in forest-dominated landscapes (20% decline) than in agricultural landscapes (15%). This pattern is probably due to the spillover effect, where a richer landscape-wide species pool in forest-dominated landscapes helps buffer local biodiversity loss[27]. Furthermore, the more intense human land use in village centres, irrespective of the surrounding landscape, led to more homogenized and impoverished flora and fauna. This pattern, previously documented in urban ecological studies in cities[28,29], was also evident in villages, despite the relatively short distances between village edges and centres. Nevertheless, creating new green infrastructures, especially in village centres, holds a great potential for restoring biodiversity in villages. This is particularly relevant in agglomerated villages, where the proportion of sealed areas is often higher. Increasing green spaces in these areas could help counteract biodiversity loss and support ecological resilience.

Linking human well-being and multitrophic diversity

We found a positive correlation between the BLI and higher HFI, both of which were more pronounced in agglomerated villages. This pattern is reflected in the greater degree of soil sealing[30] and the more intensive management of both public and private green spaces in these villages compared with those located farther from cities (personal observation by authors). While one might expect a higher HFI in agricultural versus forest-dominated landscapes due to more intensive agricultural activities, this difference was apparent only in villages far from cities. This suggests that the agglomeration effect may override the effect of landscape simplification.

Our analyses confirm the robustness of this relationship, showing that HFI consistently increases with BLI, even when controlling for key design variables in the analyses (Extended Data Table 4). This finding is particularly interesting as it challenges the assumption that rural or remote areas inherently maintain lower environmental footprints regardless of improvements in living standards. Instead, it suggests that efforts to enhance quality of life probably come at the cost of environmental sustainability[31], even in remote villages situated within forest-dominated landscapes where the HFI is typically lower.

We also found a negative effect of HFI on multitrophic diversity, highlighting a clear trade-off between human footprint and biodiversity[32]. Our multitrophic biodiversity model showed that while an increasing HFI negatively affected multitrophic biodiversity, villages in forest-dominated landscapes maintained higher biodiversity levels compared with those in agricultural landscapes (Extended Data Table 4 and Fig. 2a). This suggests that, although increasing HFI can harm biodiversity—even in forest-dominated landscapes—these areas exhibit a buffering effect due to their higher ecological and functional complexity.

Nevertheless, landscape simplification directly reduced multitrophic diversity; however, it remained relatively high in agglomerated villages within forest-dominated landscapes. This indicates that landscape complexity can mitigate the trade-off between socioeconomic advancement and biodiversity. Notably, although agglomerated villages within forest-dominated landscapes exhibited the highest BLI and correspondingly high HFI, they also had the highest multitrophic diversity, pointing to an environmental injustice. This result is probably due to the substantial species pool and greater species diversity still present in these areas[27]. Thus, we found an indirect evidence supporting the 'luxury effect', which describes a positive association between socioeconomic status and biodiversity[33]. However, in this case, the luxury effect does not appear to be driven by wealthier residents actively promoting biodiversity; instead, it probably reflects the common phenomenon of individuals relocating to greener, more natural areas within agglomerations, which in turn enhances individual well-being[34]. Further, villages situated in agricultural landscapes consistently showed lower biodiversity, whether inside or outside agglomerations. This underlines the critical role of landscape simplification as a key determinant of biodiversity in villages.

Approaches to sustainable village management

Our findings highlight that sustainable village management requires different priorities depending on landscape context, and these distinctions should be incorporated in rural development plans and policies[35]. In agglomerated villages, where development pressure is typically more intense than in villages farther from cities, future development should minimize soil sealing and reduce intensive green infrastructure management to mitigate further biodiversity loss. By contrast, for villages in forest-dominated landscapes, efforts should focus on limiting agricultural intensification and expansion to preserve biodiversity. For agglomerated villages surrounded by forest-dominated landscapes, conservation strategies should emphasize preserving semi-natural habitats and protecting their biodiversity around the settlements.

Furthermore, our findings indicate that the edge effect was more pronounced in forest-dominated landscapes than in agricultural ones, with a steeper decline in biodiversity from the village edge to the centre, starting from a higher baseline at the edges of forest-dominated landscapes. This suggests that enhancing landscape connectivity could be particularly advantageous in forest-dominated landscapes, where mitigating edge effects may result in greater biodiversity benefits. By contrast, in agricultural landscapes, active management is required to increase and improve village green infrastructure, particularly in village centres. These interior areas offer the most important potential for habitat creation or improvement for biodiversity enhancement, compared with the edges, where biodiversity is already relatively high[36]. Importantly, these improvements can also positively impact human well-being by improving the BLI[34,37]. Within villages, local residents and municipal authorities can play crucial roles in biodiversity conservation, whereas landowners, such as farmers and foresters, are the primarily responsible stakeholders in the surrounding landscapes. We propose that these conservation efforts within and outside villages can and should be pursued in parallel to maximize biodiversity conservation outcomes. To facilitate these positive changes in public and private green areas, a combination of top-down (policy-driven) and bottom-up (community-driven, that is, engagements of non-governmental organizations or local stakeholders) initiatives is needed—approaches that are currently nearly absent in the study areas. For example, new policies could regulate the development of village interior areas by restricting soil sealing in unbuilt spaces and encouraging residents to adopt low-intensity, nature-friendly management of their gardens and the areas in front of their houses. In addition, biodiversity-focused management practices such as urban tall-grass meadows, species-rich road verges and pollinator habitats—which are increasingly common in Western Europe and are now emerging in Central and Eastern Europe[38], as exemplified by the 'Wildflower Budapest' project in Hungary[39]—could be more widely implemented. Top-down policies could include incentives for sustainable agriculture, restoration projects for native habitats and village greening programmes, while bottom-up efforts might involve local non-governmental organizations engaging communities to promote biodiversity-friendly practices, such as using local seed mixtures to enhance green spaces, and raise awareness. Specifically, village-focused initiatives could support preserving traditional landscaping practices and local biodiversity-friendly farming and forestry techniques, which have long played a role in rural biodiversity conservation.

Our research highlights the urgent need for action to improve green infrastructure in villages. There is a growing body of evidence on the effectiveness of conservation strategies such as uncut grassland refuge strips and wildflower plantings in urban areas[39,40]. Similar initiatives should be tested in smaller settlements, particularly in terms of their effectiveness in spatial and temporal contexts[41], as villages appear to support richer species pools than urban areas[4]. Given that our study

highlights the important role of organism spillover between different habitats—shown by the dominant role of landscape complexity and edge–centre contrasts—as well as the strong interconnections between human well-being, human environmental footprint and biodiversity, we recommend that the EU Rural Development Strategy and related policies shift towards a stronger focus on biodiversity management, ensuring more effective conservation actions and landscape improvements both in and around villages[35].

