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Biodiversity change under human depopulation in Japan

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Global studies consistently highlight a direct relationship between habitat and species losses, and human population and economic growth. Nevertheless, countries are experiencing below-replacement human fertility and starting to depopulate; among these countries, Japan is a global forerunner. To better understand whether human depopulation automatically yields environmentally restorative outcomes, we examine the impacts of human depopulation on aspects of biodiversity in Japan. Alongside population, land use and surface temperature, we analyse biodiversity change among 464 taxonomic species of bird, butterfly, firefly and frog egg masses, and 2,922 native and non-native plant species in wooded, agricultural and peri-urban landscapes across Japan over periods of 5–17 years from 2004. Irrespective of human population increase or decrease, biodiversity losses continue among most species studied mainly because of change in agricultural land use, either due to urbanization, disuse and abandonment, or intensification. Only where human numbers are currently stable, biodiversity is also more stable, although we anticipate that this may also change as ageing deepens into depopulation in these areas. We conclude by urging countries facing depopulation to account for its outcomes in their biodiversity conservation and restoration strategies.

Earth's ecosystems are in peril. Since 1970, 73% of global wildlife has been lost, while human populations have more than doubled to more than 8 billion alive today[1,2]. Over the same period, those same people, living mainly in richer countries, grew the world economy by 3,415%, to a colossal US$105.44 trillion of global gross domestic product[3].

Global studies have consistently provided evidence of a direct relationship between habitat and species losses, and human population and economic growth[4–6]. Earth's sixth mass extinction may be underway, with losses accelerating to 100 to 1,000 times greater than pre-human influence levels[7–10]. This surge threatens human sustainability by diminishing ecosystem functionality, and damages human health, socio-economic well-being and cultural vitality, prompting intense discussion around new theoretical frameworks, including the Great Acceleration, planetary boundaries and the Anthropocene[11–14] (Appendix A in the Supplementary Information). The cumulative effects of the number of humans alive on Earth is central to these questions.

Estimates of Earth's sustainable human carrying capacity vary, with recent calculations of 3.1–3.3 billion people, which was exceeded in 1965[11,15]. Nevertheless, an emergent feature of the Anthropocene present is a global decrease in human fertility towards below-replacement levels[16]. Many hope this might yield environmentally restorative outcomes, that is, a 'depopulation dividend'[17–19]. It is a seductive logic, but is it true?

The impacts of human depopulation are an increasingly important consideration for nature conservation, yet its inclusion in sustainability research remains limited[20–22]. So far, outcomes are usually context-specific, and may vary according to sociopolitical, legal and

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conservation frameworks, and ecosystem characteristics[22–24]. An emerging question is whether and how human depopulation may contribute to recovery or whether it perhaps drives further losses[25–28].

United Nations projections anticipate that 85 countries will be continuously depopulating by 2050, and 73 will have populations 1% or more lower in 2050 than 2023, with those numbers set to rise thereafter[2]. Among these, we isolated 11 that have experienced at least 5 years of continuous depopulation through to 2023 (Supplementary Tables 1 and 2 and Appendix B in the Supplementary Information). Two countries, Japan and Italy, are noteworthy as global demographic bellwethers for their world regions—Northeast Asia and Southern Europe—because of their population size, stage of development and sociopolitical independence and stability. Continuous population decline began in each from 2010 and 2014, respectively. We call these depopulation vanguard countries (DVCs).

East Asia is a major contributor to the Great Acceleration[13]. With Japan at the vanguard, many neighbouring countries have experienced similar accelerated development pathways[29] (Supplementary Figs. 1 and 2). Habitat and species losses have been extensive[1]. As Northeast Asia's DVC, with 23 of 47 prefectures depopulating since 1995, and many remote areas losing population continuously since the 1950s or earlier, Japan is one of few countries where researching depopulation and environmental change can be conducted with sufficient rigour to carry meaning beyond its own borders[30,31].

Japan is also one of 36 biodiversity hotspots, with some of the most diverse and threatened ecosystems on Earth[32]. Unlike most hotspots, where population growth encroaches on habitats[33], Japan's population is decreasing. Yet, conservation research there has focused mainly on variables such as change in land use, without sufficiently detailed analysis of local spatial and temporal variability in human population[34–37]. Where studies examine biodiversity in the context of depopulation, the scale, range and local specificity of demographic analysis is limited and does not consider the implications of Japan's post-growth demographic transition pathways for its world region[28,38,39].

We advance sustainability studies by holistically combining multidisciplinary analysis of large micro-level and macro-level datasets in ecology and demography from Japan (Methods, Supplementary Tables 1 and 2, and Appendix B in the Supplementary Information). From the perspective of community ecology, alongside local variation in population, land use and surface temperature, we analyse aspects of biodiversity change by focusing on species richness and abundance at 158 sites across the Japanese archipelago over periods of 5–17 years from 2004 (Supplementary Table 3 and Appendix C in the Supplementary Information). Our research sites are mosaic landscapes that include agricultural fields and orchards, grasslands, ponds and watercourses, secondary and planted woodlands and coppices, and towns and villages, which together occupy the land between Japan's steep forested mountainsides, coastlines and dense urban settlements[40].

These wooded, agricultural and peri-urban (WAPU) landscapes are characterized by moderate human disturbances that create and sustain ecosystems supporting a variety of wildlife; they are maintained by human intervention in drawing resources such as fuel, food, materials and fertilizer from nature. These areas have experienced the greatest levels of human depopulation since the 1990s[30,31]. WAPU environments include not only disturbance-dependent agricultural and grassland species, but species that depend on surrounding forests and edge-dwelling organisms for their coexistence. These heterogeneous mosaic environments have markedly decreased in area in recent decades, although they include many endangered species[41].

Our biodiversity dataset encompasses a comprehensive list of taxa in the ecological trophic pyramid within Japan's WAPU landscapes. The dataset registers more than 1.5 million individual detections of 464 taxonomic species of bird, butterfly, firefly and frog egg masses, and 2,922 native and non-native plant species. Given many people's assumptions that depopulation would yield socio-environmental gains, we ask whether a biodiversity depopulation dividend is occurring for all or specific organism groups inhabiting Japan's WAPU landscapes.

Results

Irrespective of human population increase or decrease, losses continue among most of our studied species in Japan's WAPU landscapes. Only in areas where human population size is currently stable are species richness and abundance also more stable.

Depopulation and land use

Consistent with the demographic information presented elsewhere, Fig. 1 shows that in the 25-year period from 1995 to 2020 human populations increased in 43 sites we researched (27%), decreased in 64 sites (41%), with no clear trend in 51 locations (32%). Notably, depopulation nationally began midway through this period in 2008–2010. Many areas that showed an increased population in 2020 over 1995 had reached their peak population and already begun to depopulate before 2020. Therefore, the biodiversity losses that we identified are potentially accelerating more rapidly than we show in this study, as a greater proportion of Japan's WAPU landscapes begin to depopulate.

