Biodiversity and ecosystem services in cultural landscapes of Germany and Japan

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Summary

This cumulative dissertation takes a comparative approach to studying the spatial patterns of biodiversity and ecosystem services in agricultural landscapes of Germany and Japan. In both countries, biodiversity and ecosystem services maintained by the respective traditional farming systems are declining due to agricultural intensification and land abandonment. Landscape associations of bird species that are typical in agricultural landscapes of Germany and Japan were analyzed jointly, while spatial associations of ecosystem services were investigated using data from Japan only owing to the different frameworks used by public institutions for gathering data. Findings from the latter study were compared to published results from the literature in Europe. Both studies were carried out at the national level. Distribution data on bird species were obtained from nationwide monitoring programs, and metrics of landscape structure and ecosystem services linked to agroecosystems were calculated based on spatial datasets and public statistics using a geographical information system.

The first chapter demonstrates that farmland bird diversity responds to the proportions of farmland cover and semi-natural habitat cover in a similar way between Germany and Japan. The results also suggest that landscape associations can vary according to the countries. Woodland edge density had a pronounced effect on species numbers in Germany where farmland dominates. In contrast, farmland cover was more relevant in Japan than in Germany; in Japan, where forests dominate, the effect of woodland edge density was only marginal. The importance of open habitats and landscape heterogeneity for maintaining farmland bird diversity was supported by these findings. In the second chapter, landscapes in Japan specializing either in commodity production or in cultural services and habitat features were identified based on indicators for agricultural ecosystem services and farmland biodiversity. The latter landscapes coincided with areas at risk of land abandonment. The spatial aggregation of biodiversity and culturally valuable resources on marginal land, where traditional farming systems are likely to persist, underlies the importance of conserving the structural features of traditional farming systems. To conclude, this dissertation supports the notion that landscape structure, biodiversity, and ecosystem services are linked significantly, and that such links apply generally in Germany and Japan.

Zusammenfassung

Diese kumulative Dissertation verfolgt einen vergleichenden Ansatz zur Untersuchung der räumlichen Muster von Biodiversität und Ökosystemleistungen in Agrarlandschaften Deutschlands und Japans. In beiden Ländern nehmen die biologische Vielfalt und die Ökosystemleistungen, die durch die jeweiligen traditionellen landwirtschaftlichen Systeme erhalten werden, aufgrund der Intensivierung der Landwirtschaft und der Landnutzungsaufgabe ab. Für typische Vogelarten der Agrarlandschaft wurde der Zusammenhang mit der Landschaft für Deutschland und Japan zusammen analysiert. Die räumlichen Zusammenhänge von Ökosystemleistungen wurden dahingegen nur für Japan untersucht da hier andere Rahmenbedingungen für die Erhebung öffentlicher Daten gelten. Die Ergebnisse der letztgenannten Studie wurden anhand der relevanten Literatur mit denen in Europa verglichen. Beide Studien konzentrierten sich auf die nationale Ebene. Verbreitungsdaten der Vogelarten wurden aus landesweiten Monitoring Programmen gewonnen, und Metriken zur Landschaftsstruktur und zu Ökosystemleistungen im Zusammenhang mit Agrarökosystemen wurden anhand von räumlichen Datensätzen und öffentlichen Statistiken mithilfe eines geografischen Informationssystems erstellt.

Das erste Kapitel zeigt, dass die Vogelvielfalt im Ackerland auf den Anteil von Ackerlandbedeckung und naturnaher Habitatbedeckung in Deutschland und Japan ähnlich reagiert. Die Ergebnisse deuten auch darauf hin, dass landschaftliche Zusammenhänge je nach Land variieren können. In Deutschland wirkt sich, in Landschaften welche durch Ackerland dominiert werden, die Waldranddichte stark auf die Artenzahlen aus. Im Gegensatz dazu war in Japan, wo Wälder dominieren, der Effekt der Waldranddichte nur marginal aber die Ackerlandbedeckung relevanter als in Deutschland. Die Ergebnisse unterstreichen die Bedeutung offener Lebensräume und der landschaftlichen Heterogenität für die Erhaltung der Vielfalt der Ackerlandvögel. Im zweiten Kapitel identifizierte ich anhand von Indikatoren für landwirtschaftliche Ökosystemleistungen und Biodiversität Landschaften in Japan, die entweder auf landwirtschaftliche Produktion oder auf kulturelle Leistungen und Habitatelemente spezialisiert sind. Letztere Landschaften sind einem höheren Risiko der Landnutzungsaufgabe ausgesetzt. Die räumliche Aggregation von Biodiversität und kulturell wertvollen Ressourcen auf marginal Standorte, auf denen traditionelle Anbausysteme am besten erhalten sind, verdeutlicht die Notwendigkeit strukturelle Elemente traditioneller Anbausysteme zu erhalten. Zusammenfassend lässt sich sagen, dass Landschaftsstruktur, Biodiversität und Ökosystemleistungen in signifikanter Weise miteinander verknüpft sind, und dass diese Beziehungen für Deutschland und Japan allgemein gelten.

General introduction

The aim of this dissertation is to compare biodiversity and ecosystem services in agricultural landscapes of Germany and Japan. The two geographically distant countries show parallels in the development of agricultural landscapes with regard to the shaping of social-ecological systems and the divergent trends of intensification and land abandonment. Identifying similarities and differences in the spatial patterns of farmland biodiversity and agricultural ecosystem services in the face of common challenges is a prerequisite for the sustainable management of agricultural areas worldwide.

Agricultural landscapes

Sustainable social-ecological systems are 'coupled systems of people and nature,' in which feedback linkages between the two have co-produced a society in harmony with nature (Berkes *et al.*, 2000; Preiser *et al.*, 2018). Agriculture is a key determinant of many cultural landscapes for its influence on the largest part of the global land surface (Foley *et al.*, 2011; Vanbergen *et al.*, 2020). Agricultural landscapes that have developed through intertwined human-nature interactions over hundreds or even thousands of years exhibit a large variation in structure and function around the world, as they were shaped by diverse cultures under diverse socio-economic conditions in diverse climatic regions (Power, 2010). Arable land use and animal husbandry have created open areas with mosaics of diverse habitats and land use forms at different successional stages that maintain biodiversity and provide people with goods and services for their health, livelihoods, and well-being (IPBES, 2019).

Farmland biodiversity and agricultural ecosystem services, particularly those related to cultural values (Bridgewater and Rotherham, 2019), are declining due to the transition from subsistence agriculture to intensive agriculture that has taken place over the past decades (Antrop, 2005; Foley *et al.*, 2005; Stoate *et al.*, 2009). Most increases in commodity production have resulted in homogenous farming systems through agricultural intensification measures such as the use of agrochemical inputs, mechanization, and improved irrigation as well as farm specialization and farmland consolidation via removal of non-cropped habitats (IAASTD, 2009). Intensification has occurred particularly in more productive landscapes like coastal and river lowlands, wetlands, and fertile plains (Pinto-Correia and Kristensen, 2013; Levers *et al.*, 2018). On the other hand, reduced use or abandonment of agriculture is putting additional pressures on social-ecological systems, as scrub and forest encroachment on former farmland can also lead to a loss of landscape character and heterogeneity (MacDonald *et al.*, 2000;

Schirpke *et al.*, 2016; Quintas-Soriano *et al.*, 2022) as well as to a replacement of open-habitat specialists with more common generalist species (Laiolo *et al.*, 2004; Keenleyside and Tucker, 2010; Sugimoto *et al.*, 2022). Marginal land is particularly affected by farmland abandonment, where productivity is low and natural disadvantages such as steep slopes and difficult access impede modernization of agriculture (Benayas *et al*, 2007; Subedi *et al.*, 2021). Abandonment of less productive land can also be induced by agricultural intensification (Busch, 2006). Traditional rural landscapes, including the key elements that sustain biodiversity and ecosystem services, are under threat from divergent land use trends toward intensification and land abandonment, in addition to urbanization-depopulation dichotomies occurring in the process of globalization (Plieninger and Bieling, 2012; Lomba *et al.*, 2019).

Global efforts to support social-ecological systems

While indigenous and local knowledge systems are locally based, they are manifested in regional landscapes, and the diversity created in these landscapes is globally relevant (IPBES, 2019). There have been increasing efforts to protect and preserve social-ecological systems in the past few decades, starting with those possessing 'outstanding universal values' such as cultural landscapes within the World Heritage Convention (category ii – organically evolving landscapes; UNESCO, 2008) and the Globally Important Agricultural Heritage System (FAO, 2016). The 10th Conference of the Parties to the United Nations Convention on Biological Diversity (CBD-COP10) held in Japan adopted a global initiative called 'The Satoyama Initiative' to promote and sustain social-ecological systems in general to maintain biological diversity and their contributions to human well-being (IPSI, 2013). A more recent development is Other Effective area-based Conservation Measures (OECMs), which aim to increase recognition and support for *de facto* effective long-term conservation that is taking place outside protected areas under a range of governance and management regimes (CBD, 2018). Accumulating case studies from different parts of the world and sharing their information are important steps for increasing the effectiveness of global efforts for sustaining biodiversity and ecosystem services maintained by social-ecological systems (IPSI, 2013).

Biodiversity in agricultural landscapes

Species that are adapted to agroecosystems are considered to have expanded their distributions from natural grass- and shrubland, and to have synchronized their life cycle with e.g. crop growing season and management regimes of semi-natural habitats (Katano, 1998; Samu and Szinetár, 2002; Westphal *et al.*, 2003). Different forms of land use maintained by traditional management practices, including semi-natural habitats and vegetation at different successional stages within and between fields, offer a broad range of niches to fauna and flora inhabiting agroecosystems (Baldock *et al.*, 1995; Katoh *et al.*, 2009; Šálek *et al.*, 2018). These habitats aid species persistence by providing e.g. refuges for overwintering (Pfiffner and Luka, 2000), feeding areas (Maeda, 2001; Vickery *et al.*, 2009), and dispersal corridors (Pickett and Thompson, 1978). Their area, diversity, and/or connectivity have been generally identified to have a positive influence on species richness and abundance of common taxa in agricultural landscapes (Billeter *et al.*, 2007; Hendrickx *et al.*, 2007; Estrada-Carmona *et al.*, 2022; Sánchez *et al.*, 2022). For highly mobile taxa like birds, the conversion of up to 44% of natural area to human-dominated land cover can benefit open-habitat species richness without harming forest species because it adds a large area of formerly uncommon habitat and a variety of associated land uses to the landscape (Desrochers *et al.*, 2011).

The strength of associations between land use and biodiversity can vary depending on the landscape context, which moderates the effects of local land use on communities and interacts with different management schemes (Winqvist *et al.*, 2012). For example, a meta-analysis revealed that agri-environmental management in cropland enhanced species richness of several taxa in simple, but not in complex landscapes, whereas that in grassland was equally effective in both landscape types (Batáry *et al.*, 2011). Such landscape-moderated effects of land use have been reported in many cases to be related to low-intensity farming and semi-natural habitats in open landscapes (Roschewitz *et al.*, 2005; Herzon and O'Hara, 2007; Batáry *et al.*, 2010) as well as in cases like arable fields within grassland landscapes (Robinson *et al.*, 2001). Similar relationships might also hold true for farmland surrounded by vast areas of forest, as open land forms a relatively rare habitat, restricting food resources available for species that depend on farmland (Wretenberg *et al.*, 2010).

Ecosystem services in agricultural landscapes

Agricultural ecosystems are managed chiefly to meet material human needs – food, fiber, and fuel. They are traditionally considered as primary sources of provisioning services, but their contributions to other types of ecosystem services have increasingly been recognized (MEA, 2005). While conversion of natural systems to agricultural use often results in profound environmental impacts (Foley *et al.*, 2005, 2011), agroecosystems do still retain many features common to natural systems and can provide a range of regulating and supporting services (Swinton *et al.*, 2007; Bethwell *et al.*, 2021). Cultural services are also key components of cultural landscapes because they arise from intimate human-nature interactions (Chan *et al.*, 2012; Balázsi *et al.*, 2021); often, they cannot be replaced easily once they have been lost (MEA, 2005). The delivery of ecosystem services largely depends on where an agroecosystem lies on the continuum between subsistence and intensive agriculture (de Groot *et al.*, 2010).

Trade-offs and synergies may exist among ecosystem services that are provided by agroecosystems. In general, prioritizing provisioning services results in the degradation of other services because trade-offs occur most likely when resource management involves private interest acting at a local scale (Howe *et al.*, 2014). Regulating services, by contrast, are in general positively associated with many other services and biodiversity that supports them (de Groot *et al.*, 2010; Pan *et al.*, 2022). These positive and negative interactions in space have been shown to form 'bundles' or sets of ecosystem services that repeatedly appear together across a landscape (Raudsepp-Hearne *et al.*, 2010; Meacham *et al.*, 2022). Reflecting the degree of anthropogenic impact, frequently identified ecosystem service bundles include those that are typical for sections of a landscape specializing in commodity production, those that are accompanied by high provision of multiple services due to high naturalness, and those at an intermediate level (Raudsepp-Hearne *et al.*, 2010; Turner *et al.*, 2014; Spake *et al.*, 2017). Cultural services add another layer of complexity to this general gradient, influenced by accessibility (Ala-Hulkko *et al.*, 2016), landscape features and land use forms (Plieninger *et al.*, 2013), and social-cultural preferences of people (Fagerholm *et al.*, 2012). The spatial distribution of different landscape types can be explained by biophysical characteristics, socio-economic factors, and land use history (Rodríguez-Loinaz *et al.*, 2015), many of which are listed as causes of intensification and abandonment.

Agricultural landscapes in Germany and Japan

Germany belongs to the temperate climate zone which stretches from the Alps across the North European Plain to the North Sea and the Baltic Sea. More than half of the land surface is farmed, while forest takes up approximately one third (Destatis, 2015). Open land thus characterizes many cultural landscapes of the country, especially in the northern half where large farms predominate. Arable land is widespread, covering 71% of the areas utilized for agriculture (Destatis, 2015). Permanent grassland occupies 28% (Destatis, 2015) and can be found in parts of Northern Germany and the northern Alpine foreland as well as in areas where arable farming is not feasible or not economically favorable (BMELV, 2013). Within farmland, landscape elements such as hedges, field margins, and ditches are managed as part of agriculture. These semi-natural habitats, in addition to e.g. fallow land and fields with characteristic plant species, are regarded as features of high nature value (HNV) farmland in Germany (BfN, 2020). HNV farmland is estimated to occupy 15% of farmland (EEA, 2012).