Direction of future research

Although our study successfully captured notable biodiversity patterns across multiple taxonomic groups in numerous villages distributed in two countries, it is essential to acknowledge the methodological constraints imposed by the limited sampling effort per village. Each village was represented by two 100-m transects, which, while sufficient for identifying clear patterns, may not fully represent the ecological complexity of the villages. Future research should prioritize more intensive sampling efforts per site to better capture the full ecological diversity. In addition, it should extend beyond species diversity assessments, investigating a broad range of ecosystem services, studying other underrated species groups and considering the role of seasonality, given that biodiversity and people–biodiversity relationships may fluctuate with seasonal changes[42]. A major knowledge gap that remains is the need to investigate orthogonal gradients of landscape composition and configuration around villages; this would help identify critical ecological thresholds that could support more effective biodiversity conservation strategies[43]. In addition, it is essential to explore the interactive effects of other global change drivers on biodiversity, such as pollution related to agriculture and urbanization—including pesticides, transportation and heating pollutants, as well as light and noise pollution[44,45]—and, last but not least, climate change, particularly in relation to the urban heat island effect and the temperature differences between villages in warmer versus colder regions[46]. Another important research topic is the contrasting demographic trends driven by urbanization—notably, the increasing human population density in agglomerations coupled with the ongoing rural depopulation in villages far from cities[47]. Finally, given that local inhabitants are the most critical stakeholders in villages, future studies should investigate the social dimensions of biodiversity conservation. Exploring the potential for environmentally friendly behaviour changes[48] is key to achieving transformative change towards a more biodiverse and livable rural environment[49] and should be examined along landscape gradients.

Methods

Village selection and village characteristics

We developed the following GIS (Geographic Information System) protocol to select 64 villages around 16 mid-sized cities (population in thousands: mean ± s.e.m. = 99 ± 17; minimum 30, maximum 287; https://www.citypopulation.de) in Hungary and western Romania consisting of 6 major steps[50]. (1) Data collection: we used publicly available settlement polygons (cities and villages) for both countries from the web[51,52]. (2) Agglomeration identification: villages within city agglomerations were identified using existing literature[53,54]. (3) To select reference villages outside city agglomerations (that is, villages far from cities), we defined an outer ring area around the agglomeration. This was done by calculating the minimum circle encompassing the given city area and the corresponding agglomeration area (calculated by summing the areas of villages in the agglomeration). We then determined the radius of this outer ring by taking the city radius (r_{city}) and adding two times the difference between the agglomeration radius ($r_{agglomeration}$) and the city radius: $r_{city} + 2 \times (r_{agglomeration} - r_{city})$. All villages with more than 50% of their area within this outer ring (which did not contain the agglomeration) were considered potential candidates for our study. (4) Exclusion criteria: we excluded villages within both the agglomeration and outer ring that were directly neighbouring other cities and towns with populations exceeding 4,000 inhabitants, as well as 'second' villages from cities (that is, neighbours of a direct city neighbouring 'first' villages) with over 40,000 inhabitants due to their potential for having their own smaller or larger agglomerations. (5) Landscape analysis: for each potential village (either within the agglomeration or being far from the city, that is, in the outer ring; $n = 805$), we created a buffer with a 2,000-m radius to calculate the share of agricultural area (including non-irrigated arable lands, permanently irrigated land, vineyards, fruit trees and berry plantations, complex cultivation patterns) and forest area (broad-leaved forest, coniferous forest, mixed forest, transitional woodland–shrub) based on the CORINE Land Cover 2018[55]. (6) Village pair selection: for each city, we selected one village with agricultural landscape (low forest share and high agriculture share) and one village with forest-dominated landscape (high forest share and low agriculture share) within the agglomeration, and similarly one for each type in the outer ring. Although we did not set strict cut-off values for agricultural- and forest-area percentages due to differing percentages of varying numbers of villages per city, we paid careful attention to the fact that villages in forest-dominated landscapes had a high share of forest area, and villages in agricultural landscapes had a high share of agriculture areas to provide a strong contrast for each city (Extended Data Table 5). Meanwhile, we also aimed to have similar shares of these landscape elements within agglomeration and far-from-city pairs. In addition, village edges (official border of village internal area) needed to be bordered at least partly by forests and agricultural areas in forest-dominated and agricultural landscapes, respectively. We also aimed to keep the number of inhabitants consistent across the four villages per city and all cities.

This semi-quantitative selection process was checked and agreed on city by city by two authors (D. Korányi and P. B.), with subsequent site visits of one author (R. G.) alongside the six individual field survey teams. A final note on village selection: the selected cities varied in size, with populations ranging from 30,000 to 287,000. Consequently, larger cities had larger agglomerations and outer rings, leading to greater mean distances between the selected study villages as city populations increased (Pearson's $r = 0.58$; $P < 0.019$). Although we did not aim to test this effect, we accounted for it by including city ID as a random term in the statistical models.

To better characterize our study villages, we collected further data (population size[56,57] and elevation; https://en-gb.topographic-map.com). For each village, we calculated the distance to the focal city, village interior area, normalized difference vegetation index (based on the Sentinel2 images taken between April and July in the years 2016–2022; the satellite data were accessed and processed using the Google Earth Engine platform[58]) and percentage of sealed area in the village interior area (Copernicus Imperviousness Density (%)[55]). To characterize the landscapes surrounding the villages, we examined a 2,000-m radius buffer area around the village centres, excluding the village inner areas. Within this buffer zone, we calculated the soil organic content[59]. In addition, we determined the agricultural productivity index[60] by focusing on arable and grasslands, and we combined these into a compound index weighted by their share in the landscape. For calculations, we used ArcGIS 10.8[61] and QGIS 3.12[62] software and 'raster'[63], 'sf'[64] and 'rgee'[65] packages in R[66].

Multitaxa sampling

Before fieldwork, we designated 100-m-long transects at the edge and centre of each village for samplings in grassy margins bordering roads or grassy areas in the centres around churches or other public buildings. The mean distance between the centre transect and the nearest village border was approximately 200 m (mean ± s.e.m. = 203 ± 15 m). We surveyed vascular plants from late April to early June 2022 due to climatic and phenological differences between regions and estimated the relative percentage cover per species in nine 1 × 1 m quadrats ($n = 1,152$ quadrats) distributed along the transects. The quadrats were grouped