Again, irrespective of population change, agricultural land is decreasing, transitioning mainly to urban sprawl, and forested land area is little changed. In the 43 sites with increasing populations (Supplementary Fig. 3), urban land use continues to expand, with urbanization advancing in 36 (84%) and no sites showing a decrease. Forty of 43 sites (93%) experienced a decrease in agricultural land use, with no sites showing an increase. Concerning forest area, 6 of 43 sites (14%) showed a decrease, with none showing an increase.

Urban land use continues to expand even in depopulating areas. Indeed, none of 64 depopulating research sites showed a decrease in urban land use (Supplementary Fig. 3), while urbanization increased in 17 sites (27%) and the remaining 47 (73%) exhibited no significant change. Agricultural land use continues to decrease, with 31 (48%) of 64 depopulating sites showing a decrease, and just one an increase. Additionally, forest area increased in just ten (16%) of these sites, with none showing a decrease.

Long-term biodiversity in WAPU landscapes

Overall, species richness and abundance in Japan's WAPU landscapes shows clear change (Fig. 2 and Supplementary Table 4). Among the 82 sites where we analysed birds, data show an increase in bird abundance in 12 sites (15%), a decrease in 29 (35%) and no clear trend in 41 (50%). Bird species richness data showed an increase in eight of those 82 sites (10%), a decrease in 24 (29%) and no clear trend in 50 (61%). For Japanese brown frog (*Rana japonica*) abundance, ten of 28 sites (36%) showed an increase, 14 (50%) showed a decrease and 4 (14%) no clear trend. Montane brown frog (*Rana ornativentris*)and Ezo brown frog (*Rana pirica*) showed increasing abundance in ten of 31 sites researched (32%), with 20 (65%) showing a decrease and one (3%) no clear trend. For Genji firefly (*Nipponoluciola cruciata*) abundance, six of 31 sites (19%) showed an increase, 18 (58%) a decrease and seven (23%) no clear trend. With Heike firefly (*Aquatica lateralis*), nine of 26 sites (35%) showed an increase, 16 (61%) a decrease and one (4%) no clear trend. For butterfly population data, 16 of 40 researched sites (40%) showed an increase, 15 (38%) a decrease and nine (22%) no clear trend. With butterfly species richness data, eight of 40 sites (20%) showed an increase, nine (23%) a decrease and 23 (57%) no clear trend. For plant native species richness data, 45 of 103 researched sites (44%) showed an increase, 38 (37%) a decrease and 20 (19%) no clear trend. Plant invasive species richness showed an increase in 36 sites (35%), 24 (23%) showed a decrease and 43 (42%) no clear trend.

In areas experiencing human population growth, the abundance and richness of birds, and the abundance of Japanese brown frog and Genji firefly, are notably decreasing (Fig. 3 and Supplementary Tables 5 and 6). Interestingly, Montane brown frog, Heike firefly,

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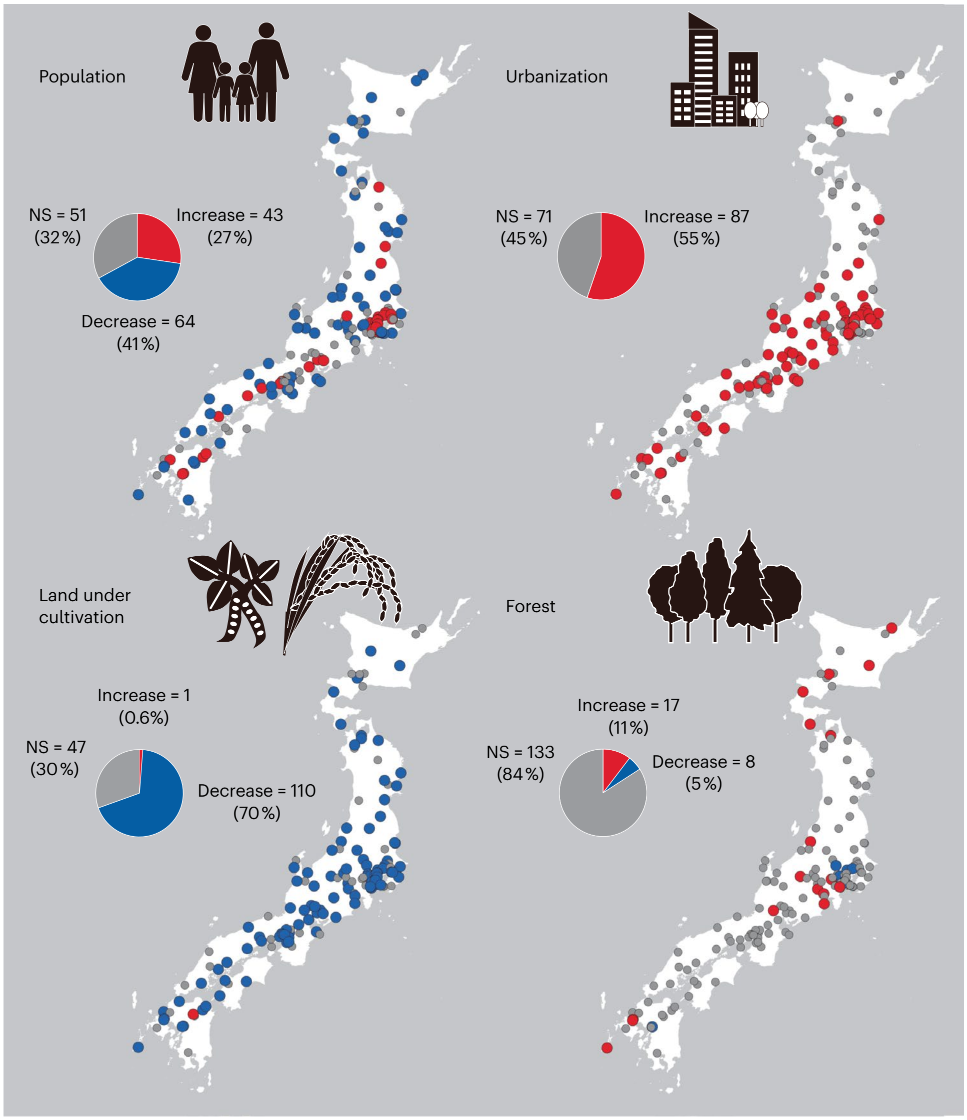

Fig. 1 | Changes in human population, urbanization and areas of land under cultivation and forest. The colour coding on the map represents the statistical results (Supplementary Table 4), with red indicating increasing trends, blue indicating decreasing trends and grey indicating no significant trend. The pie chart shows the summary of the results for the 158 sites used in the present study. NS, no significant trend.

butterfly abundance and richness, and native and non-native plant richness are increasing alongside human population growth (Fig. 3 and Supplementary Tables 5 and 6). In locations experiencing human population decline, the abundance and species richness of all organisms, except for non-native plants, decreased (Fig. 3 and Supplementary Tables 5 and 6). Notably, the slope of species richness and abundance decrease in depopulating areas for most species, excluding bird and non-native plant species richness, is steeper than in sites with stable or increasing human population size (Fig. 3 and Supplementary Tables 5 and 6).