Japan is a country composed of four main islands that extends over several climate zones ranging from subarctic in the north to subtropical in the south. It is similar in size to Germany. The land is predominantly mountainous, and forest comprises two thirds of the land surface (Statistics Bureau, 2015). Farmland accounts for only 12% (Statistics Bureau, 2015). Fifty-four percent of farmland is periodically flooded to grow rice (*Oryza sativa*), and other arable land and grassland constitute 26% and 14%, respectively (MAFF, 2016). Paddy fields are often found on lowland alluvial plains, valley bottoms, or in terraced areas, while other arable land is usually located on relatively drier and sloping parts of the terrain (Takeuchi *et al.*, 2003). Most grasslands are sown and are mainly distributed in the northernmost island Hokkaido (MAFF, 2016). Semi-natural grasslands are rare nowadays, but they used to be distributed more widely, especially in hilly areas (Ogura, 2006). Irrigation ponds and ditches as well as field margins are maintained within farmland, with the first two being managed as part of rice production. In hilly and mountainous areas, paddy fields established on the valley bottom are often surrounded by forests on the hillslopes, forming a long boundary between the two land use classes along the outline of the valley bottom (Katoh *et al.*, 2009). A strip of grassland also occurs along the same vegetation boundary (Kitagawa *et al.*, 2004). The variety of landscape elements available in small-scale farmland characterizes traditional agricultural landscapes in Japan.

Traditional agricultural landscapes in both countries have developed from prehistoric beginnings to highly organized land management systems that sustained gradually growing populations and provided employment for a large part of the workforce until the mid-20th century (Vos and Meekes, 1999; Takeuchi *et al.*, 2003). After wartime destruction, both countries recovered quickly to unprecedented economic growth that induced major shifts in economic sectors, distribution of the population between rural and urban areas, demographic structure, and land use such as intensification and increasing scales of farming practices (Stoate *et al.*, 2001; Katayama *et al.*, 2015). These trends coincided with increasing economic wealth, but they were also accompanied by land degradation and biodiversity loss (MOE, 2012; EEA, 2019). Entering the 21st century, the population has started declining in both countries (Destatis, 2015; MLIT, 2015). The effects of these demographic trends are most pronounced in marginal rural areas where they contribute to the abandonment of agricultural areas (Gellrich and Zimmermann, 2007; Su *et al.*, 2018). Funding programs to support farmers and protect the environment have been established under the agricultural policies of Germany (within the framework of the Common Agricultural Policy of the European Union) and Japan, as they both recognize the significant role that agriculture plays in safeguarding biodiversity and delivering public services beyond food production (EC, 2021; MAFF, 2021).

Rationale for taking a comparative approach

The rationale for taking a comparative approach to studying biodiversity and ecosystem services in Germany and Japan is that the two distant countries show many parallels in the development of society, technology, economy, and land use, and they face similar challenges in relation to the maintenance of cultural landscapes. Landscape mosaics maintained by local management regimes have been identified as a universally applicable characteristic that is responsible for fostering different sets of faunal and floral communities around the world (IPBES, 2019; Estrada-Carmona *et al.*, 2022). Comparing response patterns obtained from two countries that are separated by a long geographical distance while sharing biological features that are present across the Palearctic offers a unique opportunity to investigate the generality of landscape structure – biodiversity relationships. Such approach may also contribute to the identification of biodiversity responses that are region-specific (Zeller *et al*., 2017). Moreover, in countries where intensive farming predominates, traditional agricultural landscapes may represent hotspots for agricultural ecosystem services and farmland biodiversity. These may in turn face abandonment problems, but assessments on spatial patterns of farmland-related resources and their spatial congruence with abandonment pressure are scarce, where most contributions are made from European studies (e.g. MacDonald *et al.*, 2000; Keenleyside and Tucker, 2010; van der Zanden *et al.*, 2017; Quintas-Soriano *et al.*, 2022). Reviews on different geographical regions suggest that underuse problems are prevalent in Europe and East Asia (Mauerhofer *et al.*, 2018), and that from biodiversity aspect, countries in Eurasia share a negative perception about farmland abandonment (Queiroz *et al.*, 2014). Contributions from other parts of the world could foster an understanding of the impact of pressures that are often exacerbated by globalization, and such knowledge gain might be beneficial for transition countries that may face similar challenges in the future.

Research aims

By taking a comparative approach, this dissertation aims at identifying similarities and differences in how biodiversity and ecosystem services are associated with agricultural landscapes of the two geographically distant countries, i.e. Germany and Japan, respectively. The dissertation consists of two published studies, each represented by an individual chapter. The first chapter tested the generality of landscape structure – biodiversity associations in two countries belonging to the western and the eastern Palearctic, respectively. Farmland bird species were used as indicators for landscape effects. The second chapter analyzed spatial patterns of agricultural ecosystem services and farmland biodiversity indicators in landscapes where different levels of agricultural intensification have taken place. In the first study, data from agricultural landscapes in Germany and Japan were analyzed jointly, while the second study was conducted using data from Japan only; differences in the way that public statistics are gathered in both countries meant that matching indicators could not be obtained for Germany. In order to identify similarities and differences between the two countries, findings from the second study were compared to results in the literature on European areas. Both studies were carried out at the national level at which the cultural and policy background is best reflected (Hofstede, 2001), and spatial datasets and public statistics were utilized to extract metrics of landscape structure (Chapter 1 and 2) and ecosystem services (Chapter 2). Bird data were provided by the Federation of German Avifaunists and the Ministry of the Environment of Japan (Chapter 1). Data sets were collated at a resolution of approximately 10 km × 10 km grid cells according to the protocols of the breeding bird surveys in Germany and Japan (Chapter 1) or at the municipal level (Chapter 2).

The following research questions and hypotheses have been addressed in the two chapters:

1. *Does farmland bird diversity in Germany and Japan respond to landscape structure in similar ways?*
   It was hypothesized that farmland bird diversity, which is measured by species number, responds to structural characteristics of agricultural landscapes a) in similar ways regardless of different geographical settings, but also b) differently due to their contrasting land use patterns. It was also tested whether c) common ecological mechanisms underlie the patterns of farmland bird diversity in Germany and Japan.

2. *How are agricultural ecosystem services and farmland biodiversity indicators distributed in Japan?*
   The hypotheses were that a) provisioning services show trade-off relationships with other services and biodiversity indicators, and b) there is a spatial aggregation of different services and biodiversity indicators in particular parts of agricultural landscapes in Japan. It was also tested whether c) these ecosystem service and biodiversity hotspots coincide with areas affected by farmland abandonment trends.

Chapter outline

Chapter 1: Landscape associations of farmland bird diversity in Germany and Japan

Article by Keiko Sasaki, Stefan Hotes, Taku Kadoya, Akira Yoshioka, Volkmar Wolters
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The first chapter tests whether landscape structure influences farmland bird diversity in similar ways in the two geographically distant countries. Distribution data of 31 (Germany) and 29 (Japan) species were collated, and landscape associations of species richness in terms of total farmland birds and several ecological groups were analyzed using common landscape metrics. In both countries, farmland cover was the key variable determining species numbers. Species numbers also increased with increasing proportion of semi-natural habitats up to a maximum and then decreased if semi-natural habitats became more abundant. These results confirmed the first hypothesis 1a. However, significant interactions of landscape variables with the country code indicated that associations between species richness and landscape structure also vary according to the countries. In Germany, where farmland is the dominant form of land use, woodland edge density had a pronounced effect on species numbers. By contrast, associations with woodland edges were weak in Japan, where landscapes are characterized by a large extent of forest. Farmland birds in Japan showed stronger associations with farmland cover compared to Germany. Therefore, the difference between the countries is most likely to be due to the contrasting land use patterns (confirming hypothesis 1b). In line with the third hypothesis 1c, common ecological mechanisms underlying the patterns of farmland bird diversity were supported, as the direction of shifts among the ecological groups toward their preferred landscape structure was similar in both countries. Grassland and paddy field cover were the most influential cover crop types for avian species richness in agricultural landscapes of Germany and Japan, respectively. These results suggest that measures to conserve farmland bird diversity should focus on maintaining semi-natural habitats and cover crop types of ecological importance and follow different conservation strategies according to the landscape context.

Chapter 2: Hotspots of agricultural ecosystem services and farmland biodiversity overlap with areas at risk of land abandonment in Japan

Article by Keiko Sasaki, Stefan Hotes, Tomohiro Ichinose, Tomoko Doko, Volkmar Wolters
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The second chapter investigates the spatial patterns of indicators for agricultural ecosystem services and farmland biodiversity in Japan and analyzed their relationship with the distribution of farmland abandonment. Two provisioning services (rice production and other agricultural production), two cultural services (landscape aesthetics and rural tourism), and two biodiversity indicators (forest edges and irrigation ponds) were assessed, and information on the area of cultivated and abandoned fields was collated at the municipal level. Cluster analysis identified four distinct ecosystem service bundle types. The first two bundles were represented by commodity production landscapes on flat and easily-accessible land, which revealed trade-offs between provisioning services and other services as well as habitats for diverse biological communities (confirming hypothesis 2a). By contrast, the latter two bundles showed spatial aggregation of cultural services and habitat features in hilly and mountainous areas, confirming hypothesis 2b. Hilly and mountainous areas appeared to be key to sustaining food security, cultural values, and farmland biodiversity, as the two bundles together accounted for about half to three quarters of agricultural ecosystem services and landscape elements in Japan. These ecosystem service and biodiversity hotspots coincided with areas with high proportions of abandoned fields (confirming hypothesis 2c). The spatial overlap suggests that substantial losses of ecosystem services and biodiversity may occur if abandonment continues following the recent spatial trends. Revitalization measures to counteract the ongoing abandonment trends should be prioritized in hilly and mountain areas with various options to maintain valuable resources that have been shaped by farming activities.

Conclusions

This cumulative dissertation has demonstrated similarities and differences in the spatial patterns of biodiversity (Chapter 1 and 2) and ecosystem services (Chapter 2) by comparing two distant countries that show parallels in the development of agricultural landscapes, i.e. Germany and Japan. The main findings of the two studies are synthesized in Figure 1. The direct comparison of landscape associations in the case study areas provided quantitative support for the presence of common biodiversity responses that apply in both countries, while it also contributed to identifying region-specific responses that are derived from contrasting land use patterns. Landscapes important for diverse types of agricultural ecosystem services and farmland biodiversity in Japan are distributed in a similar manner to Europe, suggesting prevailing influences of agricultural intensification and land abandonment that are occurring worldwide. The dissertation supports the notion that landscape structure, biodiversity, and ecosystem services maintained by agriculture are significantly linked in both countries studied. Their spatial aggregation on marginal land, where most traditional farming systems are likely to persist, underlies the importance of conserving and sustaining their respective social-ecological systems to maintain the diversity and complexity established through a long history of human-nature interrelationships. In support of the recent discussion on the implementation of Other Effective area-based Conservation Measures outside protected areas, the findings highlight the need for increased global efforts to preserve and protect traditional land use systems against pressures that result in landscape homogeneity. Exchanging knowledge and tools for solutions across different spatial scales holds the key to implementing measures on the ground.

Similarities and differences in biodiversity responses to agricultural landscapes

Results of the first study revealed that farmland birds of the two studied countries, Germany and Japan, respond to the proportions of farmland cover and semi-natural habitat cover in a similar way (Chapter 1). In both countries, farmland cover was the key variable determining the number of farmland bird species investigated. Species richness increased with the proportion of farmland cover up to a point, but then it decreased after a peak. The latter response probably has less to do with the extent of farmland cover than with the positive correlation between farmland area and management intensity, as more farmland can lead to significant trade-offs with non-cropped habitats such as natural or semi-natural habitats (Belfrage *et al.*, 2005). Semi-natural habitats are the source of heterogeneity in time and space (Benton *et al.*, 2003) that are linked to traditional farming systems (Plieninger *et al.*, 2006). An increase in

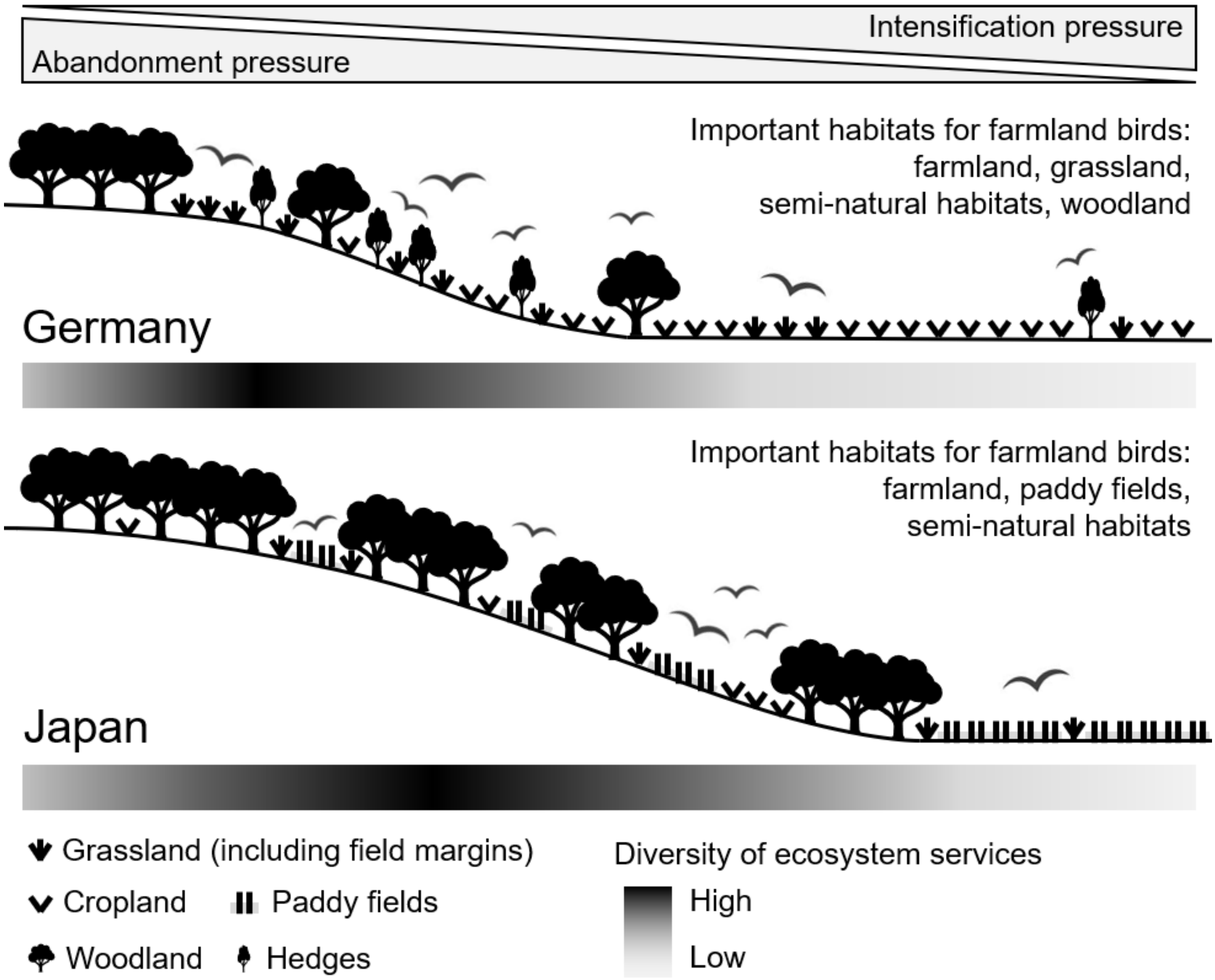

Figure 1. Diagram synthesizing the main findings of the two studies.