in 3 triplets approximately 40–50 m away from each other, and 5 m from each other within a triplet. We sampled ground-dwelling arthropods (carabids, spiders and isopods) in two 1-week periods with a 2-week break between them from May to June with 5 pitfall traps per transect spaced at least 8 m apart (n = 1,280 pitfall traps). Pitfalls had a diameter of 8.5 cm and were filled with a 50% water–propylene–glycol solution[67]. We also sampled vegetation-dwelling arthropods (spiders and true bugs) with a D-Vac suction sampler (Ryobi RBV36B 36 V leaf blower), taking 3 samples per transect at least 8 m apart twice with a 2-week break between them from May to June (n = 768 D-Vac samples)[68]. Each sample consisted of 30 suctions for 5 s. We sampled cavity-nesting bees, wasps and their parasitoids by exposing two trap nests per transect next to each other on one electricity pole at 3 m height in villages of 14 out of 16 cities from March to September (n = 224 trap nests)[69]. Villages around two cities (Salgótarján in Hungary and Oradea in Romania) were not sampled due to limited capacity. We lost only two trap nests in one transect due to damage caused by woodpeckers. For subsequent identification, we reared trap-nesting bees, wasps and parasitoids in winter. We identified all arthropods to the species level with very few exceptions, where identification was possible only at a higher taxonomic level (genus in the case of isopods (two genera), true bugs (three) and wasps (one), or family in the case of parasitoids (one genus and two families)). Finally, for each transect, we surveyed birds using one 10-minute point count within a 100 m buffer of the central point of the transect 2 times with a 3-week break between them during the peak breeding season (end of April to June)[70]. We obtained permission from the village authorities and advertized our sampling activities to village residents through leaflets and public message boards to minimize vandalism.

Multitrophic diversity index

We calculated species richness for each of the nine studied taxonomic groups by pooling spatial and temporal samples at the transect level (n = 128). We also calculated species richness at the village level by pooling edge and centre data to perform village-level analyses (n = 64). We then calculated multitrophic diversity indices at both levels on the basis of classical averaging[71] and threshold methods[43]. In the case of the averaging method, we normalized species richness data per taxon between 0 and 1 and then averaged them across all taxa. As the average approach may provide biased estimations of multitrophic diversity if there is a correlation among the individual taxa (in general, our study showed weak correlations)[72], we also used the threshold approach[43,73]. In the case of the threshold method, we identified the maximum species richness across all samples per taxon, and then the 95th percentile of it was used to minimize the effect of positive outliers[43]. Then we identified which samples attained a given threshold of this maximum. We used thresholds from 20 to 80% at each 10% interval for each taxon. Finally, we tallied the number of taxa that exceeded the given threshold and averaged it per sample across all nine taxa[43]. Thus, this threshold-based multitrophic diversity index also ranges between 0 and 1. In our case, at both the village and transect levels, the distribution of the 60% threshold turned out to be the closest to the Gaussian normal distribution. Besides, agroecological studies showed that intermediate threshold levels effectively measure multitrophic diversity[43,72]. As in our case, the 60% threshold multitrophic diversity was strongly correlated with the averaged multitrophic diversity at both the village and transect levels, and these yielded similar results, when we analysed the effects of our design variables, we presented the more complex threshold-based results only as extended data (Extended Data Fig. 5a,b).

BLI and HFI

The OECD BLI is based on the following 11 dimensions: housing, income, jobs, community, education, environment, civic engagement, health, life satisfaction, safety, and work–life balance[24,25]. Each dimension consists of one to four normalized indicators, which are then averaged per dimension and, finally, also across dimensions to get the composite BLI. We collected all possible indicators (9 indicators of 7 dimensions) available for our Hungarian villages (n = 44) at the individual village level and followed the calculation process described in the preceding for the OECD index (see Extended Data Table 3 for the dimensions and indicators considered). If an indicator depicted a negative aspect of well-being (for example, air pollution), then the normalized value was first subtracted from one[25].

The rationale for using the BLI in this study lies in its comprehensive framework, which encompasses a wide range of well-being dimensions relevant to understanding the human context in which biodiversity exists. However, we acknowledge that applying the BLI at the village level might introduce certain limitations. Well-being is inherently context-specific and may vary considerably within local environments, which could affect the comparability of results across different villages. Furthermore, our analysis is limited to Hungarian villages, preventing broader geographic comparisons. Despite these constraints, the BLI offers a robust analytical foundation to explore the intersection of socioeconomic factors and biodiversity, enriching the overall context of our ecological assessments.

The HFI is an annual composite[26], for which we used the most recent annual data (2018). Mu et al.[26] calculated this index at 1 km resolution with global coverage on the basis of 8 human pressure variables: population density, railways, roads, navigable waterways, night-time lights, built environment, cropland and pasture. They assigned different scores to each 1 km pixel according to variable contributions and calculated a composite value by summing the pressure scores of the 8 input variables (total values can range between 0 and 61). We calculated the mean HFI composite index for our study village areas using this global geospatial dataset. Finally, we divided this index by 61 so that values can range between 0 and 1 across our study villages (n = 64).

Statistical analyses

We used GLMMs implemented in the 'lmerTest' package[74] in R[66] for testing the effects of agglomeration (village in city agglomeration or far from city) and landscape simplification (village in agricultural or forest-dominated landscape) and their two-way interaction on the background variables characterizing our study design (Table 1; n = 64). We performed model diagnostics to test for the normal distribution of model residuals by investigating normal quantile–quantile plots and plotting model residuals against fitted values to visualize the error distribution and potential heteroscedasticity. If the normal distribution of model residuals was violated, we transformed the raw data to avoid this violation[75]. This was necessary for population size, village area and edge–centre distance variables, which were log-transformed before analyses. We included nested random effects in the models, with 'village' nested in 'city', and 'city' nested in 'country'. We simplified these models by backward elimination of fixed-effect terms with an alpha level ≤ 0.1 (that is, retaining marginal and significant effects) using the 'step' function of 'stats' package in R[66]. Finally, we calculated the marginal and conditional R^2 values for each minimal adequate model using the 'r.squaredGLMM' function of the 'MuMIn' package[76].

We analysed the effects of agglomeration and landscape simplification and their two-way interaction on the averaged and 60% multitrophic diversity indices, the BLI and HFI indices and the normalized species richness of individual groups at the village level with the same GLMM structure and simplification procedure as for the background variables (Figs. 2a and 3a,b and Extended Data Fig. 2). The species richness data of carabids and true bugs were square-root transformed to achieve normal model residual distributions. When we analysed the multitrophic diversity indices and species richness data of the individual taxonomic groups at the transect level (n = 128; Fig. 2b and Extended Data Fig. 3), we included the edge effect (village edge versus centre) as an additional fixed factor, and we considered all two-way interactions of the three explanatory variables (agglomeration, landscape

simplification and edge effects). In these models, we included the village ID as the last random effect to account for the fact that edge and centre transects were nested in villages.