At sites with increasing urban land use, bird, Japanese brown frog and Genji firefly abundance, and butterfly and native and non-native plant species richness, decreased (Supplementary Fig. 4 and Supplementary Tables 5 and 6). At these sites, the decreasing species richness curves for bird, butterfly and native plant species richness were steeper than for non-urbanizing sites. Significantly, there was an increase in Montane brown frog, Heike firefly and butterfly populations in these urbanizing areas. For many organisms, a decrease in species richness and abundance is occurring at sites with decreasing agricultural land, although not for Montane brown frog populations nor native and non-native plant species richness (Supplementary Fig. 5 and Supplementary Tables 5 and 6). For species richness between Heike firefly and butterfly populations, there was a decrease at sites with decreasing agricultural land, although increases were recorded at sites where agricultural land is stable.

Discussion

Human depopulation is not yet yielding automatic gains in species richness and abundance in Anthropocene Japan. Irrespective of whether human numbers are increasing or decreasing, losses are still occurring among our target species assemblages in Japan's WAPU landscapes. This is due mainly to land use change, with depopulation contributing either to urbanization, disuse and abandonment, or intensification (Supplementary Figs. 3 and 6). It is mainly areas where the human presence is currently relatively stable, and traditional wet-rice agriculture continues comparatively undisturbed, that biodiversity is more stable (Fig. 3). Hence, we are disappointed thus far not to report the achievement of a biodiversity depopulation dividend for Japan.

We focused on biodiversity change under human depopulation in Japan's WAPU landscapes, although we acknowledge the limitations of our demographic data. Even at sites showing human population stability, it is highly likely that latent depopulation is advancing because

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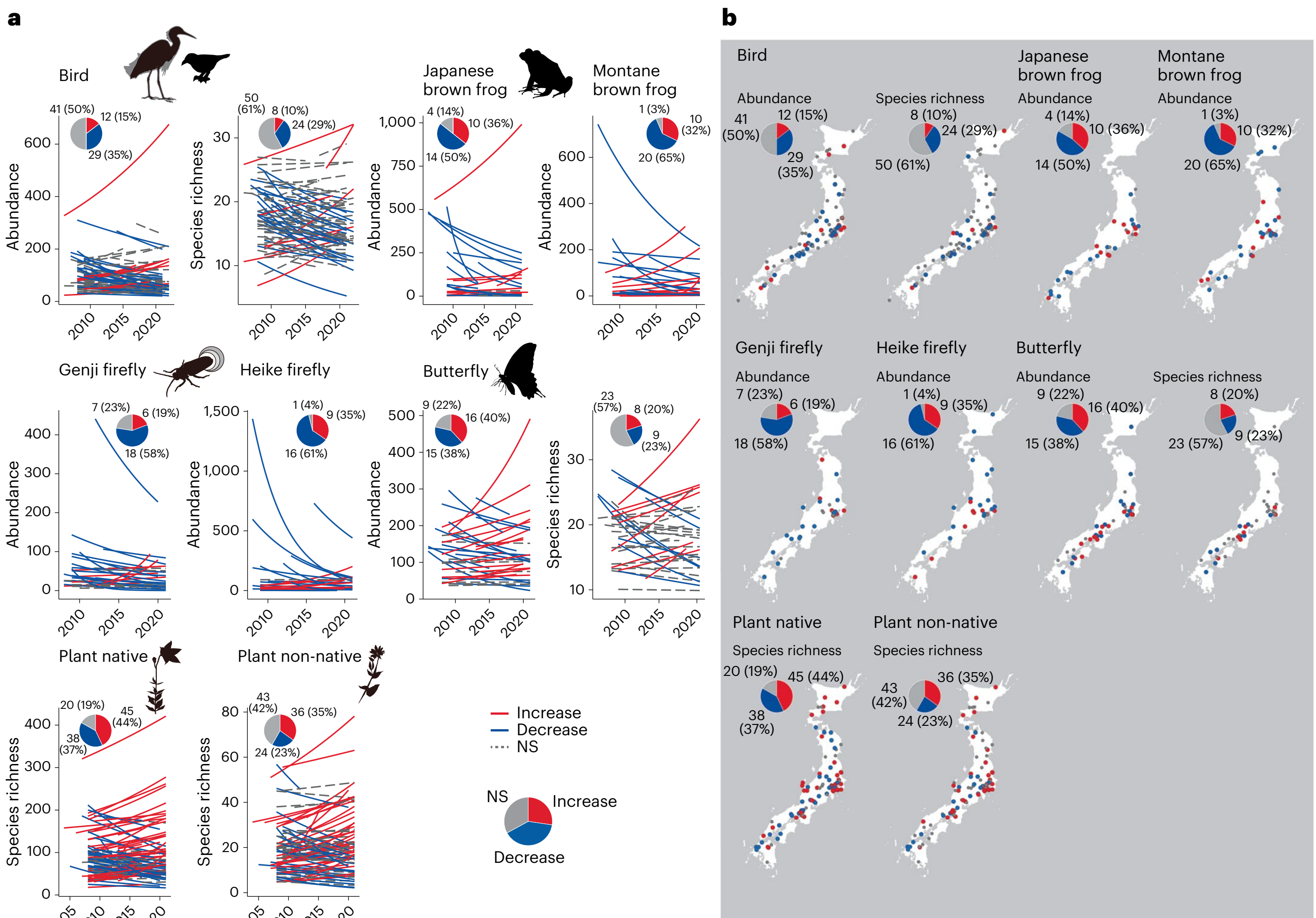

Fig. 2 | Biodiversity change in 158 sites on WAPU landscapes for five different organisms (bird, frog, firefly, butterfly and plant) across the studied area of the Japanese archipelago over periods between 5 and 17 years starting in 2004. **a**, Graphs showing aspects of biodiversity change. **b**, Maps showing the distribution of site results based on the trends in **a**. The colour coding of the trends and maps represents the statistical results (Supplementary Table 4), with red indicating increasing trends, blue indicating decreasing trends and grey indicating no significant trend. The pie chart summarizes the results for the study sites.

of ongoing population ageing, although we were unable to examine the potential impacts directly. As most ageing regions are expected to transition into population decline, our findings for depopulating areas are likely to be similar for currently stable areas in the future. Moreover, we theorize from Japan's status as Northeast Asia's DVC for similar processes and results occurring in WAPU landscapes in neighbouring countries, and connect with global research on the impacts of depopulation on ecosystems worldwide[21,22,42,43].

Our results are not surprising, and are probably attributable to niche contraction and reduction because of decline or cessation of traditional human livelihood practices that provide dynamic stability (agriculture, soil and forest management, landscape and property upkeep) and contribute to the sustainability of biological communities inhabiting WAPU-like ecosystems[34,44,45]. Even in urban and peri-urban locales, activities such as green space management and population mobility may facilitate the movement and reproduction of certain organisms[46].

The latest demographic data show all indicators pointing towards a continuation and acceleration of Japan's low fertility, ageing and depopulation in all 47 prefectures, as well as deepening rural–urban imbalances[31]. Despite 40% of surveyed areas showing population decline, urban land use in many areas continues to expand alongside agricultural disuse and intensification, with a fraction transforming into forests (Supplementary Figs. 3 and 6) because of plantation and, in most cases, natural succession. Despite limited information, some bird taxa in Japan are reported to benefit from the abandonment of agricultural land[28].