habitat heterogeneity can increase the available niche space as well as spaces for shelter, promoting biodiversity in many cases (Stein *et al.*, 2014). Positive correlations between species number and the proportion of semi-natural habitats observed for most of the ecological groups studied confirmed the general contributions of the land covers both in Germany and Japan (chapter 1). Small farmland surrounded by an abundant amount of semi-natural habitats deviated from this pattern, as the relevant habitat for farmland birds then becomes scarce. The study also showed that spatial patterns of farmland bird diversity were governed by common ecological mechanisms, as the direction of shifts among the ecological groups toward their preferred landscape structure was similar in both countries (Chapter 1). An accumulation of different species associated with different habitat types underlines the importance of maintaining mosaics in agricultural landscapes (Hendrickx *et al.*, 2007; Aue *et al.*, 2014; Estrada-Carmona *et al.*, 2022).

Significant interactions between landscape variables and the countries illustrate that the way species richness responds to landscape structure also varies according to the countries (Chapter 1). Farmland birds in Germany benefited from edge habitats provided by forest patches where landscapes are characterized by a large extent of farmland. By contrast, those in Japan showed significantly stronger associations with open habitats made available by farming activities, but were hardly related to woodland edge density where forests dominate. The observed difference in the relative importance of habitat types between the countries implied that the strength of associations for farmland bird diversity may differ according to the studied landscape context, as was also reported by previous studies (Robinson *et al.*, 2001; Herzon and O'Hara, 2007; Batáry *et al.*, 2010, 2011). This means that the difference between Germany and Japan in the biodiversity response to landscape structure was derived from the contrasting land use patterns rather than different geographical settings, which leads to a general conclusion about spatial conservation priorities for farmland avifauna: forest patches in farmland-dominated landscapes and open habitat patches in forest-dominated landscapes. In addition, the study further revealed the high ecological value of grassland and paddy fields in Germany and Japan, respectively (Chapter 1). The conservation focus in open landscapes should thus be targeted toward maintaining livestock in Germany and rice farming systems in Japan.

Similarities and differences in the spatial patterns of ecosystem services and biodiversity in agricultural landscapes

The study demonstrated that agricultural ecosystem services and farmland biodiversity in Japan are spatially aggregated and form hotspots in hilly and mountainous areas (Chapter 2). Trade-offs between provisioning services and cultural services as well as habitat features were also underlined (Chapter 2), supporting the findings of previous studies that prioritizing food production generally comes at the expense of other services (Raudsepp-Hearne *et al.*, 2010; Turner *et al.*, 2014; Früh-Müller *et al.*, 2016; Frei *et al.*, 2018). Agricultural intensification is most likely responsible for the spatial segregation observed between provisioning services on flat, fertile land and some indicators for cultural services and biodiversity on marginal land (i.e. forest edges and rural tourism). Agricultural landscapes in Europe have also experienced similar landscape transitions, where intensification induced landscape homogenization particularly on more productive land and led semi-natural habitats associated with traditional land use systems to persist mainly in more remote areas (Plieninger and Bieling, 2012; Levers *et al.*, 2018). The positive relationships between farmland bird diversity and non-cropped habitats in open landscapes in Germany and Japan also suggest that agricultural landscapes important for biodiversity conservation are found in areas where habitat heterogeneity is maintained (Chapter

1). Areas where landscape elements were maintained were found to be active in promoting rural tourism in Japan (Chapter 2), which matches the discussion in Europe that traditional cultural landscapes are associated with high heritage values (Antrop, 2005; Bridgewater and Rotherham, 2019).

Hotspots of agricultural ecosystem services and farmland biodiversity in Japan overlapped with areas at risk of land abandonment (Chapter 2). High probabilities of farmland abandonment taking place in areas with high biodiversity potential (i.e. high nature value farmland; Keenleyside and Tucker, 2010; Schmitz *et al.*, 2021) and high heritage values (MacDonald *et al.*, 2000; van der Zanden *et al.*, 2017) have also been reported in Europe. The spatial overlap observed both in Europe and Japan was possibly induced by common drivers such as agricultural intensification indirectly causing farmland abandonment on marginal land (Busch, 2006), where ecosystem service and biodiversity hotspots have persisted. Natural disadvantages inherent in hilly and mountainous areas are themselves the geo-physical causes of farmland abandonment (Gellrich and Zimmermann, 2007; Su *et al.*, 2018). The ecosystem service bundles associated with these areas were estimated to be responsible for substantial amounts of agricultural ecosystem services and farmland biodiversity in Japan (Chapter 2). The spatial overlap identified in this study indicates the possibility of losing large quantities of farmland-related resources due to land abandonment.

The identification of ecosystem service bundles and their spatial congruence with the trends of intensification and land abandonment suggest that management schemes should follow different conservation strategies. Those that aim to maintain positive externalities should target locations particularly in hilly and mountainous areas, where landscapes are vanishing due to high abandonment and depopulation pressures. Revitalization is needed to conserve the integrity of traditional farming systems through public goods-based incentives or by linking to new economic objectives such as rural tourism. In areas where intensive agriculture prevails, the focus should rather be on keeping the environment sustainable and healthy. In either case, it will be important to identify the key elements of traditional land uses that maintain and/or enhance nature’s contributions to people and to integrate these into future land use systems. Although these findings were obtained from data for Japan, they can certainly be applied in a modified form to agricultural regions in many other countries around the globe. Future studies should further evaluate the multiple functions of agricultural areas to improve policies that aim to ensure a sustainable development of rural areas.

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Chapter 1: Landscape associations of farmland bird diversity in Germany and Japan

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Landscape associations of farmland bird diversity in Germany and Japan

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ABSTRACT

Spatial heterogeneity of landscapes is a key factor for the diversity of biota. There are a rich variety of agricultural landscapes around the globe that differ with respect to composition and spatial configuration of land-use types, reflecting different levels of human impacts. To test whether landscape structure influences biodiversity in similar ways in different geographical regions, our study explored the relationship between landscape characteristics and farmland bird diversity in Germany and Japan. The two countries represent regions with similar Palearctic avifauna, but with contrasting climatic, biogeographical, and socio-economic conditions. We used distribution data for 31 (Germany) and 29 (Japan) species of farmland birds and applied multiple regression analysis to examine the effect of landscape structure on species richness of total farmland birds and of several ecological groups. In both regions, farmland cover was the key variable determining species numbers. Species numbers also increased with increasing proportion of semi-natural habitats up to a maximum and then decreased if semi-natural habitat became more abundant. Optimum landscape structure for each ecological group differed according to their respective habitat needs, but the direction of shifts toward their preferred habitats was similar in both regions, suggesting common ecological mechanisms underlying the patterns of farmland bird diversity. Significant interactions of structural characteristics with the region variable indicated that associations between species richness and landscape structure varied regionally. In Germany, where landscapes are covered by a large extent of farmland, woodland edge density had a pronounced effect on species numbers. By contrast, associations with woodland edges were weak in Japan, where forest is the dominant form of land-use. The differences in landscape associations imply that different conservation strategies should be taken according to the landscape context. In farmland-dominated landscapes, edge habitats provided by forest patches are an important feature for maintaining farmland bird diversity, whereas maintaining open habitats is crucial in forest-dominated landscapes. The importance of maintaining grassland, paddy fields, and semi-natural habitats as part of agricultural landscapes was also underlined by the results of our study. Measures for conserving farmland bird diversity should focus on maintaining heterogeneity of agricultural landscapes.

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1. Introduction

Agricultural landscapes, consisting of various land-use types with different levels of human impact, occupy the largest part of Earth's terrestrial surface (Foley et al., 2011). The composition and spatial configuration of land-use types differ greatly among such landscapes. The effects of these differences on biological diversity at different spatial scales have been the focus of many studies, not least because of the need for effective management strategies to address the dramatic decline of farmland biodiversity that has been observed worldwide (Tscharntke et al., 2005, 2012; Batáry et al., 2011). In most cases, local to landscape scales have been considered. However, only a few studies have tested the generality of landscape structure – biodiversity relationships in agricultural regions of different continents (Václavík et al., 2016), or have taken a comparative approach to differentiate between region-specific responses and those that are universally applicable across biogeographical regions (Queiroz et al., 2014; Zeller et al., 2017). We tested the effects of landscape structure on the diversity of farmland birds using information from agricultural landscapes in Germany and Japan.

The two regions provide an opportunity to test the generality of landscape structure – diversity associations beyond regional scales because they have different climatic, biogeographical, and socio-economic conditions. Germany is located in the temperate deciduous forest biome, whereas Japan stretches across several biomes ranging from subboreal coniferous forest in the north to subtropical evergreen broad-leaved forest in the south (see supplementary material 1; SM1). Climatic conditions as well as geological and topographical settings determine land-use options available to farmers, and agricultural land-use at a given point in time is likely to reflect the efforts of land managers to optimize household income within the given environmental and socio-economic constraints. Such interactions between farming practices and natural ecosystems over long time periods have shaped the landscapes in both regions (Berglund, 1991; Takeuchi et al., 2003). Germany is characterized by open landscapes with 52% farmland and 30% forest, and non-irrigated land such as cropland and grassland represent 71% and 28% of farmland, respectively (Destatis, 2015). In contrast, Japan has higher forest cover, comprising 67% of the land, and farmland takes up only 12% (Statistics Bureau, 2015). Irrigated land, i.e. paddy fields, is the major land-cover accounting for 54% of farmland, while cropland and grassland contribute 26% and 14%, respectively (MAFF, 2016). In both regions, agriculture started during the Neolithic (Crawford, 2011; Bollongino et al., 2013), and broad distribution patterns of agricultural areas that persist today were established by the medieval period (with the notable exception of Hokkaido where large-scale forest clearance and wetland reclamation for agriculture started in the second half of the 19th century). The resulting cultural landscapes, especially those maintained by traditional agricultural management, are considered to be of importance for biodiversity conservation (Queiroz et al., 2014), as they harbor unique floral and faunal communities through long-term interactions between human and nature (Katoh et al., 2009; Bignal and McCracken, 2000).

Biogeographically, Germany and Japan belong to the Palearctic realm; 155 bird species occur in both regions (BirdLife International, 2016), and their ecological niches are broadly similar (Fig. 1). In a large-scale analysis regarding landscape structure – biodiversity relationships, Stein et al. (2014) found a general trend across biomes that environmental

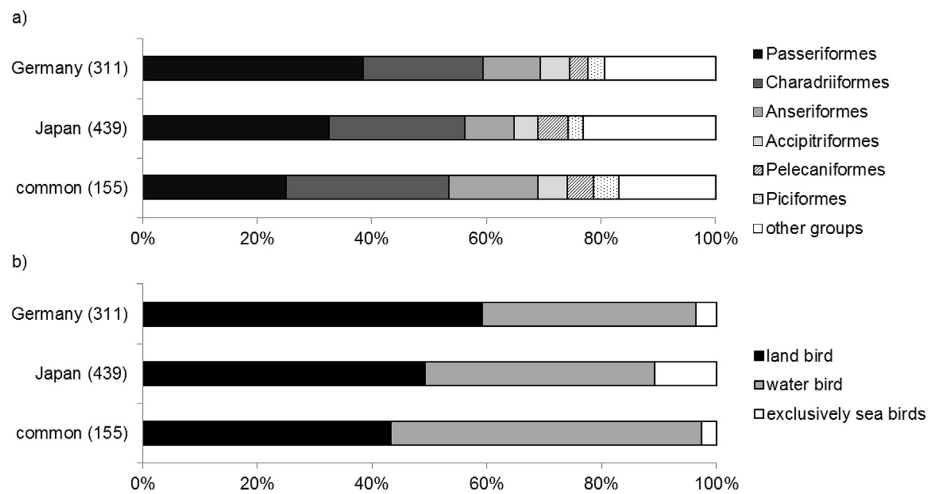

Fig. 1. Proportion of a) taxonomic groups and b) broad ecological groups of birds occurring in Germany, in Japan, or in both regions. Numbers in brackets indicate the number of species. Data extracted from BirdLife International (2016).

heterogeneity has positive effects on biodiversity. According to Benton et al. (2003), this also applies to farmland biodiversity. Metrics describing farmland-woodland mosaics have often been used to express landscape heterogeneity (Berg, 2002; Herzon and O'Hara, 2007; Desrochers et al., 2011). Moreover, semi-natural elements along field margins, water courses, and reservoirs are generally thought to enhance farmland biodiversity in agricultural landscapes (Maeda, 2001; Amano, 2009; Doxa et al., 2010; Zhou et al., 2018), though there are some cases where the strength of statistical relationships was weaker than expected (e.g. Aue et al., 2014) or such relationship did not hold (Tscharntke et al., 2016).