Finally, when we analysed the single direct effects of BLI on HFI and HFI on multitrophic diversity at the village level (Fig. 3c,d), we restructured the random terms to consider our cross-nested study design, where villages were nested both in agglomeration (Aggl.) status (agglomeration or far from city) and in landscape (Landsc.) type (agricultural or forest-dominated landscape). The model formulae in R-syntax:

$$\text{lmer}(\text{HFI} \approx \text{BLI} + (1|\text{City/Aggl\_status}) + (1|\text{City/Landsc\_type}))$$

$$\text{lmer}\,(\text{Multitrophic\_diversity} \approx \text{HFI} + (1|\text{Country/City/Aggl\_status}) + (1|\text{Country/City/Landsc\_type}))\,.$$

We also modified these two models by adding our two main design variables, landscape simplification and agglomeration effect, as fixed instead of random factors while considering all two-way interactions. We simplified these models by backward elimination of fixed-effect terms with an alpha level ≤ 0.1. Finally, we also analysed the direct effect of BLI on multitrophic diversity at the village level with the same random structure as in the case of the HFI model.

Figures were created using Microsoft Office Excel 2016, QGIS 3.12[62] and 'stats' package in R[66].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Species presence, multitrophic diversity and socioeconomic data used in the analyses are available via Zenodo (https://doi.org/10.5281/zenodo.15516259)[77]. Population data were obtained from the City Population database (https://www.citypopulation.de/)[78]; village elevation data were obtained from the Topographic Map database (https://en-gb.topographic-map.com/map-cvtgt/Europe/)[79]; housing, job and education data were obtained from the Hungarian Census database (https://nepszamlalas2022.ksh.hu/en/database/)[80]; and income, health and civic engagement data were obtained from the TIMEA database (https://map.ksh.hu/timea/?locale=en)[81].

Code availability

A complete description of the models is provided in Methods, and all code is available from the corresponding author on reasonable request.

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Author contributions

P.B. conceived the study. P.B., R.G., D. Korányi, T.L., B.D., K. Szitár and E.T. developed the study. P.B., R.G., D. Korányi, T.L., B.D., N.G.-S., M.K., C.K., D. Kotowska, R.M., B.P., B.S., A.T., A.B., Z.L., J.J.P., G. Seress, I.U., D.P., K. Sándor, L.S., G. Süle, O.V., A.R.Z., K. Szitár and E.T. contributed to data collection. D. Korányi, N.G.-S., A.T. and E.H. identified arthropods. P.B. analysed data. Z.M., C.F., L.M. and T.T. provided insights for analyses and assisted in the interpretation of results. P.B. wrote the paper with substantial input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41893-025-01592-y.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-025-01592-y.

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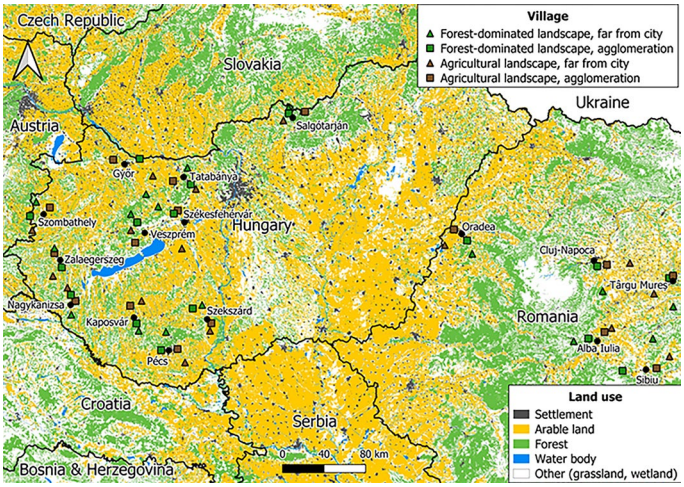
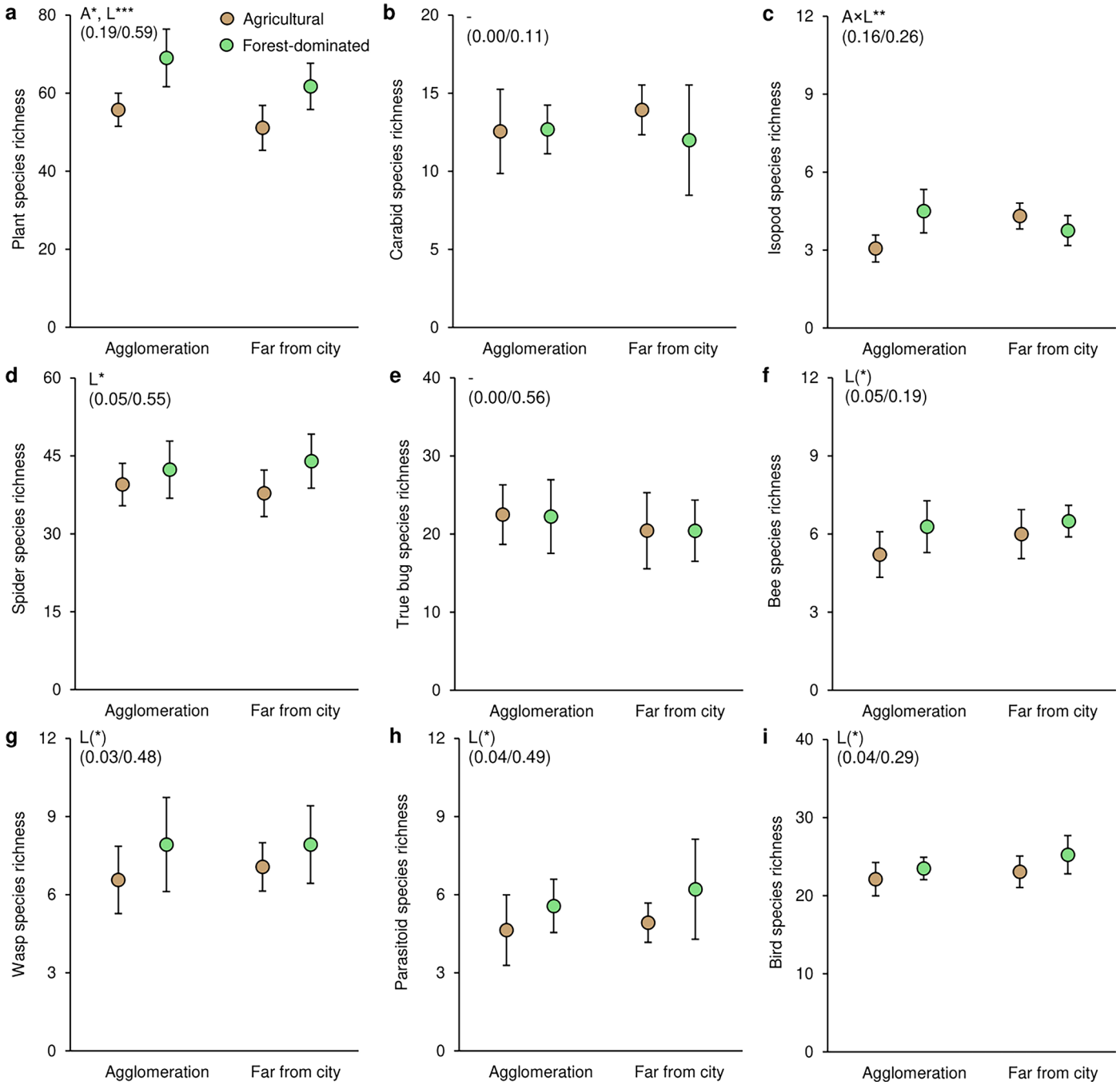