We argue that humans are a deeply embedded and essential agent of ecosystem sustainability within Japan's WAPU environments through traditional agricultural and livelihood practices. However, existing alongside these regions approximately 67% of Japan's land area is forested, of which about 40% is plantations[47]. Most are sparsely inhabited or uninhabited by humans because of their steep-sided mountainous terrain, high elevation, inhospitable climates and difficulties in accessing basic utilities and services. Human population decline occurred in these areas mainly during the 1950–1990 period of rapid national economic and population growth because of the local push–pull effects of the decline of the forestry industry alongside industrial and urban expansion attracting mostly younger adults to move away, rather than below-replacement fertility leading to ageing and national-scale depopulation, which is the situation now with WAPU regions[43].

Mosses, lichens, mammals and invertebrates—including soil organisms such as nematodes and molluscs—are important biological groups closely associated with forest habitats that we did not include[48,49]. Moreover, in recent decades, knowledge about functional biodiversity has improved, emphasizing the traits of species and

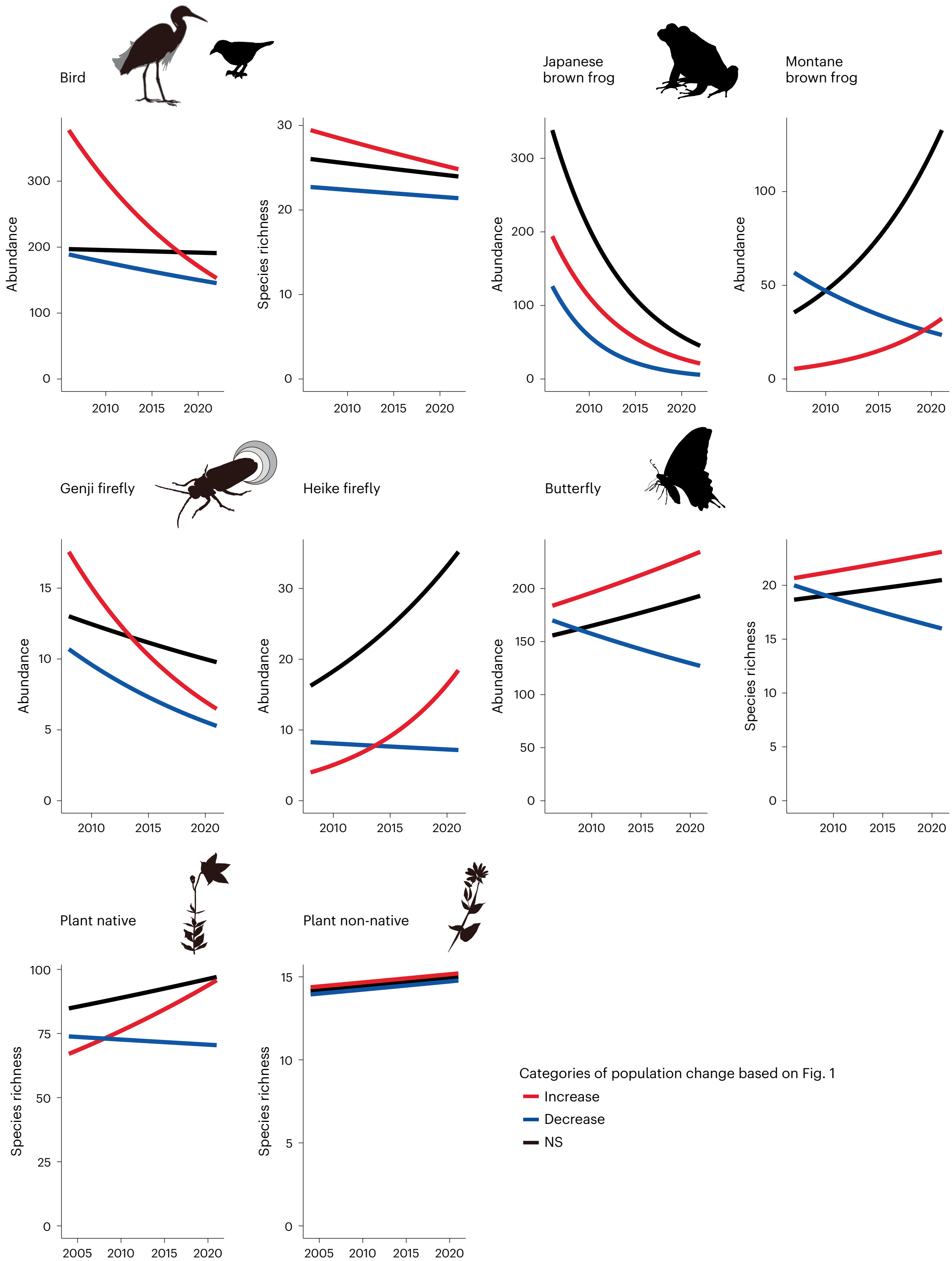

Fig. 3 | Relationships between biodiversity change and human population change at the study sites. The colour coding of the trends represents the statistical results of population demography based on Fig. 1, with red indicating increasing trends, blue indicating decreasing trends and grey indicating no significant trend. Essentially, the graph shows the changes in biodiversity for the study sites, categorized according to increasing trends, decreasing trends or no significant trend in human population. The solid lines are regression curves based on coefficients estimated from the best models.

organism groups and their roles in ecosystems[50], although we did not consider this in our analysis. Incorporating these biological groups and functional diversity indicators in future research could enhance our understanding of depopulation–biodiversity interactions.

Notwithstanding, our research shows that human depopulation in Japan's WAPU landscapes can be ecologically highly disruptive and even destructive. Some species thrive in disruptive environments. These are often non-native and present additional conservation challenges, such as the drying and choking of formerly wet-rice paddy fields by plains forb species (for example, *Solidago altissima*). Fewer species survive in destructive environments, whether the human population is growing or decreasing.

Globally, change in land use and agricultural intensification, due to population and economic growth and lifestyle changes, are the major drivers of ecosystem degradation and biodiversity loss[51,52]. Biodiversity loss is manifested most prominently in primary forest clearance in developing countries for the production of meat and ultra-processed foods, and associated human settlement[53]. However, Japan is not Brazil. Rather than expanding into areas where contemporary human civilization has not had a large-scale presence, the number of people living and farming in Japan's long-settled agricultural regions is declining. These areas evolved into human-settled, rice-based, semi-natural agroecosystems from the time of the Jōmon-Yayoi transition, beginning roughly 3,000 years ago, and spreading south and east from northern Kyushu thereafter[54]. They depend on the maintenance provided by human livelihood practices, although their agrobiodiversity stability and sustainability are often overlooked[55,56].

Japan is not Chernobyl either, where a one-time exogenous factor caused a sudden, almost total human population loss, leading to some startling, although contested, accounts of biodiversity revival[56,57]. Instead, an expanding mosaic of under-occupied and abandoned farms and properties emerges gradually from within ostensibly still-functioning inhabited settlements. As demographic circumstances persist, so depopulation deepens and spreads across the national space over a period of decades to include broader regions and larger settlements[30]. Grey infrastructure also falls into disuse but is rarely removed. The outcome has been a simultaneous neglect of the built and transformation of the natural environments.