Farmland birds have experienced population declines and range contractions over the last decades in both regions (Amano and Yamaura, 2007; DDA, 2014) mainly due to loss of habitat heterogeneity in time and space arising from agricultural intensification and land abandonment (Benton et al., 2003; Amano, 2009; Koshida and Katayama, 2018). Similar ecological characteristics of birds and the parallels in their historical development of cultural landscapes set the rationale for the comparison between Germany and Japan. The application of common landscape measurements allows us to derive information on the effects of landscape structure on the diversity of farmland birds in regions with parallel socio-economic trends but with contrasting environmental conditions. Our comparative approach contributes to addressing common applicability of landscape drivers underlying the enhancement of species richness in a quantitative manner and thus broadens our understanding of biodiversity patterns shared among agroecosystems of different regions.

Using bird distribution data and common landscape measurements, our study compared how species richness was associated with structural characteristics of German and Japanese agricultural landscapes, and identified ecological mechanisms underlying the patterns of farmland bird diversity. We provide suggestions for maintaining the key characteristics of landscape structure that support the diversity of farmland birds beyond regional scales.

2. Methods

2.1. Bird data

We used breeding bird data compiled by the Federation of German Avifaunists (Dachverband Deutscher Avifaunisten e.V., DDA) and the Ministry of Environment Japan. Data for the German breeding bird atlas project (ADEBAR) were collected between 2005 and 2009 mostly by volunteers. The atlas accumulates data on the distribution and population sizes of breeding birds in Germany at a resolution of approximately 11 km × 11 km, corresponding to the size of a quadrant of the standard 1:25,000 topographical map (Gedeon et al., 2014). Birds meeting the possible, probable, and confirmed breeding criteria of the European Bird Census Council (EBCC, 2015) were recorded, and different survey methods were used according to the frequency levels of species occurrence: frequent (45 species), semi-frequent (156), and rare (75) (Gedeon et al., 2014). The distributions of frequent species were derived from modeling outputs of observations gathered under the German Common Breeding Bird Survey scheme, in which 903 sampling plots of 1 km^2 established across Germany were surveyed along transects of approximately 3–4 km. Semi-frequent species were surveyed in all habitat types present in 11 km × 11 km grid cells, and rare species were recorded through specifically designed projects. The Japanese data were collected under the 6th National Survey of the Natural Environment organized between 1997 and 2002, where distribution data of breeding birds were compiled at a 10 km × 10 km resolution based on field studies and questionnaire surveys among bird experts (MOE, 2004). We only used data derived from field observations of individual birds whose breeding status was A (confirmed breeding), B (probable breeding), or C50 (species observed in breeding season in possible nesting habitat) to be consistent with the EBCC breeding criteria (see SM2 for further details about the categories). Half of the grid cells were evenly chosen across the land, and each contained a 3-km transect. The sampling intensity is thus lower, and the distribution data are more heterogeneous than Germany. Nevertheless, the spatial resolution of the data sets for Germany and Japan is roughly similar, and it is the best distribution data available in Japan, which have been successfully used to answer important ecological questions (e.g. Amano and Yamaura, 2007; Yamaura et al., 2009; Kadoya and Washitani, 2011).

For the selection of farmland species, we used lists published by NABU (2004) and Amano and Yamaura (2007) for Germany and Japan, respectively. Both references defined farmland species as birds that utilize agricultural landscapes for nesting or foraging during the breeding period, and listed 47 species for Germany and 58 for Japan. We assumed that agricultural areas had been surveyed if grid cells contained at least one of the farmland species above. This corresponded to 2966 grid cells in Germany and 2280 in Japan. Next, we excluded species that were infrequently encountered and those whose geographic ranges are known to cover only a small part of the study regions (MOE, 2004; Gedeon et al., 2014). As a result, 31 species occurring in at least 500 out of 2966 grid cells across Germany and 27 species occurring in at least 100 out of 1728 grid cells on the islands of Honshu, Shikoku, and Kyushu were retained (SM3). Grid cells on the northernmost island Hokkaido, the Ryukyu Islands south of Kyushu as well as the Japanese Pacific islands were excluded ($n = 552$) because their avifauna differs considerably from the three main islands. Common buzzard *Buteo buteo* and Gray lapwing *Vanellus cinereus* were added to the list of Japan because the former is also included in the list of Germany and the latter has a similar ecological niche to Lapwing *Vanellus vanellus* in Germany. Thus, the final list from Japan included a total of 29 species. The lists for Germany and Japan had six species in common (SM3).

Habitat use such as foraging or nesting was extracted from the literature, namely Cramp (1977–1994) for species in Germany and Nakamura and Nakamura (1995a; 1995b) for species in Japan. The following broadly defined habitat types were noted based on the density of tree cover and hydrological conditions: dry grassland i.e. farmland including dry grassland and non-irrigated arable land, wet grassland i.e. farmland including wet grassland and irrigated arable land, and woodland.

Species were then assigned to one of the following ecological groups of each category according to the habitat types defined above (SM3): (1) edge-habitat species (those that use both dry/wet grassland and woodland), open-habitat species (mainly dry/wet grassland), or woodland species (mainly woodland) and (2) agricultural land species (those that prefer dry grassland, including species that mainly use woodland) or agricultural wetland species (wet grassland). The former category considered multi-habitat uses with regard to forested and open land, while the latter took into account the preferred level of soil moisture of farmland.

The number of species per grid cell was calculated using ArcView GIS 9.3 (ESRI Inc., Redlands, CA, USA; Table 1).

2.2. Landscape data

2.2.1. Land-cover data

The European CORINE Land Cover inventory 2006 version 17 (EEA, 2014a) and the actual vegetation map (Environment Agency and Asia Air Survey Co. Ltd., 1999) were used as base land-cover maps for Germany and Japan, respectively. CORINE land-cover data consist of 44 land-cover types. The raster format has a standard resolution of 100 m and a minimum mapping unit of 25 ha. To distinguish between farmland and woodland in the CORINE classes “Complex cultivation patterns” and “Land principally occupied by agriculture, with significant areas of natural vegetation” at higher spatial resolution, the Forest Type Map 2006 provided by the Joint Research Centre of the European Union (EC, 2015) was overlaid on the CORINE land-cover map, which was converted to 25 m resolution beforehand. We also integrated maps of water bodies from ESRI (2004) and Degree of Soil Sealing (EEA, 2014b), which accumulates information on the percentage of sealed area, e.g. built-up and non-built-up impervious areas such as pavement, per 20 m raster cell. The Japanese land-cover map was compiled at the scale of 1:50,000 with a minimum mapping unit of 1 ha, and consists of 774 types of vegetation communities. Both land-cover maps were converted to raster data with a spatial resolution of 50 m.

The Land Cover Classification System developed by the Food and Agriculture Organization (Gregorio and Jansen, 2000) was used to reclassify the 44 and 774 land-cover types in Germany and Japan, respectively. The categories are cropland, grassland, paddy fields, bamboo, natural shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, snow/ice, broad-leaved forest, mixed forest, coniferous forest, mangrove, trees in open landscapes, tree crop, shrub crop, vegetated urban, urban, and unknown. The resulting maps for Germany and Japan consisted of 18 and 22 land-cover types, respectively.

2.2.2. Landscape variables

Nine farmland-based variables related to landscape structure that were considered relevant for farmland birds were derived from the land-cover maps (Table 2). The first four variables relate to the proportion of farmland to the total land area and were calculated per grid cell. ‘Farmland cover’ accounts for the extent of open farmland (3 types: cropland, grassland, and paddy fields; hereafter addressed as farmland). The other three variables were separate proportions for cropland (‘cropland cover’), grassland (‘grassland cover’), and paddy fields (‘paddy field cover’) to the total land area. Note that paddy field cover did not apply to Germany and that grassland cover was not computed for Japan, as this land cover type was scarce in the Japanese study area. ‘Number of habitat types’ is the combined number of land-cover types per grid cell including ten land-cover types belonging to semi-natural habitats (bamboo, natural shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, and snow/ice) and five land-cover types belonging to woodland (broad-leaved forest, mixed forest, coniferous forest, mangrove, and trees in open landscapes).

To examine the effects of land-cover types neighboring farmland, we generated agricultural landscape sections by buffering 250 m around farmland edges. Within these sections, we calculated the proportions of semi-natural habitats (‘semi-natural habitat cover’) and woodland (‘woodland cover’) to the area of agricultural landscape sections for each grid cell. In Germany, semi-natural habitats in agricultural land sections were composed of 69% water body, 19% wetland, and 7% natural herbaceous cover, while those in Japan were 41% natural herbaceous cover, 33% water body, and 10% wetland. To assess effects of edges between farmland and non-farmland on bird distributions, edge densities of semi-natural habitats and woodland adjacent to farmland were extracted by dividing the edge length of semi-natural habitats (‘semi-natural habitat edge density’) and woodland (‘woodland edge density’) by total farmland area.

Table 1
Summary of descriptive statistics of species richness per grid cell in Germany and Japan.

	Germany				Japan			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Total farmland birds	2	31	24.0	4.8	1	23	9.7	4.3
Edge-habitat species	0	9	7.5	1.4	0	11	4.5	2.3
Open-habitat species	0	19	14.2	3.6	0	12	3.8	2.3
Agricultural land species	2	22	18.6	3.0	0	15	7.8	3.1
Agricultural wetland species	0	9	5.4	2.4	0	10	1.9	1.8

Table 2
List of landscape variables used. Values refer to mean ± 1 standard deviation.

Variables	Description	Unit	Germany	Japan
Farmland cover	Proportion of farmland to total land area	%	54.5 ± 22.1	18.9 ± 17.1
Cropland cover	Proportion of cropland to total land area	%	43.0 ± 23.0	5.4 ± 7.4
Grassland cover	Proportion of grassland to total land area	%	11.6 ± 13.7	N.A.
Paddy field cover	Proportion of paddy fields to total land area	%	N.A.	13.4 ± 14.1
Number of habitat types	Number of semi-natural habitat and woodland types per grid cell	n	4.9 ± 1.3	5.9 ± 1.2
Semi-natural habitat cover	Proportion of semi-natural habitats to agricultural landscape section	%	2.0 ± 4.3	5.9 ± 6.0
Woodland cover	Proportion of woodland to agricultural landscape section	%	23.2 ± 15.2	49.6 ± 24.0
Semi-natural habitat edge density	Edge density of semi-natural habitats adjacent to farmland per hectare of farmland	m ha^{-1}	1.2 ± 1.4	2.5 ± 2.7
Woodland edge density	Edge density of woodland adjacent to farmland per hectare of farmland	m ha^{-1}	10.5 ± 5.8	12.4 ± 10.7
Elevation	Mean elevation	m	252.4 ± 247.2	367.1 ± 368.9

Total land area: area of each grid cell covered by the study area.
Agricultural landscape section: area within 250 m from farmland edges.
Farmland: cropland, grassland, and paddy fields.
Woodland: broad-leaved forest, mixed forest, coniferous forest, mangrove, and trees in open landscapes.
Semi-natural habitat: bamboo, shrub, natural herbaceous, sparse vegetation, lichen/moss, water body, wetland, salt marsh, bare area, and snow/ice.
Tree crop, shrub crop, vegetated urban, urban, and unknown land-cover type were not considered.
N.A.: data not available.

All variables were calculated based on 50 m pixels except for edge density, which was derived using vector data converted and smoothed from the raster data. Permanent crops were different from other land-cover categories in terms of management intensity and woody structure over an extended period of time. However, the cover of permanent crops was too small to establish its own category and to be included in landscape analysis (0.68% of the land surface in Germany and 1.89% in Japan), so tree crop and shrub crop were considered non-informative for the study. Vegetated urban, urban, and unknown land-cover type were not considered.

2.2.3. Elevation data

We selected elevation as a variable accounting for large-scale bird distributions since it showed strong correlations with average precipitation in Germany (Spearman's rank correlation = 0.84) and average temperature in Japan (Spearman's rank correlation = 0.66) during the surveyed breeding period. German data were acquired from the Digital Terrain Model with a grid width of 200 m (Federal Agency for Cartography and Geodesy, 2013), and the Japanese data were obtained from the Elevation, Degree of Slope Tertiary Mesh Data (MLIT, 2011). Mean values were calculated per grid cell ('elevation').

The German and Japanese datasets were combined, and the landscape variables were standardized together based on the mean and standard deviation.

2.3. Statistical analysis

Grid cells that contained missing data for calculating the landscape variables were excluded, resulting in a total of 2957 grid cells in Germany and 1728 in Japan. Relationships among the landscape variables were then examined using Spearman's rank correlations in each region. Variables that showed correlations higher than the absolute value of 0.5 (i.e. number of habitat types, woodland cover, and semi-natural habitat edge density; SM4; Booth et al., 1994) were not used in the subsequent regression analysis, even if correlations existed only in one of the regions, to keep consistency in the datasets.

Using the first set of landscape variables as multiple explanatory variables (farmland cover, semi-natural habitat cover, woodland edge density, and elevation), we modeled the species richness, i.e. the number of species, in generalized linear models with a log link function for the following ecological groups: total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species. The woodland group was excluded from analysis as it contained only three species in both regions that are not specifically dependent on open agricultural fields (SM3). The assumption of a Poisson distribution was verified by visual inspection of the frequency distribution of species numbers and the regression residuals. Linear and quadratic terms of each landscape variable were included to account for non-linear relationships, and interaction terms encoding the regions as a two-level factor parameter were added to address whether landscape associations vary regionally. Correlograms of Moran's I (Legendre and Legendre, 1998) were then constructed to assess the degree of spatial autocorrelation in the regression residuals using the 'ncf' package in R (Bjornstad and Cai, 2019). Intersample distance classes were formed using a lag of 50 km up to the maximum distance. Since significant autocorrelation was not detected, no further methods were applied. A full model approach was taken to compare the effects of different explanatory variables on the distributions of farmland bird diversity (Whittingham et al., 2006).