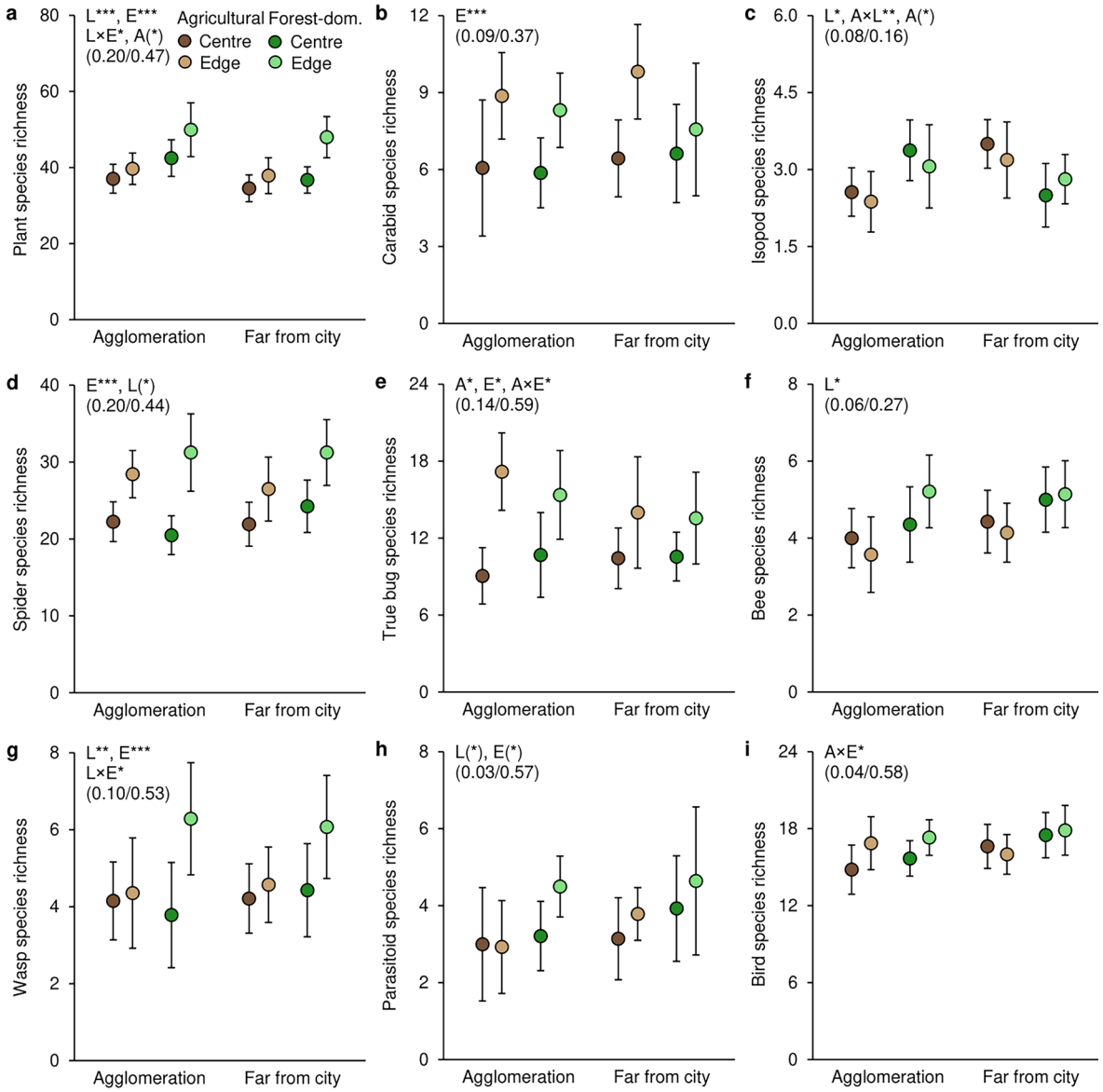
Extended Data Fig. 1 | Map showing the study areas in Hungary and Romania with the four village types around the 16 focal mid-sized cities (black dots with city names). Map based on the CORINE Land Cover 2018[55].

https://doi.org/10.1038/s41893-025-01592-y



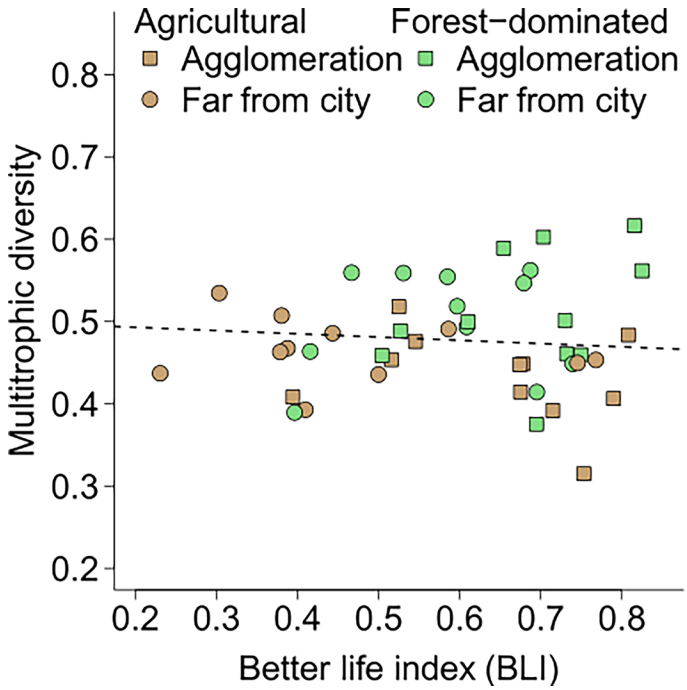
Extended Data Fig. 2 | Effects of agglomeration (agglomerations vs. far from cities) and landscape simplification (agricultural vs. forest-dominated landscapes) on species richness of plants (a), carabids (b), isopods (c), spiders (d), true bugs (e), bees (f), wasps (g), parasitoids (h) and birds (i) (n = 64, for f-h n = 56 villages). A: agglomeration effect; L: landscape simplification effect. Error bars represent mean ± 95% confidence intervals. Significance levels (two-sided t-test): (*)$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. (R_m/R_c): marginal/conditional R-squared.