Crucially, the number of *akiya* (empty or abandoned homes) is steadily increasing to more than 9 million nationwide by October 2023 (5.8 million in 1998), or 13.8% of the housing stock[58]. This has consequences for attached paddy fields, fruit orchards and coppiced woodland becoming *akichi* (disused or abandoned land). Total agricultural output value has declined by 25% since 1984, with rice production falling 64%, indicating a substantial decline in wet-rice land use. The number of farmers is also declining, with their average age rising to 68.4, signalling a crisis of human sustainability[59]. Hence, while reports of increasing take-up of sustainable and traditional agricultural practices appear (areas awarded Globally Important Agricultural Heritage System status increased to 15 in 2023; Appendix D in the Supplementary Information), the overall agricultural land area is decreasing and dilapidated, and abandoned farmland is expanding. Land use transformation to either urban sprawl, or consolidation and intensification under a business-oriented agricultural policy, is advancing[40,59].

Partly because of high demolition and disposal costs, and punitive land taxes, housing and land in many rural areas are almost valueless and unsalable, exacerbating the problem of abandonment and neglect. However, under the continuing legacy of Japan's developmental and construction state[60], land is often sold to developers for transformation to urban functions, such as road transport and ribbon development, or shopping malls, sports facilities, new residential development and car parking, or consolidation of family farms into larger-scale agro-industrial intensification, such as vegetable and fruit horticulture under vast plastic hothouses[61].

Future prospects for biodiversity under depopulation

It is imperative that we halt the catastrophic decline of Earth's biodiversity and strive to restore the biosphere. The current situation is more than urgent[62]. Natural ecosystems hold intrinsic value and are indispensable for sustaining human life. Humans are integral to sustaining Japan's semi-natural areas; we know that depopulation will continue to deepen and expand spatially. These human outcomes are incompatible with either halting habitat and biodiversity losses or achieving revival and recovery under the current regime.

By introducing our theory of DVCs and positioning Japan as the DVC for Northeast Asia, we have established an agenda for further research into the relationship between human depopulation and its socio-environmental outcomes globally. In this study, our research suggests that depopulation and the associated change in land use may be a significant contributor to habitat and biodiversity loss for other ancient wet-rice anthropogenic biomes in Northeast China, South Korea and Taiwan, where human development patterns and geographical conditions are similar[23,29]. Consequently, we advise that passively waiting for spontaneous habitat and biodiversity recovery to occur in depopulating areas anywhere will probably result in an underwhelming outcome[25,63].

Rewilding is gaining attention worldwide as a strategy for recovering habitats and restoring ecosystem functionality and sustainability. Although a few rewilding projects are underway in Japan, these are small-scale and usually in mountainous areas, such as Akaya Forest in Gunma prefecture and Mount Diasen in Tottori prefecture[64,65]. Our findings show that large-scale spontaneous rewilding is unlikely in Japan's depopulating WAPU landscapes because urban expansion and land disuse and abandonment patterns as yet prevent widespread succession. Therefore, counterintuitively, we find that the reduction of human influence from depopulation does not necessarily result in restorative ecological outcomes.

This prompts the question of what an interventionist rewilding would look like in this context. What type of ecosystem would or should rewilding revert to, given that wet-rice agriculture and associated human practices have long been present? The experience of the Knepp Estate in the UK suggests that a true rewilding of ancient agricultural landscapes is impossible, but that a new interventionist wilding could be successful[66]. As a keystone species in Japan's WAPU landscapes, what role would humans have in such a wilding, even as their numbers continue to decline?

Human depopulation presents substantial opportunities for achieving socio-environmentally (re)generative solutions. Global research indicates that investment in biodiversity conservation works in most cases[67]. Hence, long-term monitoring of biodiversity alongside human activities, and understanding the significance of these interrelationships in the context of local and global change, is essential. Although population decline and land use change have often not been analysed together in sufficient detail in biodiversity studies, we consider it necessary for Japan and other depopulating countries in Northeast Asia, Southern Europe and elsewhere in future. Careful consideration of the maintenance of wildlife-friendly human livelihood practices in depopulating WAPU landscapes in these countries is crucial. Achieving a biodiversity depopulation dividend demands coordinated long-term monitoring of the human–environment nexus with active habitat and biodiversity management for conservation and recovery. In the absence of such coordination, habitat and biodiversity losses in Japan's WAPU landscapes are likely to continue, even as the number of people living there decreases. Therefore, we urge all countries facing depopulation now or in the future to account for its outcomes in their biodiversity conservation and restoration strategies.

Methods

Study area

Alongside other countries, over the past 100 years, significant loss of natural and semi-natural habitat has occurred in Japan, mainly because of urbanization and agricultural expansion in the course of Japan's demographic and economic development (Supplementary Fig. 6).

Our research revealed aspects of biodiversity trends relating to depopulation, land use and climate change in WAPU locations across the Japanese archipelago. We focused on these areas because they represent regions of greatest interaction between nature and humans;

they are where the greatest human population decline has been occurring in recent decades under national-scale depopulation. Moreover, these regions bear important geographical and ecological similarities to equivalent landscapes in South Korea, Northeast China and beyond, where wet-rice agriculture and its associated human livelihood practices are an embedded feature of local ecosystems.

Macro-level demographic data

Japan is already well known as the first Asian country to encounter long-term below-replacement human fertility, leading to demographic ageing and depopulation. To demonstrate Japan's role as the DVC for Northeast Asia, we set it within both the world and regional contexts using the United Nations Population Division World Population Prospects 2024[2]. While noting this dataset's limitations for future fertility projections[16], it presents globally comparable and actual national population change to 2023, and models projections from 2024 onwards. Our research measures only changes among selected biodiversity assemblages against changes in human population size, without considering the impact of changes in the population-age structure. We assume that ageing will have a similar, perhaps more muted, effect because of the tendency for older farmers to reduce productivity in labour-intensive agriculture[68,69].

Adopting strict inclusion criteria, we narrowed the dataset pool of 233 countries and territories to 11 independent countries showing the earliest onset for indicators of long-term continuous depopulation caused primarily by natural causes (Supplementary Table 1). Among these 11, Japan was the only Asian country. Next, to demonstrate Japan's position at the vanguard of a region-wide trend of low fertility leading to depopulation, we used the same indicators to compare Japan's situation in relation to its Northeast and Southeast Asian neighbours. Supplementary Table 2 shows that the whole East Asian region is in the grip of a long-term depopulation trend, with Japan at the vanguard. The table also shows Northeast and Southeast Asian countries as distinct groups, with Northeast Asia depopulating and Southeast Asia growing but with decreasing human fertility leading to depopulation in the future.

Local-level population, land use and climate change data

To account for temporal and local spatial inconsistencies between our demographic and biodiversity data, we combined local-area mesh statistics with the National Census for 1995–2020. Mesh statistics divide a region into local-area grids (meshes) based on latitude and longitude and organize statistical data for each grid. Combining these datasets enables precise observation of demographic and biodiversity change over smaller geographical scales.