Based on the parameter estimates of linear and quadratic terms, shapes of landscape structure − farmland bird diversity relationships were visualized, and values at which the maxima of species richness were reached (hereafter addressed as optimum values) were calculated for each landscape variable and each ecological group. In order to determine the relative importance of subclasses of agricultural land for farmland bird diversity, a second set of models was similarly constructed using cropland, grassland, paddy field cover as individual variables instead of including farmland cover. The explanatory variables here were centered on zero mean so that the changes in species richness could be compared based on the original unit of measurement (i.e. cropland, grassland, paddy field, and semi-natural habitat cover in percent, woodland edge density in meters per hectare, and elevation in meters).

Statistical analyses were conducted using R-3.2.4 (R Development Core Team, http://www.r-project.org/).

3. Results

In general, heterogeneity in the bird data among grid cells was smaller in Germany compared to Japan due to the differences in sampling intensity (see 2.1. Bird data; Table 1). Of the 31 and 29 farmland species used in Germany and Japan, the former consisted of 9 edge-habitat species, 19 open-habitat species, 22 agricultural land species, and 9 agricultural wetland species, while the latter included 12, 14, 17, and 12 species, respectively.

Multiple regression analysis revealed that species richness of total farmland birds and the ecological groups was negatively correlated with elevation in both regions (Table 3), indicating a decline in species richness with increasing altitude (Fig. 2).

Among the variables related to landscape structure, farmland cover was the key variable determining species numbers in Germany and Japan (Table 3). The coefficients for the linear term were positive for total farmland birds and all ecological groups considered, and they were larger than those for semi-natural habitat cover and woodland edge density. Significant interactions between farmland cover and region indicated that the effects of farmland cover on species richness differed in Germany and Japan. The difference in slopes revealed that the associations between species richness and farmland cover were stronger in Japan (Table 3). Moreover, the unimodal relationship between farmland cover and species richness suggested that there is an optimal proportion of farmland for the diversity of farmland birds (Fig. 2). In Germany, the optimum values of farmland cover where the maxima of species numbers were reached were located around the mean or slightly larger (mean farmland cover 54.5%, range of optimum values 48.5–69.6%). In Japan, the maxima were found more or less in the same range (44.7–62.8%), but landscapes with such farmland extent were rare as these values lay beyond 89th percentile of its distribution (mean 18.9%).

Models including the cover of particular subclasses of agricultural land (i.e. cropland, grassland, and paddy fields) showed that the proportion of grassland and paddy fields had larger positive effect size on species richness than cropland cover (except for agricultural land species in Germany; SM5). Furthermore, there was only a small difference in R^2 between the first (considering farmland cover) and second (considering the cover of subclasses of agricultural land) sets of models (Table 3; SM5).

Species richness showed a unimodal relationship with semi-natural habitat cover (Fig. 2), and the effects of the linear term were significantly stronger in Japan (Table 3). Species numbers increased with increasing proportion of semi-natural habitats up to a maximum and then decreased if semi-natural habitat became more abundant. In both regions, the optimum values were larger than the mean for most of the ecological groups considered (mean Germany 2.0%, Japan 5.9%; Fig. 2). Edge-habitat species and agricultural land species in Germany deviated from this pattern. They were negatively related to semi-natural habitat cover (Table 3), and their maxima were estimated at zero (Fig. 2). Low species richness in grid cells with high semi-natural habitat cover was associated with a small number of data points which had special land cover patterns. At these points, small farmland areas were surrounded by larger areas of semi-natural habitats such as sparse vegetation and salt marshes in Germany and herbaceous cover and water body in Japan (range of farmland cover with the top ten highest proportion of semi-natural habitats: Germany 0.9–18.4%, Japan 0.2–9.9%). Such land cover patterns were apparently not conducive to the diversity of farmland birds and led to a drop in species numbers.

The most pronounced differences between Germany and Japan were observed in the effect of woodland edge density on farmland bird diversity (Table 3; Fig. 2). In Germany, species richness showed a unimodal relationship with woodland edge density, with maximum richness close to the mean value of woodland edge density (mean 10.5 m ha^{-1}, range of optimum values 7.5–11.7 m ha^{-1}). In Japan, on the other hand, the relationship was an almost horizontal line, suggesting that species richness was only marginally influenced by woodland edge density. The effects of the quadratic term were significantly stronger in Germany compared to those in Japan where the coefficients were all close to zero. The shape of relationship confirmed such differences in the landscape associations (Fig. 2).

Different ecological groups responded differently to landscape structure according to their respective habitat needs. However, the direction of change how the numeric values of optima shifted among the ecological groups was similar between Germany and Japan (Fig. 2). For example, it was common to both regions that edge-habitat species showed preference for higher woodland edge density (optimum values Germany 11.7 m ha^{-1}, Japan 30.2 m ha^{-1}) but required less farmland cover compared to other groups (Germany 48.5%, Japan 44.7%). By contrast, open-habitat species required higher farmland cover (Germany 66.9%, Japan 61.2%) and higher semi-natural habitat cover instead (Germany 19.3%, Japan 22.4%). Agricultural land species showed intermediate responses compared to edge-habitat species and open-habitat species. The positive effect of farmland cover was most pronounced for agricultural wetland species (Table 3). Models including the cover of subclasses of agricultural land indicated that this was driven mostly by grassland and paddy field cover in Germany and Japan, respectively (SM5). The proportion of semi-natural habitats was also most relevant for these species. Maxima in species richness in this group were found at 31.4% in Germany and at 24.6% in Japan (Fig. 2).

Table 3
Results of generalized linear models explaining the species number of total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species as a function of farmland cover, semi-natural habitat cover, woodland edge density, and elevation. Note that landscape variables were standardized based on the mean and standard deviation before model construction. The number of species used in Germany and Japan is shown in brackets. Linear and quadratic terms of each landscape variable were included in the analysis. Regression coefficients are expressed as means ± standard errors.

	Total farmland birds						
	Germany (31)			Japan (29)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	3.203 ± 0.007	462.94	<0.001	2.501 ± 0.019	131.90	<0.001	<0.001
Farmland cover	0.061 ± 0.007	8.85	<0.001	0.107 ± 0.019	5.73	<0.001	<0.05
(Farmland cover)^2	−0.044 ± 0.006	−6.79	<0.001	−0.147 ± 0.019	−7.82	<0.001	<0.001
Semi-natural habitat cover	0.007 ± 0.008	0.87	0.38	0.049 ± 0.012	3.89	<0.001	<0.01
(Semi-natural habitat cover)^2	−0.005 ± 0.001	−3.56	<0.001	−0.009 ± 0.002	−3.51	<0.001	0.15
Woodland edge density	−0.026 ± 0.007	−3.55	<0.001	0.011 ± 0.010	1.07	0.29	<0.01
(Woodland edge density)^2	−0.050 ± 0.006	−8.71	<0.001	−0.003 ± 0.003	−1.06	0.29	<0.001
Elevation	−0.131 ± 0.007	−19.22	<0.001	−0.086 ± 0.014	−6.19	<0.001	<0.01
(Elevation)^2	−0.021 ± 0.005	−4.49	<0.001	0.008 ± 0.004	1.74	0.08	<0.001
	Edge-habitat species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	2.078 ± 0.012	170.10	<0.001	1.681 ± 0.028	59.22	<0.001	<0.001
Farmland cover	0.018 ± 0.012	1.52	0.13	0.040 ± 0.028	1.42	0.16	0.48
(Farmland cover)^2	−0.034 ± 0.012	−2.95	<0.01	−0.161 ± 0.028	−5.72	<0.001	<0.001
Semi-natural habitat cover	−0.010 ± 0.016	−0.66	0.51	0.042 ± 0.019	2.26	<0.05	<0.05
(Semi-natural habitat cover)^2	−0.007 ± 0.003	−2.49	<0.05	−0.009 ± 0.004	−2.38	<0.05	0.65
Woodland edge density	0.009 ± 0.013	0.67	0.50	0.030 ± 0.015	2.00	<0.05	0.30
(Woodland edge density)^2	−0.071 ± 0.010	−6.80	<0.001	−0.006 ± 0.004	−1.57	0.12	<0.001
Elevation	−0.036 ± 0.012	−2.98	<0.01	−0.174 ± 0.021	−8.32	<0.001	<0.001
(Elevation)^2	−0.019 ± 0.007	−2.60	<0.01	0.016 ± 0.007	2.28	<0.05	<0.001
	Open-habitat species						
	Germany (19)			Japan (14)			
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	P^2
Intercept	2.655 ± 0.009	289.37	<0.001	1.638 ± 0.029	55.60	<0.001	<0.001
Farmland cover	0.103 ± 0.009	11.28	<0.001	0.237 ± 0.028	8.48	<0.001	<0.001
(Farmland cover)^2	−0.054 ± 0.008	−6.41	<0.001	−0.160 ± 0.029	−5.55	<0.001	<0.001
Semi-natural habitat cover	0.026 ± 0.011	2.40	<0.05	0.072 ± 0.020	3.61	<0.001	<0.05
(Semi-natural habitat cover)^2	−0.004 ± 0.002	−2.80	<0.01	−0.010 ± 0.004	−2.63	<0.01	0.16
Woodland edge density	−0.039 ± 0.009	−4.19	<0.001	−0.033 ± 0.016	−2.06	<0.05	0.74
(Woodland edge density)^2	−0.043 ± 0.007	−5.85	<0.001	0.004 ± 0.004	1.01	0.31	<0.001
Elevation	−0.189 ± 0.009	−21.01	<0.001	−0.051 ± 0.022	−2.30	<0.05	<0.001
(Elevation)^2	−0.028 ± 0.007	−4.12	<0.001	0.017 ± 0.006	2.66	<0.01	<0.001
	Agricultural land species						
	Germany (22)			Japan (17)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	2.965 ± 0.008	377.61	<0.001	2.267 ± 0.021	106.44	<0.001	<0.001
Farmland cover	0.030 ± 0.008	3.96	<0.001	0.056 ± 0.022	2.60	<0.01	0.26
(Farmland cover)^2	−0.036 ± 0.007	−4.85	<0.001	−0.149 ± 0.022	−6.90	<0.001	<0.001
Semi-natural habitat cover	−0.022 ± 0.010	−2.29	<0.05	0.038 ± 0.014	2.77	<0.01	<0.001
(Semi-natural habitat cover)^2	−0.003 ± 0.002	−1.95	0.05	−0.008 ± 0.003	−2.87	<0.01	0.12
Woodland edge density	−0.015 ± 0.008	−1.88	0.06	0.036 ± 0.012	3.07	<0.01	<0.001
(Woodland edge density)^2	−0.038 ± 0.006	−5.96	<0.001	−0.008 ± 0.003	−2.65	<0.01	<0.001
Elevation	−0.071 ± 0.008	−9.19	<0.001	−0.052 ± 0.015	−3.36	<0.001	0.27
(Elevation)^2	−0.036 ± 0.005	−7.09	<0.001	0.000 ± 0.005	−0.03	0.98	<0.001
	Agricultural wetland species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	
Intercept	1.626 ± 0.015	107.95	<0.001	0.894 ± 0.042	21.10	<0.001	<0.001
Farmland cover	0.175 ± 0.016	11.25	<0.001	0.262 ± 0.037	7.13	<0.001	<0.05
(Farmland cover)^2	−0.083 ± 0.014	−6.01	<0.001	−0.163 ± 0.039	−4.18	<0.001	0.05
Semi-natural habitat cover	0.091 ± 0.017	5.53	<0.001	0.090 ± 0.028	3.17	<0.01	0.98
(Semi-natural habitat cover)^2	−0.009 ± 0.002	−3.64	<0.001	−0.011 ± 0.005	−2.08	<0.05	0.65
Woodland edge density	−0.068 ± 0.015	−4.45	<0.001	−0.078 ± 0.022	−3.63	<0.001	0.71

(continued on next page)

Table 3 (*continued*)

	Agricultural wetland species						
	Germany (9)			Japan (12)			P^2
	Coefficient±SE	*Z*	P^1	Coefficient±SE	*Z*	P^1	
(Woodland edge density)^2	−0.102 ± 0.013	−7.91	<0.001	0.016 ± 0.005	2.98	<0.01	<0.001
Elevation	−0.358 ± 0.015	−23.83	<0.001	−0.240 ± 0.033	−7.30	<0.001	<0.01
(Elevation)^2	0.029 ± 0.011	2.60	<0.01	0.043 ± 0.010	4.26	<0.001	0.33

P^1 *p*-values for the explanatory variables in each region.
P^2 *p*-values for interaction terms of the variables between the regions.

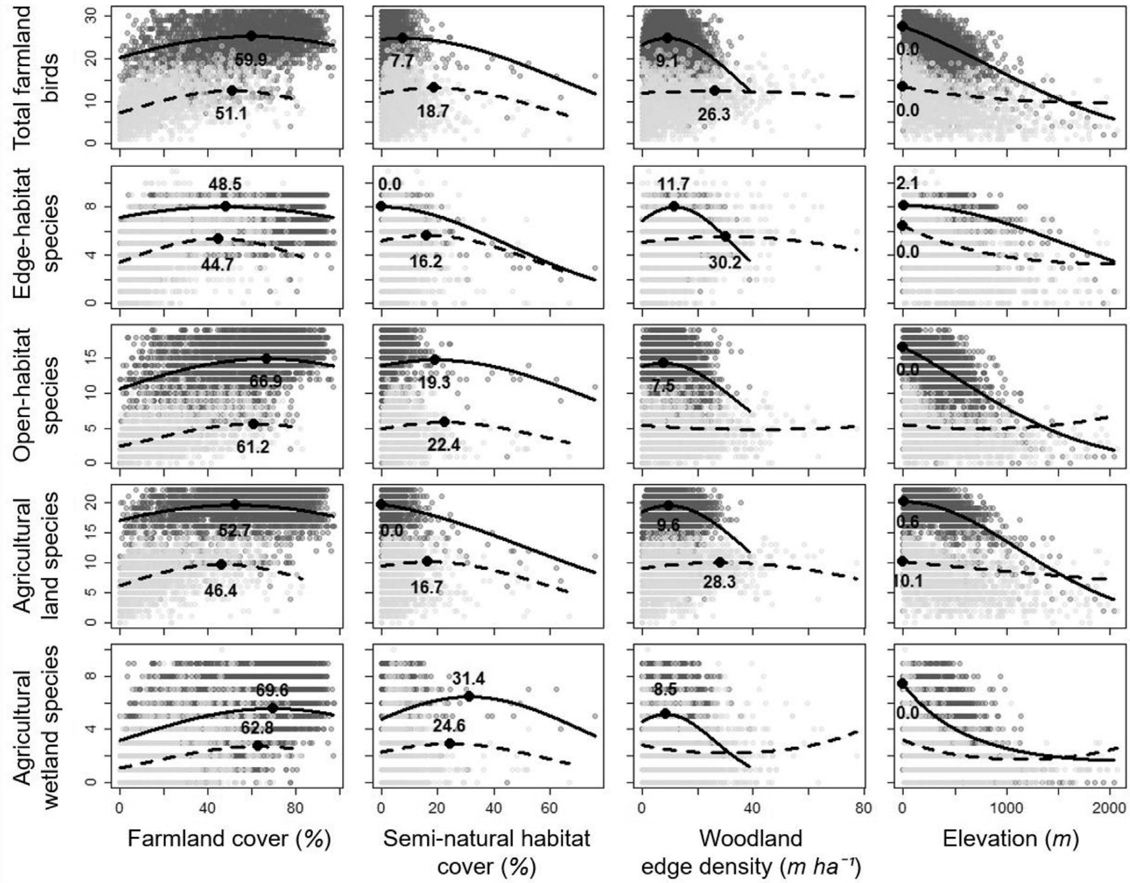

Fig. 2. Changes in the species number of total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species as a function of farmland cover, semi-natural habitat cover, woodland edge density, and elevation in Germany (dark gray circles) and Japan (light gray circles). The regression lines for changes in species richness (Germany solid lines, Japan dashed lines) are shown using the estimated mean coefficients, with values of all other significant variables being zero. The optimum values at which the maxima of species richness are reached are also represented (closed circles, values shown below or above).