https://doi.org/10.1038/s41893-025-01592-y



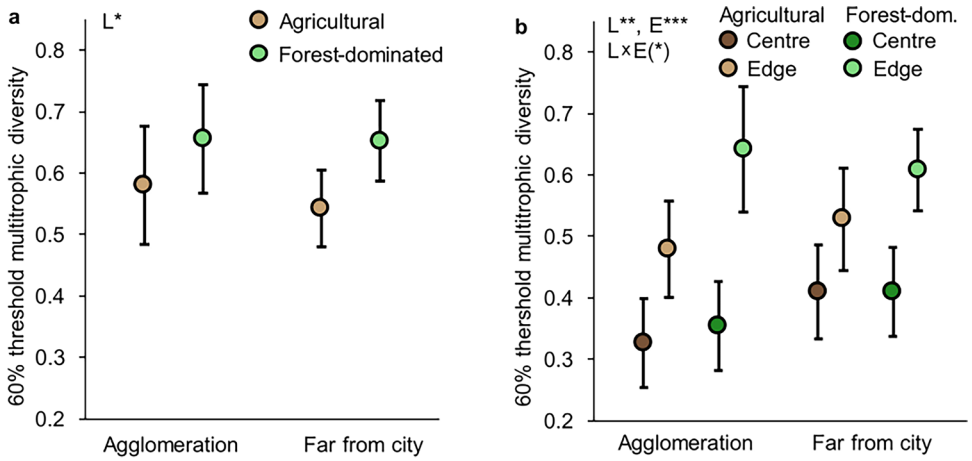
Extended Data Fig. 3 | Effects of agglomeration (agglomerations vs. far from cities), landscape simplification (agricultural vs. forest-dominated landscapes) and edge effect (edge vs. centre) on species richness of plants (a), carabids (b), isopods (c), spiders (d), true bugs (e), bees (f), wasps (g), parasitoids (h) and birds (i) (n = 128, for f-h n = 111 transects). Error bars represent mean ± 95% confidence intervals. Forest-dom.: Forest-dominated. A: agglomeration effect; L: landscape simplification effect; E: edge effect. Significance levels (two-sided t-test): (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001. (R_m/R_c): marginal/conditional R-squared.

https://doi.org/10.1038/s41893-025-01592-y



Extended Data Fig. 4 | Relationships between Better Life Index and multitrophic diversity in villages (n = 44 villages). Dashed line represents non-significant fitted regression lines.

https://doi.org/10.1038/s41893-025-01592-y



Extended Data Fig. 5 | Effects of agglomeration (agglomerations vs. far from cities) and landscape simplification (agricultural vs. forest-dominated landscapes) on 60% threshold multitrophic diversity (a) in villages, and on 60% threshold multitrophic diversity (b) at transect level including edge effects (village centre vs. village edge). Marginal and conditional R-squared values for at village level model: R2m = 0.07, R2c = 0.30 and at transect level model: R2m = 0.28, R2c = 0.35. Error bars represent mean ± 95% confidence intervals (n = 64 villages for a, n = 128 transects for b). Forest-dom.: Forest-dominated. E: edge effect; L: landscape simplification effect. Significance levels (two-sided t-test): (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

https://doi.org/10.1038/s41893-025-01592-y

Extended Data Table 1 | Summary statistics of GLMMs on the effects of agglomeration, landscape simplification and their interaction on multitrophic diversity (Fig. 2a), species richness of study taxa (Extended Data Fig. 2), Better Life Index (Fig. 3a) and Human Footprint Index (Fig. 3b) in villages (n=64)

Model	Variable	Estimate ± 95% CI	P	R^2_m/R^2_c
Multitrophic diversity	Landscape simplification (L)	-0.07 ± 0.03	<0.001	0.20/0.51
Species richness				
Plant	Agglomeration (A)	0.08 ± 0.06	0.018	0.19/0.59
	Landscape simplification (L)	-0.16 ± 0.06	<0.001	
Carabid	–	–	–	0.00/0.26
Isopod	Agglomeration (A)	0.11 ± 0.12	0.083	0.16/0.26
	Landscape simplification (L)	0.08 ± 0.12	0.190	
	A × L	-0.29 ± 0.17	0.002	
Spider	Landscape simplification (L)	-0.12 ± 0.09	0.012	0.05/0.55
True bug	–	–	–	0.00/0.56
Bee	Landscape simplification (L)	-0.10 ± 0.10	0.071	0.05/0.19
Wasp	Landscape simplification (L)	-0.09 ± 0.09	0.073	0.03/0.49
Parasitoid	Landscape simplification (L)	-0.10 ± 0.10	0.059	0.03/0.49
Bird	Landscape simplification (L)	-0.10 ± 0.10	0.064	0.04/0.29
Better Life Index (BLI)	Agglomeration (A)	0.14 ± 0.06	<0.001	0.27/0.60
	Landscape simplification (L)	-0.08 ± 0.06	0.013	
Human Footprint Index (HFI)	Agglomeration (A)	0.13 ± 0.05	<0.001	0.27/0.49
	Landscape simplification (L)	0.08 ± 0.05	0.006	
	A × L	-0.08 ± 0.07	0.049	

The statistical values presented are estimates with their corresponding 95% confidence intervals (CI), P-values (two-sided t-test), and marginal/conditional R-squared values (R2m/R2c).

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Extended Data Table 2 | Summary statistics of GLMMs on the effects of agglomeration, landscape simplification, edge effect and their interaction on multitrophic diversity (Fig. 2b), and species richness of study taxa (Extended Data Fig. 3) in villages at transect level (n=128; for bees wasps and parasitoids n=111 transects)

Model	Variable	Estimate ± 95% CI	P	R^2_m/R^2_c
Multitrophic diversity	Landscape simplification (L)	-0.07 ± 0.03	<0.001	0.29/0.49
	Edge effect (E)	-0.11 ± 0.03	<0.001	
	L × E	0.05 ± 0.05	0.040	
Species richness				
Plant	Agglomeration (A)	0.04 ± 0.05	0.075	0.20/0.47
	Landscape simplification (L)	-0.14 ± 0.06	<0.001	
	Edge effect (E)	-0.13 ± 0.06	<0.001	
	L × E	0.09 ± 0.08	0.035	
Carabid	Edge effect (E)	-0.13 ± 0.06	<0.001	0.09/0.37
Isopod	Agglomeration (A)	0.09 ± 0.10	0.065	0.08/0.16
	Landscape simplification (L)	0.11 ± 0.10	0.025	
	A × L	-0.24 ± 0.14	0.001	
Spider	Landscape simplification (L)	-0.05 ± 0.05	0.094	0.20/0.44
	Edge effect (E)	-0.18 ± 0.05	<0.001	
True bug	Agglomeration (A)	0.09 ± 0.07	0.021	0.14/0.59
	Edge effect (E)	-0.08 ± 0.07	0.017	
	A × E	-0.12 ± 0.09	0.015	
Bee	Landscape simplification (L)	-0.10 ± 0.07	0.013	0.06/0.27
Wasp	Landscape simplification (L)	-0.16 ± 0.10	0.003	0.10/0.53
	Edge effect (E)	-0.19 ± 0.09	<0.001	
	L × E	0.17 ± 0.13	0.012	
Parasitoid	Landscape simplification (L)	-0.08 ± 0.09	0.073	0.03/0.57
	Edge effect (E)	-0.06 ± 0.07	0.079	
Bird	Agglomeration (A)	0.01 ± 0.09	0.838	0.04/0.58
	Edge effect (E)	0.01 ± 0.08	0.844	
	A × E	-0.12 ± 0.11	0.031	

The statistical values presented are estimates with their corresponding 95% confidence intervals (CI), P-values (two-sided t-test), and marginal/conditional R-squared values (R2m/R2c).