First, we aggregated human population data for the areas surrounding the study sites. After determining the latitude and longitude coordinates for each research site, we used R to identify the 1-km mesh code. We selected two scales, 25 km^2 (5 × 5 km) and 100 km^2 (10 × 10 km), as the basic unit range for the analysis. The process for obtaining data within a 25-km^2 range involved identifying the 1-km mesh code, using ArcGIS to open the grid map, taking the confirmed 1-km mesh as the centre, and then counting two grids on the top, bottom, left and right to determine a square area with a side length of 5 km containing twenty-five 1-km grids. We obtained the population size of each 25-km^2 range by aggregating the population size of these 25 grids. Similarly, for the 100-km^2 range, after confirming the mesh code, we counted four grids to the left and upper sides of the confirmed 1-km grid, and five grids on its right and lower sides, to determine a square area with a side length of 10 km containing one hundred 1-km grids. Finally, we aggregated the population of each grid to obtain the population size within a 100-km^2 range.

Next, we included data on land use change from 1997 to 2016, the closest available period. We applied the same scoping method as above, then combined it with national land numerical information data. National land numerical information statistics include data on the area of each land use category (paddy field, forest, wasteland, built site, highway site, river area, lake). Change in land use was divided for later analysis into three groups: urban; forested; and land under cultivation. The proportion of land under cultivation surrounding each survey site in 1997 averaged 21.9% with an s.e. of 1.2%, while forests averaged 42.9% (s.e. = 2.2%) and artificial land averaged 28.0% (s.e. = 1.9%). In 2016, the proportion of land under cultivation decreased to an average of 17.7% (s.e. = 1.2%), while forests increased slightly to 44.4% (s.e. = 2.2%) and artificial land expanded to 31.4% (s.e. = 2.1%).

We then compared the demographic and data on land use and found that they were highly significantly correlated between the 25-km^2 and 100-km^2 areas (population demography, $r = 0.67$, $P < 0.001$; urbanization, $r = 0.95$, $P < 0.001$; land under cultivation, $r = 0.88$, $P < 0.001$; forestation, $r = 0.94$, $P < 0.001$). Considering human movement distances, we used the 100-km^2 (10 × 10 km) data in the subsequent analyses.

Finally, when analysing long-term biodiversity change, the impact of climate change cannot be ignored. As a covariate factor, we consequently included annual average temperatures from the Japan Meteorological Agency from 1995 to 2020, using data from the nearest meteorological station to each survey site.

Biodiversity data

We used unpublished biodiversity data for the period spanning 2004 to 2021 from Monitoring Sites 1000 (Appendix E in the Supplementary Information). The data used are from surveys conducted in WAPU landscapes. These landscapes account for approximately 40% of the land area in Japan[70]. The study sites were selected from agricultural secondary natural areas on land, excluding locations of newly created habitat by humans, such as artificial biotopes. Furthermore, we did not include 'pristine' natural environments free from obvious signs of human disturbance in our study. Over the past 50 years, from 1970 through to the present, Japan's forest cover has remained approximately 67%, with around 40% consisting of plantations, such as Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*) for timber production. The WAPU areas surveyed in our study include both succession forests and plantations. However, as already stated, our study sites are settled rural and peri-urban areas where agricultural land, forests and artificial land are intermingled in a mosaic pattern.

The survey area for each site was set to encompass a contiguous ecosystem, with a target size of approximately 30–100 hectares. Data from sites with a survey duration of less than 4 years were excluded; analysis was conducted on 158 sites within the latitude and longitude ranges of 24–44° and 123–145°, respectively, and with surveys conducted continuously for over 5 years. Detailed data for each site can be found in Supplementary Table 4. While the survey methods were generally standardized across all sites, we accounted for climate and topography variations at each survey location. Consequently, surveys differed in terms of survey area coverage and the number of surveys conducted annually for each individual site. Hence, we analysed individual sites to understand the cumulative fluctuating trends in biodiversity among selected species across Japan as a whole.

For this study, we focused on reliable information obtained through censuses for specific taxa, including birds (community data), frogs (population data for three species), insects (population data for two species of fireflies and community data for butterfly species) and plants (community data for both native and non-native species). Among the Monitoring Site 1000 data, camera trap data for mammals were included. However, because of changes in camera trap methods over time, direct comparisons with past data are challenging. To avoid drawing incorrect conclusions, we excluded these data from our analysis. Additionally, surveys of habitat area for the harvest mouse were conducted but abundance was not measured for this species. Hence, we excluded it from our analysis. The selected taxa cover a broad range of the ecological pyramid in semi-natural ecosystems, from top predators (birds) to producers (plants). Consequently, they provide a suitable dataset for evaluating the impacts of demographic and environmental change on organisms in semi-natural ecosystems (Supplementary Table 3).

During the breeding (April–August) and wintering (October–March) seasons, observers recorded the names and number of species, and the number of individuals, of birds observed within a 50-m radius along survey routes for subsequent analysis. Surveys were conducted three times per season, totalling six annually; the same routes were traversed to minimize survey biases for each round.

We conducted surveys of frogs, a key indicator species for both terrestrial and aquatic ecosystems, during the breeding season (October–June). Each survey location had a markedly different latitude, so the breeding season for each site was surveyed over a wide range. We counted the total number of egg masses for three frog species (*R. japonica*, *R. ornativentris* and *R. pirica*) because counting egg masses made the survey easier. Adult frogs inhabit areas such as farmland and mountain lowlands, making it preferable to focus on surveying their congregations during the breeding season to quantify their population. Moreover, as *R. pirica* inhabits a limited number of regions, we analysed it alongside *R. ornativentris*, which is phylogenetically close[71].

Among insects we surveyed butterflies, whose larval host plants and adult nectar sources are located in semi-natural grasslands and forests around farmlands. Additionally, fireflies live close to water resources in the agricultural environment. For butterflies, we recorded the species name and number of individuals observed within a 5-m radius along the survey routes, with surveys conducted one or more times per month. For fireflies, we recorded the number of individuals during the breeding season for two key species, Genji fireflies (*N. cruciata*) and Heike fireflies (*A. lateralis*), which serve as indicators for aquatic organisms.

For plant species, once a month we recorded the names of plants with reproductive organs, such as flowers and fruits, observed along the survey routes. Each survey route was set to include a variety of landscape types, such as forests, forest edges, rice fields, fallow fields, wetlands, grasslands and roads; we recorded plant species observed along these routes. The surveyed plants included herbaceous species (seed plants and ferns) and woody species. Assessing plant abundance was not feasible, so we opted to analyse the number of species instead.

For taxonomic groups with available data on individual counts, we conducted analyses of annual variation in abundance using the method described below. Additionally, for birds, butterflies and plants with data on species numbers, we also conducted analyses of annual variation in species richness. We categorized plants into native and non-native species because the impact of population and land use changes may vary for each category. Separate analyses were conducted for the number of species for each group. For birds and butterflies, we analysed only native species because the number of non-native species was seven and one, respectively.

Analysis overview

Our analysis consisted of three components. First, we analysed and mapped human population transitions, change in land use and average temperature change (158 sites). Then, we analysed and mapped fluctuations in species abundance and richness (Supplementary Table 4). Finally, we analysed the relationships between population and change in land use, and changes in species abundance and richness (Supplementary Table 4).