4. Discussion

Our study tested the generality of relationships between species richness of farmland birds and landscape structure using two distant geographical regions with similar Palearctic avifauna. Germany and Japan represent regions of contrasting land-use patterns with respect to farmland extent and farming systems, i.e. irrigated and non-irrigated agriculture. Nevertheless, given the differences, our results suggest that farmland cover plays a central role in enhancing species numbers of farmland bird communities of both study regions, with maxima found within similar ranges. Species numbers also increased with increasing proportion of semi-natural habitats up to maxima reached above the mean (except for edge-habitat species and agricultural land species). In addition, the direction of shifts of the ecological groups toward their respective preferred landscape structure was similar in both regions, suggesting common ecological mechanisms underlying the patterns of farmland bird diversity. One should note, however, that the landscape associations observed here concerned only common species; those of rare or threatened species were not examined. As demonstrated by Katayama et al. (2014), wide- and narrow-ranging species show different responses to landscape structure, with the former being more associated with heterogeneous landscapes and the latter with homogeneous landscapes. The inclusion of narrow-ranging species, which are often open-landscape specialists of high conservation priority, may thus increase the relevance of farmland extent than it was observed in our study.

Our analysis revealed several significant regional interactions, indicating that the way species richness responds to landscape structure varies between the regions. Such regional differences in landscape associations could be related to structural characteristics in agricultural landscapes as well as to different responses of farmland species included in the bird data sets. Furthermore, differences in the methodologies of the land-use surveys in Germany and Japan could have played a role. For example, different minimum mapping units might have influenced the strength and direction of relationships, as different levels of information loss may have occurred, especially with regard to small habitat features. In Germany, adopting a coarser minimum mapping unit (25 ha) compared to Japan (1 ha) may have resulted in a remarkably low proportion of semi-natural habitats across the grid cells (mean 2.0%). With the frequency distribution of semi-natural habitat cover in Germany being strongly skewed to the right, much of the variability of species numbers occurred in a narrow range of this variable. In such a situation, statistical relationships are weak. Aggregation of presence data into species numbers should have reduced possible effects arising from the use of different bird lists. There was also no apparent influence of species composition on the response to landscape composition, as the number of species included in each ecological group did not differ greatly between the regions. Our results suggest regional differences in the response to farmland cover and woodland edge density. Because Germany and Japan are characterized by contrasting farmland-woodland mosaics, i.e. the former by larger farmland extent and the latter by larger forest extent, we consider structural differences in agricultural landscapes to be the main reasons for the observed associational differences between the regions.

In Germany, agricultural landscapes structured by average amounts of farmland cover and woodland edge density supported the highest species numbers, suggesting that forest patches and edge habitats are beneficial to the diversity of farmland bird communities in farmland-dominated landscapes. Such landscapes structured by mosaics of farmland and woodland are known to support high farmland bird diversity (Berg, 2002; Herzon and O'Hara, 2007). For instance, Herzon and O'Hara (2007), who studied farmland bird communities along a gradient of farmland-woodland mosaics in the Baltic States, found that the abundance of farmland birds was frequently associated with semi-open landscapes. Berg (2002) also observed higher abundance and richness of farmland birds in mosaic farmland landscapes, and emphasized the importance of woodland edges as they provide nesting habitats, especially if they are rich in shrubs and deciduous trees. The presence of forest patches might also be important for providing food resources for insectivorous farmland birds since farmland landscapes surrounded by a high proportion of non-crop habitats are known to harbor a high amount of prey animals such as spiders, beetles, and butterflies (Weibull et al., 2000; Schmidt and Tscharntke, 2005; Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Increasing woodland edges can, however, also increase the risk of nest predation on ground-nesting farmland birds (Krüger et al., 2018). Further fragmentation of remaining forest patches should thus be avoided.

Farmland birds in Japan showed significantly stronger associations with farmland cover compared to Germany, with maxima reached at high farmland extent, but were hardly related to woodland edge density. The importance of open land in forest-dominated landscapes is in line with previous studies in mountain areas (Pino et al., 2000; Ichinose, 2007; Zakkak et al., 2014, 2015). Desrochers et al. (2011) showed that loss of natural land cover up to 44% led to an overall increase in avian richness through a gain of 20 open-habitat species with a loss of two forest species. They explained that conversion of small amounts of natural areas to human-dominated land covers contributed to habitat heterogeneity and benefited especially open-habitat species as only a few natural open habitats remain nowadays. In Japan, open land has been made available by converting natural areas into agricultural land as well. Over the past century, agricultural fields have been lost substantially due to abandonment and development of rural areas (Statistics Bureau, 2018), especially grasslands that were historically more widespread than it is in today's landscape (<1% of total area; MOE, 2011). There, a number of breeding bird species have declined significantly in recent decades (Fujioka and Yoshida, 2001), and the loss, fragmentation, and degradation of open land have been identified as possible causes for their range contractions and narrow ranges (Amano and Yamaura, 2007; Katayama et al., 2014). Remaining open-habitats might have become more critical for the survival of farmland bird species, thus resulting in strong associations between the two variables. The effects of woodland edge density could have been mediated by the functional link between farmland cover and woodland edge density, i.e. woodland edges become available where agricultural land is extended ($r = 0.57$).

The difference in the relative importance of habitat types between the regions (i.e. higher relevance of forest patches in farmland-dominated landscapes vs. higher relevance of open-habitat patches in forest-dominated landscapes) may imply that the strength of associations for farmland bird diversity differs according to the studied landscape context. Similar landscape-moderated effects of habitat patches were also reported in landscape and regional level studies, where effects of hedges and agri-environment schemes were found to be more pronounced in simple than in complex landscapes (Batáry et al., 2010, 2011), residual habitats in open landscapes (Herzon and O'Hara, 2007), and arable fields in grassland landscapes (Robinson et al., 2001). These previous studies argued that food resources and nesting sites were probably the limiting factors in landscapes where relevant habitats were scarce, so increasing these habitats in such landscapes had contributed to increasing richness up to a threshold of the local or regional species pool. Our study supports these findings based on observations in two distant regions. This is an important difference because it points out the need for different management strategies according to landscape context, as suggested by Batáry et al. (2011) and Aue et al. (2014).

Similar responses of edge-habitat species and open-habitat species to landscape structure between the regions imply common ecological mechanisms underlying how farmland bird diversity is distributed in space. The edge-habitat species studied here are known to show preferences for forest edges (Cramp, 1977–1994; Nakamura and Nakamura, 1995a, 1995b) because they provide both necessary foraging areas and nesting sites. Among the edge-habitat species in Germany, *Buteo*, *Corvus corax*, *Milvus milvus*, and *Turdus pilaris* in particular require such combinations of habitats as they prefer to nest in woodland nearby farmland in structurally-rich landscapes (Cramp, 1977–1994; Gedeon et al., 2014). In Japan, Ardeidae and *Butastur indicus* are the species that particularly depend on the simultaneous presence of paddy fields and surrounding forest (Fujioka and Yoshida, 2001; Katoh et al., 2009). The pronounced responses of edge-habitat species to landscapes with farmland-woodland mosaics were also observed elsewhere (e.g. Pino et al., 2000; Sanderson et al., 2009) as such landscapes provide high accessibility to a variety of resources necessary for species that make use of multiple habitats.

Open-habitat species in contrast showed a stronger association with open land that has been created by farming practices. In open landscapes, farmland birds are known to have strong associations with local management practices and habitat heterogeneity. This includes management intensity of fields and the presence of non-cropped habitats between fields (Maeda, 2001; Berg, 2002; Benton et al., 2003; Doxa et al., 2010; Zhou et al., 2018). Low-intensity farming and mosaics of semi-natural habitats (e.g. hedges, field margins, and ditches), which are classified as farming areas of high nature value in the European Union's Rural Development Program (Andersen et al., 2003), are acknowledged to offer an array of habitats for plant and animal species (Doxa et al., 2010; Aue et al., 2014). In irrigated farming systems, simultaneous management of irrigation channels, irrigation ponds, paddy levee, and grassland patches creates spatial and temporal habitat heterogeneity, allowing organisms to move among different habitats (e.g. fish, amphibians and Odonata; Fujioka and Lane, 1997; Lane and Fujioka, 1998; Kadoya et al., 2009), which then results in enhanced farmland biodiversity (Amano, 2009; Katoh et al., 2009). In our study, although small habitat features may have been underrepresented due to the coarse mapping unit of the land-cover maps, we still observed an increase in species richness with increasing proportion of semi-natural habitats on agricultural land, especially in the case of open-habitat species and agricultural wetland species. Exceptions found in edge-habitat species and agricultural land species in Germany were probably due to a lack of relevant habitat types included in the land-cover map (breakdown of the composition in Germany: water body 69%, wetland 19%, and herbaceous cover 7%).

Grassland and paddy field cover were the most influential cover crop types for avian species richness in agricultural landscapes of Germany and Japan, respectively (except for agricultural land species in Germany). Many of the bird species studied here are known to show some level of association with pastoral landscapes or rice paddy landscapes because grassland and paddies under traditional management practices host a diverse and rich amount of food resources (Vickery et al., 1999; Fujioka et al., 2010). Grassland, which covers only 12.9% of the total land (Destatis, 2015), supports half of the native plant species in Germany (BMELV, 2013), and a high proportion of grassland invertebrates and a rich soil fauna are found above- and below-ground, respectively (Curry, 1994). The availability of small birds and mammals also make it suitable as a foraging site for birds of prey (Vickery et al., 1999). In Japan, paddy fields serve as foraging sites for many species. The wetland habitat created by rice farming provides aquatic prey animals (i.e. earthworms, fish, and frogs) for carnivorous birds (Fujioka et al., 2010), and associated paddy levees facilitate foraging activity of water and land birds (Maeda, 2001). Moreover, grassland and paddy fields function as alternative habitats for many avian species, especially for agricultural wetland species, because much of their original habitats such as natural marsh and floodplains have been lost (Fujioka and Yoshida, 2001; BMELV, 2013).

Grasslands and paddy fields are both under pressure due to socioeconomic trends. Factors such as conversion to cropland and land abandonment have led to substantial losses over the past decades (MAFF, 2012; BfN, 2014). Land abandonment, which occurs as a result of agricultural intensification and market globalization (Cramer and Hobbs, 2007), is known to have both positive and negative influences on biodiversity (Queiroz et al., 2014; Pereira and Navarro, 2015; MacDonald et al., 2000). Abandoned farmland is seen as an opportunity for rewilding in some parts of Europe, as it can facilitate plant succession and provide habitats for organisms that suffered from the past expansion and intensification of agriculture (Pereira and Navarro, 2015). However, since abandonment is likely to occur in less favored areas where high nature value farming systems remain (Keenleyside and Tucker, 2010), withdrawal of agricultural management can lead to a significant loss of semi-natural habitats and associated species of conservation importance as well (Pointereau et al., 2008). The contribution of abandoned farmland to ecological restoration has also been tested in Japan. Although some studies reported its high conservation values for open-habitat bird communities (Kitazawa et al., 2019; Hanioka et al., 2018), a meta-analysis specifically done for rice-farming systems depicted a pronounced decline in biodiversity, indicating that abandonment is not likely to contribute to or even have negative impacts on ecological restoration (Koshida and Katayama, 2018). A continuation of livestock and rice farming systems is thus crucial for conservation of farmland biodiversity. In addition to the decrease in the area of these habitats, agricultural intensification like mechanization, increased use of agrochemicals, improvement of irrigation and drainage to maximize productivity, and loss of field margins due to enlargement of fields have simplified the diversity and structural complexity of vegetation. The habitat suitability of grassland and paddy fields has thus been reduced (for further details, see Vickery et al. (2001) and Amano (2009) for livestock and rice farming systems, respectively), and policies that reverse these trends are needed.