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Extended Data Table 3 | Indicators of Better Life Index of Hungarian villages in agglomeration of mid-sized cities versus far from cities and in agricultural versus forest-dominated landscapes (mean ± 95% confidence interval) (n = 44 villages)

	Agglomeration		Far from city		Estimate ± 95% CI		R^2_m/R^2_c
	Agricultural	Forest-dom.	Agricultural	Forest-dom.	Agglomeration	Landsc. simp.	
Housing (equipement %)[1]	69.6 ± 7.4	73.9 ± 6.1	50.5 ± 9.8	64.0 ± 9.0	14.68 ± 7.8***	-8.86 ± 7.8*	0.28/0.36
Income (€/capita/year)[2]	4802 ± 206	4727 ± 429	3749 ± 690	4078 ± 488	850 ± 316***	–	0.18/0.72
Jobs (unemployment %)[3]	3.38 ± 1.02	3.19 ± 0.71	4.61 ± 1.72	3.46 ± 0.90	–	–	0.00/0.36
Education							
Secondary education (%)[4]	49.1 ± 4.5	52.5 ± 3.7	35.2 ± 6.9	40.4 ± 6.9	12.96 ± 5.37***	–	0.32/0.39
Higher education (%)[5]	16.2 ± 2.9	17.6 ± 3.1	8.9 ± 2.9	11.6 ± 3.1	6.50 ± 2.78***	–	0.28/0.42
Environment							
PM2.5 ($\mu m/m^3$)[6]	12.5 ± 0.4	12.0 ± 0.2	12.3 ± 0.4	11.8 ± 0.4	0.20 ± 0.22(*)	0.57 ± 0.22***	0.19/0.71
NO_2 (ppb)[7]	5.73 ± 1.08	5.60 ± 0.69	6.03 ± 0.49	4.58 ± 0.80	–	0.79 ± 0.78(*)	0.08/0.14
Health (death/1000 capita)[8]	15.7 ± 3.1	14.0 ± 3.3	14.8 ± 2.0	15.8 ± 3.7	–	–	0.00/0.32
Civic engagement (voting %)[9]	70.4 ± 2.9	70.6 ± 2.7	64.2 ± 4.5	67.3 ± 2.7	4.69 ± 2.73**	–	0.15/0.44

Effects of agglomeration (reference: far from city) and landscape simplification (Landsc. simp.; reference: complex) are shown as effect estimates ± 95% confidence interval (CI) from general linear mixed-effects models (GLMM). Unemployment rate was arcsine-transformed prior to analysis. R2m: marginal R-squared. R2c: conditional R-squared. –: effect was discarded from the minimal adequate model during model simplification (the interaction between agglomeration and landscape simplification was discarded in all models). Significance levels based on GLMM outputs (two-sided t-test): (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001. Footnote: [1]Proportion of dwellings with all amenities in total occupied dwellings in % in 2022 (ref. 80). [2]Amount of personal income tax base per permanent capita in Euro in 2021 (changed from Hungarian Ft to Euro with the currency exchange rate of 390 HUF/Euro)[81]. [3]Proportion of unemployment in population aged 15–64 in % in 2022 (ref. 80). [4]Proportion of people aged >20 having completed at least secondary level of education (high school) in 2022 (ref. 80). [5]Proportion of people who completed university, college, etc. with degree in population aged >20 in % in 2022 (ref. 80). [6]Average concentration of particulate matter (PM) smaller than 2.5 micrometres per cubic meter in the air in 2022 (ref. 82). [7]Nitrogen dioxide surface-level annual average concentration in 2019 in parts per billion [ppb][83]. [8]Number of deaths per 1000 capita in 2021 (ref. 81). [9]Voter turnout in the 2022 parliamentary elections [%][81].

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Extended Data Table 4 | Summary statistics of GLMMs on the effects of Better Life Index, agglomeration, landscape simplification and their interaction on Human Footprint Index (n=44) and on the effects of Human Footprint Index, agglomeration, landscape simplification and their interaction on multitrophic diversity (n=64)

Model	Variable	Estimate ± 95% CI	P	R^2_m/R^2_c
Human Footprint Index (HFI)	Better Life Index (BLI)	0.30 ± 0.18	0.002	0.38/0.63
	Agglomeration (A)	0.08 ± 0.05	0.003	
	Landscape simplification (L)	0.10 ± 0.05	0.001	
	A × L	-0.10 ± 0.07	0.011	
Multitrophic diversity	Human Footprint Index (HFI)	-0.15 ± 0.15	0.048	0.24/0.51
	Landscape simplification (L)	-0.07 ± 0.03	<0.001	

The statistical values presented are estimates with their corresponding 95% confidence intervals (CI), P-values (two-sided t-test), and marginal/conditional R-squared values (R2m/R2c).

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Extended Data Table 5 | Landscape structure (in 2,000 m buffer) of villages in agglomeration of mid-sized cities versus far from cities, and separately in agricultural versus forest-dominated landscapes (mean ± 95% confidence interval) (n=64 villages)

	Agglomeration	Far from city	Agricultural	Forest-dom.
Agricultural area (%)	50.8 ± 9.5	52.7 ± 7.1	73.4 ± 4.5	30.0 ± 7.0
Forest area (%)	23.7 ± 9.1	23.9 ± 7.2	6.5 ± 6.0	41.0 ± 4.3
Distance to city (km)	10.1 ± 1.3	20.0 ± 2.5	14.8 ± 2.4	15.1 ± 2.9

Forest-dom.: Forest-dominated.