Fluctuation trends in environmental factors

To examine annual change in environmental factors at each site, we used linear models with the population, land use or mean temperature as the response variables and year as the explanatory variable for each study site. In other words, the environmental factors in each sample E_i were defined as:

$$E_i \approx N(\lambda_i)$$

Expectations under a Gaussian process λ_i were:

$$\lambda_i = \beta_1 \times Y_i + \beta_2$$

where β_1 and β_2 are the parameters estimated using linear models and Y_i is the year. Based on the significance of the slope for the year ($\alpha = 0.05$), each study site was classified into three environmental change categories: increase (significantly positive); decrease (significantly negative); and no significant trend.

Fluctuating biodiversity trends

To examine annual changes in biodiversity among our selected taxonomic species at each site, we used generalized linear models (GLMs) (family = Poisson; link = log) with abundance or species richness as the response variables and year and month as the explanatory variables for each study site. The exception was where the survey date was included in the bird model as a random effect (generalized linear mixed models (GLMMs)) because bird surveys were performed multiple times per day. In other words, species richness or abundance in each sample N_i were defined as:

$$N_i \approx \text{Poisson}(\lambda_i)$$

In this case, expectations under a Poisson process λ_i were:

$$\lambda_i = \begin{cases} \exp\left(\beta_1 \times Y_i + \beta_2 + M_i + d_i\right), & \text{if birds} \\ \exp\left(\beta_1 \times Y_i + \beta_2 + M_i\right), & \text{other organisms} \end{cases}$$

where β_1 and β_2 are the parameters estimated using GLMs or GLMMs, Y_i is the year and d_i is the random effect of the survey date. The effects M_i of the month on species richness or abundance were:

$$M_i = \beta_3 \times m_{1,i} + \beta_4 \times m_{2,i} + \cdots + \beta_{n+1} \times m_{n-1,i}$$

where $\beta_3, \beta_{4\ldots}\beta_{n+1}$ were the parameters estimated using GLMs or GLMMs, and $m_{1,i}, m_{2,i\ldots}m_{n-1,i}$ are the dummy variables of n month.

We excluded from the analysis some sites where the target taxa were not observed in any individuals. Based on the significance of the slope for the year ($\alpha = 0.05$), each study site was classified into three change categories: increase (significantly positive); decrease (significantly negative); and no significant trend.

Effects of human anthropogenic factors on biodiversity

We evaluated how the population and land use change categorizations (increase, decrease, no significant trend) affect biodiversity. The response variable was the abundance or species richness of each taxon. The explanatory variables were: year, month; changes to population, urbanization, land under cultivation, forest and temperature; and interactions between year and each environmental change. Site identity and spatial autocorrelation were incorporated as random effects in GLMMs (family = Poisson, link = log). The spatial autocorrelation matrix was fitted using the spaMM package[72] with the Matérn structure of pairwise correlations between the coordinates of each site location, accounting for spatial dependencies that might otherwise bias the results. In other words, species richness or abundance observed in each sample i was defined as:

$$N_i \approx \text{Poisson}(\lambda_i).$$

In this case, expectations under a Poisson process λ_i were:

$$\begin{aligned}\lambda_i = \exp(&(\beta_1 \times P_{\text{inc},i} + \beta_2 \times P_{\text{dec},i} + \beta_3 \times U_{\text{inc},i} + \beta_4 \times C_{\text{dec},i} + \beta_5 \times F_{\text{dec},i} \\ &+\beta_6 \times F_{\text{inc},i} + \beta_7 \times T_{\text{inc},i} + \beta_8) \times Y_i + \beta_9 \times P_{\text{inc},i} \\ &+\beta_{10} \times P_{\text{dec},i} + \beta_{11} \times U_{\text{inc},i} + \beta_{12} \times C_{\text{dec},i} + \beta_{13} \times F_{\text{dec},i} \\ &+\beta_{14} \times F_{\text{inc},i} + \beta_{15} \times T_{\text{inc},i} + \beta_{16} + M_i + s_i + \xi_i)\end{aligned}$$

where $\beta_1, \beta_{2}, _{\ldots}\, \beta_{16}$ are parameters estimated using GLMMs, Y_i is the year, $P_{\text{inc},i}$ and $P_{\text{dec},i}$ are the dummy variables of the population change categories, $U_{\mathrm{inc},i}$ is the dummy variable of the urbanization change categories, $C_{\mathrm{dec},i}$ is the dummy variable of the land under cultivation change categories, $F_{\mathrm{dec},i}$ and $F_{\mathrm{inc},i}$ are the dummy variables of the forest change categories, $T_{\mathrm{inc},i}$ is the dummy variable of the temperature change categories and s_i is the random effect of study site ('inc' = increase, 'dec' = decrease in all variable labels). ξ_i is the random effect accounting for spatial autocorrelation. Also, the effects of the month (M_i) on species richness or abundance were:

$$M_i = \beta_{17} \times m_{1,i} + \beta_{18} \times m_{2,i} + \cdots + \beta_{n+15} \times m_{n-1,i}$$

where $\beta_{17}, \beta_{18}, \ldots \beta_{n+15}$ are the parameters estimated using GLMMs, and $m_{1,i}, m_{2,i} \ldots m_{n-1,i}$ are the dummy variables of n month.

Before the analysis, we calculated the variance inflation factor values for each model to check for issues of multicollinearity (all variance inflation factors were less than 3.3). The best model was selected based on the minimum Akaike information criterion by evaluating all possible combinations of the explanatory variables. We conducted all analyses in R v.4.4.2 (ref. 73) using the fitme function with the spaMM package[72].

Reporting summary

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

Data availability

The raw population data were obtained from the Statistics Bureau of Japan (www.stat.go.jp/data/jinsui/). The raw land-use map data were sourced from the National Land Information Division, National Spatial Planning and Regional Policy Bureau, MLIT of Japan (https://nlftp.mlit.go.jp/ksj/). The raw climate data were obtained from the Japan Meteorological Agency (www.data.jma.go.jp/stats/etrn/index.php). The raw biodiversity data were provided by the Biodiversity Center of Japan (www.biodic.go.jp/index_e.html). To use biodiversity data for research purposes, researchers must apply to the Biodiversity Center of Japan for permission regarding the purpose and use of the data. The Biodiversity Center of Japan can provide information on the time frame for responses to requests and the details of any restrictions imposed on data use via data use agreements. The data that we curated and analysed from the raw data are available via Figshare at https://doi.org/10.6084/m9.figshare.26347669 (ref. 74).

Code availability

The code used for the analyses is available via Figshare at https://doi.org/10.6084/m9.figshare.26347669 (ref. 74).

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Author contributions
K.U., P.M. and M.K.H. conceived and designed the study theme and analyses. K.U. and M.K.H. performed all the statistical analyses of the data. K.U., Y.L. and T.F. curated the sourcing of biodiversity, population and land-use materials. P.M. and Y.L. contributed population data and materials, specifically the national-level population data, tables and calculations. K.U. and M.K.H. contributed the climate data materials. K.U., P.M. and M.K.H. wrote the first draft of the paper, with Y.L. drafting the initial version of the section on collecting gridded population and data on land use. All authors contributed subsequent revisions.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-025-01578-w.