5. Conservation implications

Based on the finding that the relative importance of a habitat type changes according to the landscape context, we conclude that conservation of farmland bird diversity should follow different strategies in Germany and Japan. In Germany where the extent of farmland is large in most areas, policies should aim at maintaining the cover of woodland in farmland-woodland mosaics. By contrast, the focus should be on maintaining open habitats in Japan where forest dominates in most areas. This is a particular challenge in Japan because socio-economic trends are putting pressure on the farming sector, leading to a decline in the farming population and to farmland abandonment. Policies that promote farming as an attractive profession are thus needed as part of a conservation strategy. In addition, our study revealed the importance of grassland and paddy fields for farmland bird diversity. Given the increasing trends in agricultural intensification and abandonment of livestock and rice farming systems, conservation focus in open landscapes should be targeted toward maintaining or expanding these land-cover types through environmentally friendly farming practices.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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Electric supplementary material

Landscape associations of farmland bird diversity in Germany and Japan

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Supplementary Material 1 Comparison of environmental characteristics between Germany and Japan

Variable	Germany	Japan
Longitude [E]	5°52’ - 15°02’	122°59’ - 153°58’
Latitude [N]	47°16’ - 55°03’	20°25’ - 45°31’
Area [km^2]	357,050	377,835
Mean temperature [°C]	9.6 / 11.3	8.5 / 22.7
Mean precipitation [mm]	470 / 898	1123 / 2279
Max. elevation [m]	2,962	3,776
Major biomes	temperate deciduous forest	subboreal coniferous forest to subtropical evergreen broadleaved forest

Supplementary Material 2 Correspondence table for breeding criteria in Germany and Japan

Criteria of EBCC Atlas of European Breeding Birds	Germany	Japan
0. Non breeding (species observed but suspected to be still on migration or to be summering non-breeder)		C(51); D
A. Possible breeding		
1. Species observed in breeding season in possible nesting habitat	I	C(50)
2. Singing male(s) present (or breeding calls heard) in breeding season	I	B(30)
B. Probable breeding		
3. Pair observed in suitable nesting habitat in breeding season	II	-
4. Permanent territory presumed through registration of territorial behavior (song, etc.) on at least two different days a week or more apart at same place	II	-
5. Courtship and display	II	B(31)
6. Visiting probable nest-site	III	B(34)
7. Agitated behavior or anxiety calls from adults	III	B(33)
8. Brood patch on adult examined in the hand	III	-
9. Nest-building or excavating of nest-hole	III	B(35); B(36)
C. Confirmed breeding		
10. Distraction-display or injury-feigning	IV	A(15)
11. Used nest or eggshells found (occupied or laid within period of survey)	IV	A(16); A(17)
12. Recently fledged young (nidicolous species) or downy young (nidifugous species)	IV	A(21)
13. Adults entering or leaving nest-site in circumstances indicating occupied nest (including high nests or nest holes, the contents of which cannot be seen) or adult seen incubating	IV	A(10)
14. Adult carrying a fecal sac or food for young	IV	A(13); A(14)
15. Nests containing eggs	IV	A(11)
16. Nests with young seen or heard	IV	A(19); A(20)

Germany: The Breeding Bird Atlas Project (Gedeon et al., 2014)
Japan: The 6th National Survey of the Natural Environment (MOE, 2004)
In Japan, species records with C(51) and D were excluded from the data due to association to non-breeding criteria.

Supplementary Material 3 List of breeding bird species associated with agricultural landscapes in Germany and Japan. The number of species is shown in brackets.

Germany (31)	Agricultural land species (22)	Agricultural wetland species (9)
Edge-habitat species (9)	Common buzzard (*Buteo buteo*)[SF]* Carrion crow (*Corvus corone*)[F]* Eurasian tree sparrow (*Passer montanus*) [F]* European goldfinch (*Carduelis carduelis*) [F] Northern raven (*Corvus corax*) [SF] Red kite (*Milvus milvus*) [SF] Common starling (*Sturnus vulgaris*) [F] Fieldfare (*Turdus pilaris*) [SF]	White stork (*Ciconia ciconia*) [R]
Open-habitat species (19)	Eurasian skylark (*Alauda arvensis*) [F]* Barn swallow (*Hirundo rustica*) [SF]* Common pheasant (*Phasianus colchicus*) [F]* Common linnet (*Carduelis cannabina*) [SF] Common quail (*Coturnix coturnix*) [SF] Yellowhammer (*Emberiza citrinella*) [F] Red-backed shrike (*Lanius collurio*) [SF] Corn bunting (*Miliaria calandra*) [SF] House sparrow (*Passer domesticus*) [F] Grey partridge (*Perdix perdix*) [SF] Common whitethroat (*Sylvia communis*) [F]	Marsh warbler (*Acrocephalus palustris*) [F] Meadow pipit (*Anthus pratensis*) [SF] Corn crake (*Crex crex*) [SF] Common reed bunting (*Emberiza schoeniclus*) [F] Common snipe (*Gallinago gallinago*) [SF] Western yellow wagtail (*Motacilla flava*) [SF] Whinchat (*Saxicola rubetra*) [SF] Northern lapwing (*Vanellus vanellus*) [SF]
Woodland species (3)	Eurasian wryneck (*Jynx torquilla*) [SF] Common redstart (*Phoenicurus phoenicurus*) [SF] Song thrush (*Turdus philomelos*) [F]	

Japan (29)	Agricultural land species (17)	Agricultural wetland species (12)
Edge-habitat species (12)	Common buzzard (*Buteo buteo*)* Carrion crow (*Corvus corone*)* Eurasian tree sparrow (*Passer montanus*)* Oriental greenfinch (*Carduelis sinica minor*) Jungle crow (*Corvus macrorhynchos*) Black kite (*Milvus migrans*) Oriental turtle dove (*Streptopelia orientalis*) Grey starling (*Sturnus cineraceus*)	Grey heron (*Ardea cinerea*) Grey-faced buzzard (*Butastur indicus*) Little egret (*Egretta garzetta*) Black-crowned night heron (*Nycticorax nycticorax*)
Open-habitat species (14)	Eurasian skylark (*Alauda arvensis*)* Barn swallow (*Hirundo rustica*)* Common pheasant (*Phasianus colchicus*)* Common cuckoo (*Cuculus canorus*) Siberian meadow bunting (*Emberiza cioides*) Bull-headed shrike (*Lanius bucephalus*)	Great reed warbler (*Acrocephalus arundinaceus*) Spot-billed duck (*Anas poecilorhyncha*) Little ringed plover (*Charadrius dubius*) Fan-tailed warbler (*Cisticola juncidis*) Grey wagtail (*Motacilla cinerea*) Japanese wagtail (*Motacilla grandis*) White wagtail (*Motacilla lugens*) Grey-headed lapwing (*Vanellus cinereus*)
Woodland species (3)	Chinese bamboo partridge (*Bambusicola thoracica*) Masked grosbeak (*Eophona personata*) Brown-eared bulbul (*Hypsipetes amaurotis*)	

* Species in common

[F] frequent [SF] semi-frequent [R] rare species

Germany: Nature and Biodiversity Conservation Union (NABU, 2004)

Japan: Amano and Yamaura (2007)

Supplementary Material 4 Spearman's rank correlation coefficients between pairs of landscape variables. Abbreviations: Pfarm farmland cover, Pcrop cropland cover, Pgrass grassland cover, Ppaddy paddy field cover, Nhabitat number of habitat types, Pnature semi-natural habitat cover, Pwood woodland cover, EDnature semi-natural habitat edge density, EDwood woodland edge density, MeanEV elevation. Significant correlations were shown by . $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Germany	Pfarm	Pcrop	Ppasture	Ppaddy	Nhabitat	Pnature	Pwood	EDnature	EDwood	MeanEV
Pfarm	1									
Pcrop	0.81***	1								
Ppasture	0.14***	-0.33***	1							
Ppaddy	N.A.	N.A.	N.A.	1						
Nhabitat	-0.14***	-0.19***	0.13***	N.A.	1					
Pnature	0.03.	-0.08***	0.14***	N.A.	0.56***	1				
Pwood	-0.73***	-0.60***	0.02	N.A.	0.03	-0.28***	1			
EDnature	0.05**	-0.08***	0.3***	N.A.	0.35***	0.74***	-0.08***	1		
EDwood	-0.14***	-0.07***	0.15***	N.A.	-0.13***	-0.32***	0.60***	0.07***	1	
MeanEV	-0.42***	-0.30***	-0.09***	N.A.	-0.25***	-0.41***	0.59***	-0.26***	0.42***	1

Japan	Pfarm	Pcrop	Ppasture	Ppaddy	Nhabitat	Pnature	Pwood	EDnature	EDwood	meanEV
Pfarm	1									
Pcrop	0.67***	1								
Ppasture	N.A.	N.A.	1							
Ppaddy	0.91***	0.37***	N.A.	1						
Nhabitat	0.06**	0.01	N.A.	0.09***	1					
Pnature	0.04.	0.07**	N.A.	0.03	0.27***	1				
Pwood	-0.65***	-0.40***	N.A.	-0.58***	-0.21***	-0.21***	1			
EDnature	0.75***	0.44***	N.A.	0.73***	0.20***	0.41***	-0.54***	1		
EDwood	0.57***	0.53***	N.A.	0.49***	-0.03***	-0.11***	0.02	0.42***	1	
MeanEV	-0.67***	-0.44***	N.A.	-0.61***	-0.13***	-0.17***	0.58***	-0.62***	-0.31***	1

N.A. data not available

Supplementary Material 5 Results of generalized linear models explaining the species number of total farmland birds, edge-habitat species, open-habitat species, agricultural land species, and agricultural wetland species as a function of cover crop types (cropland cover, grassland cover, paddy field cover), semi-natural habitat cover, woodland edge density, and mean elevation. Note that landscape variables were standardized based on the mean before model construction. The number of species used in Germany and Japan is shown in brackets. Linear and quadratic terms of each landscape variable were included in the analysis. Regression coefficients are expressed as means ± standard errors.

	Total farmland birds											
	Germany (31)					Japan (29)						
	Coefficient±SE			Z	P^1	Coefficient±SE			Z	P^1	P^2
Intercept	3.21E+00	±	7.20E-03	445.48	<0.001	2.47E+00	±	2.90E-02	85.22	<0.001	<0.001
Cropland cover	2.38E-01	±	3.08E-02	7.72	<0.001	4.86E-01	±	2.07E-01	2.35	<0.05	0.24
(Cropland cover)^2	-3.98E-01	±	7.84E-02	-5.07	<0.001	-9.98E-01	±	6.82E-01	-1.46	0.14	0.38
Grassland cover	2.62E-01	±	5.18E-02	5.06	<0.001			NA	NA	NA	NA
(Grassland cover)^2	-5.49E-01	±	1.34E-01	-4.11	<0.001			NA	NA	NA	NA
Paddy field cover			NA	NA	NA	1.35E+00	±	1.06E-01	12.74	<0.001	NA
(Paddy field cover)^2			NA	NA	NA	-2.22E+00	±	3.04E-01	-7.30	<0.001	NA
Semi-natural habitat cover	2.83E-01	±	1.57E-01	1.80	0.07	9.62E-01	±	2.34E-01	4.11	<0.001	<0.05
(Semi-natural habitat cover)^2	-1.90E+00	±	4.50E-01	-4.23	<0.001	-3.04E+00	±	8.48E-01	-3.59	<0.001	0.24
Woodland edge density	-2.32E-03	±	8.38E-04	-2.77	<0.01	2.19E-03	±	1.28E-03	1.72	0.09	<0.01
(Woodland edge density)^2	-7.49E-04	±	8.98E-05	-8.33	<0.001	-6.59E-05	±	4.23E-05	-1.56	0.12	<0.001
Elevation	-3.99E-04	±	2.28E-05	-17.49	<0.001	-3.04E-04	±	4.56E-05	-6.67	<0.001	0.06
(Elevation)^2	-2.84E-07	±	5.03E-08	-5.63	<0.001	9.14E-08	±	4.80E-08	1.90	0.06	<0.001
R^2											0.783

Supplementary Material 5 (continued)

	Edge-habitat species												
	Germany (9)					Japan (12)						
	Coefficient±SE			*Z*	*P*[1]	Coefficient±SE			*Z*	*P*[1]	*P*[2]
Intercept	2.08E+00	±	1.26E-02	164.91	<0.001	1.61E+00	±	4.33E-02	37.05	<0.001	<0.01
Cropland cover	5.08E-02	±	5.40E-02	0.94	0.35	1.90E-01	±	3.09E-01	0.62	0.54	0.66
(Cropland cover)^2	-2.23E-01	±	1.40E-01	-1.59	0.11	-8.11E-01	±	1.02E+00	-0.80	0.42	0.57
Grassland cover	2.03E-01	±	9.30E-02	2.18	<0.05			NA	NA	NA	NA
(Grassland cover)^2	-7.21E-01	±	2.47E-01	-2.92	<0.01			NA	NA	NA	NA
Paddy field cover			NA	NA	NA	1.11E+00	±	1.56E-01	7.16	<0.001	NA
(Paddy field cover)^2			NA	NA	NA	-2.05E+00	±	4.49E-01	-4.56	<0.001	NA
Semi-natural habitat cover	-9.68E-02	±	2.92E-01	-0.33	0.74	8.66E-01	±	3.51E-01	2.47	<0.05	<0.05
(Semi-natural habitat cover)^2	-2.65E+00	±	9.66E-01	-2.74	<0.01	-3.19E+00	±	1.31E+00	-2.44	<0.05	0.74
Woodland edge density	1.68E-03	±	1.52E-03	1.11	0.27	5.69E-03	±	1.88E-03	3.03	<0.01	0.10
(Woodland edge density)^2	-1.08E-03	±	1.63E-04	-6.61	<0.001	-1.36E-04	±	6.25E-05	-2.17	<0.05	<0.001
Elevation	-9.49E-05	±	4.03E-05	-2.36	<0.05	-6.09E-04	±	6.88E-05	-8.85	<0.001	<0.001
(Elevation)^2	-2.60E-07	±	7.76E-08	-3.36	<0.001	1.89E-07	±	7.57E-08	2.50	<0.05	<0.001
R^2											0.502

Supplementary Material 5 (continued)