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Corresponding author(s): Dr. Péter Batáry

Last updated by author(s): May 26, 2025

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
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☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	For GIS data collection, we used ArcGIS 10.8 and QGIS 3.12 software and 'raster', 'sf' and 'rgee' packages in R, as well as, Google Earth Engine platform. We cited all of them with references in the Methods section.
Data analysis	For analysing the data we used the following R packages: 'lmerTest', 'stats' and 'MuMIn'. We cited all of them with references in the Methods section. For creating figures we used Microsoft Office Excel 2016.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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Species presence, multitrophic diversity and socioeconomic data used in the analyses are archived at the research data repository Zenodo (https://zenodo.org/

records/15516260). Population data were sourced from the City Population database (https://www.citypopulation.de/), and village elevation data were obtained from the Topographic Map database (https://en-gb.topographic-map.com/map-cvtgt/Europe/).

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	We did not collect sex- or gender-based data.
Population characteristics	We did not perform surveys on human research participants.
Recruitment	We did not recruit participants.
Ethics oversight	There is no ethical issue.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We selected sets of four villages in Hungary and Romania, situated around 16 mid-sized cities: two villages were located in city agglomerations, and two were located far from cities, and further categorised as two being in simple and two in complex landscapes (n = 64 villages). We collected human footprint index index and socio-economic variables at the village level - the latter were available only from Hungary (n = 44 villages). For collecting multitrophic diversity, we designated two transects per village, at village edge and centre (n = 128). These data were analysed both at village and at transect levels.
Research sample	- The human footprint index was collected by GIS from the global geographic dataset of Mu et al. 2022. Sci. Data. - To calculate better life index for Hungarian villages, socio-economic variables (housing, income, jobs education, health) were collected from Hungarian Statistical Office and Hungarian National Election Office (civic engagement), and environmental data (PM2.5 and NO2) from Wei et al. 2023. Nat. Commun., respectively, from Anenberg et al. 2022. Lancet Planetary Health. - For calculating multitrophic diversity, we sampled all taxa at village edges and centres. We estimated estimated the relative percentage cover of vascular plants per species in nine 1 × 1 m quadrats (n = 1,152 quadrats). We sampled ground-dwelling arthropods (carabids, spiders, and isopods) in two one-week periods with a two-week break between them from May to June with five pitfall traps per transect (n = 1,280 pitfall traps). We also sampled vegetation-dwelling arthropods (spiders and true bugs) with a D-Vac suction sampler, taking 3 samples per transect twice with a two-week break between them from May to June (n = 768 D-Vac samples). We sampled cavity-nesting bees, wasps and their parasitoids by exposing two trap nests per transect in villages of 14 out of 16 cities from March to September (n = 224 trap nests; villages around two cities were not sampled due to limited capacity). We surveyed birds using one 10-minute point count within a 100 m buffer of the central point of the transect two times with a 3-week break between them during the peak breeding season.
Sampling strategy	Socio-economic data were directly collected at village level. Multitrophic diversity data were collected at transect level with spatial and/or temporal replicates within transects; all of these replicates were pooled at transect level, and also at village level to perform statistical analyses at both levels. To achieve a sufficiently robust sample size, we engaged five additional research groups for biodiversity samplings to include as many villages (64) as possible from the Carpathian basin.
Data collection	Data were collected as described at Research sample. GIS data were collected by D. Korányi and P. Palotás. Human footprint index and socio-economic variables were collected by D. Kotowska and P. Batáry. Biodiversity data were collected by all co-authors with exception of Z. Molnár, C. Fischer, L. Marini and T. Tscharntke.
Timing and spatial scale	Please, see timing and spatial scale at Research sample.
Data exclusions	We lost only two trap nests in the centre of one village. We did not apply any data imputation, and did not exclude any data.
Reproducibility	We prepared detailed site selection and biodiversity sampling protocols (described in the Methods section), which have been discussed with the participating research groups in one online and one in-person meetings.
Randomization	Each collaborating research group surveyed biodiversity in villages around two focal cities, which were close to their affiliation, whereas my own (leading) research group surveyed biodiversity in villages around six further cities. Thus we did not apply a randomization among survey teams due to logistic constraints, but considered heterogeneity among focal cities and villages by

including random factors in the models ('village' nested in 'city', and 'city' nested in 'country').

Blinding

Blinding was not necessary for this study, as we a priori selected all study sites based on a site selection protocol according to our hierarchical nested study design.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

We performed the biodiversity surveys in spring-summer of 2022 under calm and dry weather conditions. There was no heavy rain, which would have destroyed the pitfall traps. To conduct the D-Vac surveys, we waited in the mornings until the vegetation had dried. Bird surveys were conducted under dry weather conditions from sunrise plus 4h.

Location

Village ID and thus location will be stored openly in the repository Zenodo. Exact geographic locations within villages are stored on local computers and cloud server of the first author's research centre, and can be made available upon reasonable request.

Access & import/export

We asked permission for biodiversity sampling from each village authority. We accessed the villages by institutional or private cars. The collected pitfall trap and D-vac samples were stored in 70% alcohol right from the sampling, and in case of hot weather they were transported in cooling boxes in the cars. Trap nests were exposed with the permission and assistance of the German electricity company, E.ON. As we did not sample arthropods in protected areas or protected species, we did not need special permissions. Thus our sampling complied all laws.

Disturbance

To minimize the cause of disturbance, we avoided samplings during bad weather conditions. We collected the trap nests containing living animals (trap nesting bees, wasps and natural enemies) as quick as possible, noting the upper side of traps for undisturbed storing, and keeping them as short as possible in transport to deliver in safe and cool chambers at the institutes for overwintering. We marked each pitfall trap, and notified the local public in order to avoid any disturbance. If mowing of road verges occurred on sites of vegetation survey, then we postponed survey by a few weeks, so that it does not hamper species level identification.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals

We did not work with laboratory animals.

Wild animals

We sampled ground-dwelling arthropods (carabids, spiders, and isopods) by pitfall traps, which were killed by the trapping material (50% water–propylene–glycol solution) on site, and the captured animals were transferred to a 70% alcohol solution for transport and storage. We also sampled vegetation-dwelling arthropods (spiders and true bugs) with a D-Vac suction sampler, and captured arthropods were killed in putting them in 70% alcohol solution on site for transport and storage. We capture trap nesting bees, wasps, and their natural enemies by exposing trap nests from March to September. The collected trap nests were stored in cooling chambers to let the arthropod larvae overwinter and develop to adults. Each reed stem with animal has been stored after opening in individual glass test tube in the autumn, and the emerging adults next spring were killed by 70% alcohol solution for later species level identification and storage. It was necessary to kill these arthropods (approximately 0 to 1 year in age) to identify all adults to the species level.

Reporting on sex

No, sex was not considered at all in this study, although for some species groups (bees, wasps, spiders), experts noted the sex, which can be used for later analyses in separate studies.

Field-collected samples	The trap nests, respectively the trap nesting arthropod larvae were stored in the 5 degree C and dark cooling chambers for overwintering.
Ethics oversight	No ethical approval was required.

Note that full information on the approval of the study protocol must also be provided in the manuscript.