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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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☐	☒	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	The diversity of all organisms were quantified with visual count survey method. The bird diversity was conducted both visual and acoustic survey. All surveys are the result of researches have conducted by researchers, advanced amateurs, non-profit organizations, and citizens throughout Japan. All data are compiled by the Ministry of the Environment, Government of Japan. To use biodiversity data for research purposes, the researchers have to apply to the Biodiversity Center of Japan for permission regarding the purpose and use of the data (https://www.biodic.go.jp/index_e.html). Population, land-use, and meteorology data can be downloaded by Ministry of Internal Affairs and Communications, Ministry of Land, Infrastructure, Transport and Tourism, and Japan Meteorological Agency, respectively (see Data Availability section).
Data analysis	All analyses were conducted using R version 4.4.2. The code used for the analyses has been uploaded to [figshare]. [figshare]:https://doi.org/10.6084/m9.figshare.26347669

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We used unpublished biodiversity data for the period spanning 2004 to 2021 from Monitoring Sites 1000 (project in the Ministry of the Environment, Government of Japan). The data used for the analyses have been uploaded to [figshare]. Although, the raw data including the distribution of endangered organisms cannot be made open due to conservation concerns, the raw data can be obtained by submitting an application for use. To use biodiversity data for research purposes, the researchers have to apply to the Biodiversity Center of Japan for permission regarding the purpose and use of the data (https://www.biodic.go.jp/index_e.html). The researchers need ask the data availability for the Biodiversity Center of Japan about the timeframe for response to requests and details of any restrictions imposed on data use via data use agreements.
Population, land-use, and meteorology data can be downloaded by Ministry of Internal Affairs and Communications, Ministry of Land, Infrastructure, Transport and Tourism, and Japan Meteorological Agency, respectively (see Data Availability section).
[figshare]:https://doi.org/10.6084/m9.figshare.26347669

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	We did not use any Human research materials.
Reporting on race, ethnicity, or other socially relevant groupings	We did not use any Human research materials.
Population characteristics	We did not use any Human research materials.
Recruitment	We did not use any Human research materials.
Ethics oversight	We did not use any Human research materials.

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.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

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

Study description	We analysed biodiversity change in 158 sites in semi-natural and peri-urban areas across the Japanese archipelago over periods of between 5 to 17 years starting in 2004, alongside actual local spatial and temporal variability in human population, land use, and average annual surface temperature. Our biodiversity dataset encompasses a comprehensive list of taxa in the ecological trophic pyramid within semi-natural ecosystems, registering more than 1.5 million individual detections of 464 taxonomic species of bird, butterfly, firefly, and frog egg masses, and 2,922 native and non-native plant species.
Research sample	We used unpublished biodiversity data for the period spanning 2004 to 2021 from Monitoring Sites 1000. Established in 2003 to continuously gather and store data on species diversity and environmental conditions collected by researchers and citizens, this dataset is compiled and archived by the Ministry of the Environment's Biodiversity Center, Government of Japan. More details here. https://www.biodic.go.jp/moni1000/findings/newsflash/. Data from sites with a survey duration of less than 4 years were excluded, and analysis was conducted on 158 sites within latitude and longitude ranges 24°–44° and 123°–145° 396 respectively, and with surveys conducted continuously for over 5 years duration.
Sampling strategy	This study utilized national-level biological monitoring data that had been collected prior to the design of this research. Although statistical methods were not used to determine the sample size, all samples were included in the analysis except for those excluded based on the criteria outlined in the data exclusions section. As a result, there was no bias in the selection of samples. Furthermore, even after exclusions, data from 158 sites covering the Japanese archipelago were analyzed, which is considered sufficient for this study.

Data collection	The diversity of all organisms were quantified with visual count survey method. The bird diversity was conducted both visual and acoustic survey. All surveys are the result of researches have conducted by researchers, advanced amateurs, non-profit organizations, and citizens throughout Japan. All data are compiled by the Ministry of the Environment, Government of Japan, and raw data can be obtained by submitting an application for use. Population, land-use, and meteorology data can be downloaded by Ministry of Internal Affairs and Communications, Ministry of Land, Infrastructure, Transport and Tourism, and Japan Meteorological Agency, respectively.
Timing and spatial scale	We analyzed biodiversity change in 158 sites in semi-natural and peri-urban areas across the Japanese archipelago over periods of between 5 to 17 years starting in 2004. At each site, multiple surveys were conducted annually during the active periods of the target taxa.
Data exclusions	Data were excluded from the analyses if they were from sites with a survey duration of less than 4 years, as this duration is too short to observe temporal changes. Additionally, we excluded from the analysis sites where the target taxa were not observed at all during the survey period. These criteria were determined prior to the analysis.
Reproducibility	To ensure reproducibility, all protocols and procedures used in this study were meticulously documented. The data and code used for the analyses are publicly available at [figshare]. By using data from 158 sites, we confirmed that the results were not due to site-specific phenomena.
Randomization	This study involved numerous field surveyors conducting research at various locations, ensuring that no specific surveyor was disproportionately represented. Additionally, all site data were used except for the locations excluded as mentioned in the data exclusions section, ensuring that there was no bias in the selection of survey sites.
Blinding	This study used data from the long-term biological monitoring program, Monitoring Site 1000, which has been conducted nationwide since 2003. This program was established prior to the initiation of this study, ensuring that data collection was not influenced by any biases related to this research.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The sampling was carried out during the peak season of biomass production and active period for all species. All sampling was not conducted in rainy condition or excluding sampling data in the rain condition before analysing.
Location	Data from sites with a survey duration of less than 4 years were excluded, and analysis was conducted on 158 sites within latitude and longitude ranges 24°–44° and 123°–145° 396 respectively, and with surveys conducted continuously for over 5 years duration.
Access & import/export	On-site work permits were issued by the landowner and the local administration. At each of the survey areas, the surveys were conducted after the respective permits were obtained.
Disturbance	Activity of investigators was spatially limited at each site.

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
☐	☒	Plants

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	No laboratory animals were involved in the study.

Wild animals	We did not collected wild animals for the study. We collected species data using the visual and the acoustic methods.
Reporting on sex	No sex-related data were collected for this study.
Field-collected samples	We did not collected wild animals for the study. We collected species data using the visual and the acoustic methods.
Ethics oversight	We did not collected wild animals and plants for the study. We collected species data using the visual and the acoustic methods.

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

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☒	☐	Public health
☒	☐	National security
☒	☐	Crops and/or livestock
☒	☐	Ecosystems
☒	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
☒	☐	Demonstrate how to render a vaccine ineffective
☒	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐	Increase transmissibility of a pathogen
☒	☐	Alter the host range of a pathogen
☒	☐	Enable evasion of diagnostic/detection modalities
☒	☐	Enable the weaponization of a biological agent or toxin
☒	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	We did not collect the plant seeds.
Novel plant genotypes	We did not collect the plant genes.
Authentication	We did not collect the plants.