	Open-habitat species						
	Germany (19)			Japan (14)			
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	P^2
Intercept	2.66E+00 ± 9.61E-03	276.47	<0.001	1.63E+00 ± 4.47E-02	36.47	<0.001	<0.001
Cropland cover	3.97E-01 ± 4.09E-02	9.71	<0.001	8.67E-01 ± 3.24E-01	2.67	<0.01	0.15
(Cropland cover)²	-5.18E-01 ± 1.03E-01	-5.05	<0.001	-1.79E+00 ± 1.08E+00	-1.66	0.10	0.24
Grassland cover	4.09E-01 ± 6.74E-02	6.07	<0.001	NA	NA	NA	NA
(Grassland cover)²	-5.34E-01 ± 1.70E-01	-3.14	<0.01	NA	NA	NA	NA
Paddy field cover	NA	NA	NA	1.96E+00 ± 1.68E-01	11.68	<0.001	NA
(Paddy field cover)²	NA	NA	NA	-2.66E+00 ± 4.65E-01	-5.72	<0.001	NA
Semi-natural habitat cover	6.24E-01 ± 2.00E-01	3.12	<0.01	1.38E+00 ± 3.71E-01	3.71	<0.001	0.07
(Semi-natural habitat cover)²	-1.81E+00 ± 5.44E-01	-3.33	<0.001	-3.57E+00 ± 1.34E+00	-2.67	<0.01	0.22
Woodland edge density	-3.78E-03 ± 1.09E-03	-3.48	<0.001	-4.24E-03 ± 2.01E-03	-2.11	<0.05	0.84
(Woodland edge density)²	-6.67E-04 ± 1.17E-04	-5.72	<0.001	6.25E-05 ± 6.59E-05	0.95	0.34	<0.001
Elevation	-5.82E-04 ± 3.00E-05	-19.41	<0.001	-1.80E-04 ± 7.21E-05	-2.49	<0.05	<0.001
(Elevation)²	-3.85E-07 ± 7.57E-08	-5.09	<0.001	1.88E-07 ± 7.04E-08	2.67	<0.01	<0.001
R^2							0.820

Supplementary Material 5 (continued)

	Agricultural land species						
	Germany (22)			Japan (17)			
	Coefficient±SE	*Z*	P^1	Coefficient±SE	*Z*	P^1	P^2
Intercept	2.96E+00 ± 8.13E-03	364.08	<0.001	2.26E+00 ± 3.28E-02	68.83	<0.001	<0.001
Cropland cover	1.34E-01 ± 3.45E-02	3.89	<0.001	1.96E-01 ± 2.43E-01	0.81	0.42	0.80
(Cropland cover)²	-2.84E-01 ± 8.86E-02	-3.20	<0.01	-1.92E+00 ± 7.91E-01	-2.43	<0.05	<0.05
Grassland cover	2.75E-04 ± 5.92E-02	0.01	1.00	NA	NA	NA	NA
(Grassland cover)²	-2.86E-01 ± 1.55E-01	-1.85	0.06	NA	NA	NA	NA
Paddy field cover	NA	NA	NA	9.80E-01 ± 1.19E-01	8.27	<0.001	NA
(Paddy field cover)²	NA	NA	NA	-1.74E+00 ± 3.47E-01	-5.01	<0.001	NA
Semi-natural habitat cover	-1.51E-01 ± 1.82E-01	-0.83	0.41	7.47E-01 ± 2.61E-01	2.87	<0.01	<0.01
(Semi-natural habitat cover)²	-1.58E+00 ± 5.37E-01	-2.94	<0.01	-2.83E+00 ± 9.49E-01	-2.98	<0.01	0.25
Woodland edge density	-6.60E-04 ± 9.51E-04	-0.69	0.49	5.49E-03 ± 1.44E-03	3.80	<0.001	<0.001
(Woodland edge density)²	-5.56E-04 ± 1.00E-04	-5.55	<0.001	-1.59E-04 ± 4.88E-05	-3.25	<0.01	<0.001
Elevation	-2.03E-04 ± 2.57E-05	-7.88	<0.001	-1.97E-04 ± 5.05E-05	-3.90	<0.001	0.92
(Elevation)²	-4.16E-07 ± 5.53E-08	-7.53	<0.001	1.25E-09 ± 5.36E-08	0.02	0.98	<0.001
R^2							0.502

Supplementary Material 5 (continued)

	Agricultural wetland species							
	Germany (9)			Japan (12)				
	Coefficient±SE	Z	P^1	Coefficient±SE	Z	P^1	P^2
Intercept	1.65E+00 ± 1.60E-02	103.13	<0.001	7.59E-01 ± 6.30E-02	12.04	<0.001	<0.001
Cropland cover	5.92E-01 ± 6.88E-02	8.62	<0.001	1.50E+00 ± 3.88E-01	3.86	<0.001	<0.05
(Cropland cover)^2	-7.57E-01 ± 1.70E-01	-4.46	<0.001	2.55E+00 ± 1.33E+00	1.92	0.06	<0.05
Grassland cover	1.05E+00 ± 1.08E-01	9.64	<0.001	NA	NA	NA	NA
(Grassland cover)^2	-1.29E+00 ± 2.69E-01	-4.79	<0.001	NA	NA	NA	NA
Paddy field cover	NA	NA	NA	2.79E+00 ± 2.37E-01	11.78	<0.001	NA
(Paddy field cover)^2	NA	NA	NA	-4.39E+00 ± 6.41E-01	-6.84	<0.001	NA
Semi-natural habitat cover	1.63E+00 ± 3.09E-01	5.29	<0.001	1.86E+00 ± 5.32E-01	3.49	<0.001	0.72
(Semi-natural habitat cover)^2	-2.95E+00 ± 8.31E-01	-3.55	<0.001	-3.79E+00 ± 1.89E+00	-2.01	<0.05	0.68
Woodland edge density	-7.58E-03 ± 1.80E-03	-4.20	<0.001	-9.57E-03 ± 2.73E-03	-3.50	<0.001	0.54
(Woodland edge density)^2	-1.68E-03 ± 2.06E-04	-8.18	<0.001	2.58E-04 ± 8.44E-05	3.06	<0.01	<0.001
Elevation	-1.12E-03 ± 5.01E-05	-22.32	<0.001	-7.84E-04 ± 1.08E-04	-7.27	<0.001	<0.01
(Elevation)^2	5.23E-08 ± 1.32E-07	0.40	0.69	4.93E-07 ± 1.09E-07	4.53	<0.001	<0.01
R^2							0.578

P^1 *p*-values for the explanatory variables in each region.
P^2 *p*-values for interaction terms of the variables between the regions.
N.A. data not available.

Chapter 2: Hotspots of agricultural ecosystem services and farmland biodiversity overlap with areas at risk of land abandonment in Japan

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Hotspots of Agricultural Ecosystem Services and Farmland Biodiversity Overlap with Areas at Risk of Land Abandonment in Japan

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Abstract: Agriculture provides a wide range of ecosystem services and has the potential to contribute to biodiversity conservation. In Japan, many of the resources associated with agroecosystems are threatened by farmland abandonment. Identifying where and to what extent agricultural ecosystem services and farmland biodiversity are affected by farmland abandonment is essential for developing effective strategies to counter the potential loss of these services and the biological communities that support them. Our study aimed to examine how a set of indicators for ecosystem services and biodiversity linked to agroecosystems (proportions of land dedicated to rice production and other agricultural production, proportion of agricultural land on slopes potentially providing landscape aesthetics, proportion of villages promoting rural tourism, and densities of forest edges and irrigation ponds in agricultural land) are distributed at the municipal level across the Japanese Archipelago, and to analyze their spatial patterns in relation to the distribution of farmland abandonment. It was hypothesized that hotspots of agricultural ecosystem services and farmland biodiversity occur in areas at risk of farmland abandonment owing to shared drivers. The cluster analysis identified four distinct ecosystem service bundle types, two of them representing areas specializing in agricultural production, while the other two provided high levels of cultural services and habitats for diverse biological communities. The latter two bundles were located in hilly and mountainous areas and accounted for 58% of rice production, 27% of other agricultural production, 77% of landscape aesthetics, 77% of rural tourism, 64% of forest edges, and 87% of irrigation ponds in Japan. In support of the hypothesis, farmland abandonment was pronounced in these areas, with 64% of recently abandoned fields located where 44% of agricultural land was found. This spatial overlap suggests that substantial losses of ecosystem services and biodiversity may occur if current patterns of farmland abandonment continue. In order to prevent large-scale losses of agricultural ecosystem services and farmland biodiversity, measures to counteract the ongoing abandonment trends should prioritize hilly and mountainous areas, and future studies should further evaluate the multiple functions of agricultural areas to improve policies that aim to ensure sustainable development of rural areas in Japan.

Keywords: agriculture; farmland loss; hilly and mountainous area; socio-ecological system; spatial pattern

1. Introduction

Farmland abandonment is changing rural landscapes worldwide [1–3]. The trend towards abandonment is driven by a combination of ecological and socio-economic factors [2,4]. Affected areas often have unfavorable environmental conditions such as low productivity soils, climatic constraints or topographic challenges—steep slopes or high elevation—which make them particularly prone to abandonment [5,6]. Low farm income, rural-urban migration, aging population of farmers, limited access to modern agriculture and market globalization are socio-economic factors contributing to this trend [6,7]. Areas where farming is no longer viable are often located in remote and mountainous areas where traditional farming systems have been maintained until now [1,7].

Agricultural landscapes show a large variation in structure and function [8]. Traditional farming systems that have evolved from long-term interactions between humans and nature play a key role in shaping and maintaining this diversity [9,10]. The unique values of traditional agriculture have been discussed with regard to biodiversity (e.g., wildlife and habitats; [11–13]) and cultural aspects (e.g., traditional knowledge and cultural landscapes; [14–16]), reflecting the fact that such land use systems create coupled social-ecological systems [17]. In regions dominated by intensive agricultural practices, traditional agricultural landscapes represent hotspots in particular for regulating and cultural ecosystem services and biodiversity [18].

Given the multifunctional nature of traditional farming systems [12,19], there may be spatial aggregation of different agricultural ecosystem services and farmland biodiversity in those parts of agricultural landscapes where such farming systems persist. In conjunction with farmland abandonment being pronounced in traditional farming systems [20], it is possible that areas with high levels of multiple ecosystem services and high biodiversity are concentrated in areas which are disproportionately affected by abandonment trends. If such spatial overlap exists, agricultural ecosystem services and farmland biodiversity may decline due to vegetation succession following the cessation of agricultural management. An obvious consequence of farmland abandonment is the loss of production potential for food, feed, and fiber. Environmentally, scrub and tree encroachment can lead to a loss of landscape heterogeneity and mosaic features and threaten a range of species that have adapted to farming systems over time [2,19,21,22]. The loss of landscape character induced by vegetation succession can also affect cultural and heritage values of landscapes shaped by humans [2,23]. Negative environmental impacts of farmland abandonment have been reported, particularly from regions with high forest cover [2] where small-scale/low intensity agriculture is often retained [21]. By contrast, some ecosystem services and elements of biodiversity have been found to increase during secondary succession on former farmland [4]; these include the stabilization of soils [24] along with soil recovery [25], carbon sequestration [26], and water regulation [27]. Successional vegetation development allows biodiversity recovery in simple landscapes (rewilding; [28]), and shifts biological communities towards species favoring woody vegetation [29,30]. However, findings from previous studies in mountain areas reveal that species colonizing old field sites were predominantly common ones [29,30], suggesting that there may be only a small gain in species diversity from adding shrubs and trees in areas where woody vegetation is already abundant. In regions where forests cover most of the land, negative effects of farmland loss may outweigh positive effects of forest gain.

This study focused on agricultural ecosystem services and elements of biodiversity that are linked to agroecosystems; these variables are negatively affected when agricultural management ceases, and the effects may be difficult to reverse once they have occurred [31]. We elucidated the relationships between ecosystem services and biodiversity across basic types of agricultural landscapes in different topographic settings, and we tested whether the spatial distribution of these ecosystem services and biodiversity elements is systematically linked to the distribution of areas where farmland abandonment is pronounced. Such information on the spatial relationships between ecosystem services, biodiversity and farmland abandonment is important for decision makers tasked with improving policy design and spatial planning for sustainable development, including the International Partnership for the Satoyama Initiative, that aims to accomplish societies in harmony with nature [9,32].

We used the concept of ecosystem service bundles to capture key patterns in the distribution of agricultural ecosystem services and farmland biodiversity across the Japanese archipelago. Ecosystem service bundles have been defined as sets of ecosystem services that repeatedly occur together across space [33]; this approach has been applied successfully to link such bundles to socio-ecological subsystems of a landscape [33–36]. We applied this method to identify hotspots of agricultural ecosystem services and farmland biodiversity in landscapes with different topographic characteristics and levels of agricultural land use intensity. Our study aimed to investigate (i) whether there is spatial aggregation of different agricultural ecosystem services and farmland biodiversity in Japan, and (ii) whether the identified hotspots coincide with areas affected by farmland abandonment trends.

2. Methods

2.1. Agricultural Areas in Japan

Japan extends over several biomes ranging from subboreal coniferous forest in the north to subtropical evergreen broad-leaved forest in the south. It has a wide topographic gradient ranging from coastal plains to high mountain zones. Due to the dominance of hilly and mountainous areas, the land is mainly covered by forests, comprising 67% of the land surface, whereas farmland makes up only 12% [37]. The main crop is rice (*Oryza sativa*), accounting for 54% of the total cultivated land [38]. Traditional rural landscapes in Japan are referred to as 'satoyama,' where a mosaic of forests, semi-natural grasslands, agricultural fields, irrigation channels, ponds and settlements are managed as an integral part of socio-ecological systems (see [9,11,12] for images of satoyama landscapes). In these landscapes, farmland abandonment has become a major challenge owing to an aging population, migration to urban areas, a shortage of farm labor, and a set-aside program for rice production [39,40]. Abandoned fields occupy approximately 10% of the total farmland area [41], and the trend towards abandonment is expected to continue [39]. Japan is thus suited to study how spatial patterns of multiple agricultural ecosystem services and farmland biodiversity are related to the distribution of abandoned fields.

2.2. Quantification of Ecosystem Services and Biodiversity

We screened nationwide public statistics and land-use datasets for proxies of ecosystem services and biodiversity. Two provisioning services (rice production and other agricultural production), two cultural services (landscape aesthetics and rural tourism), and two landscape indicators (forest edges and irrigation ponds) relevant for biodiversity were assessed across Japan. This selection of indicators was based on their relationship to agroecosystems, their susceptibility to farmland abandonment, and on data availability. Regulating services were not included, because many of them would be expected to recover with secondary succession, or because their provision relies on conditions and management intensity at the local level. Extensively managed grassland, which is equally relevant for biodiversity, was not included in the analysis because grasslands are rare at the national scale, making up less than 1% of the total land surface [42]. Table 1 provides a summary of ecosystem services and biodiversity indicators assessed.

Table 1. List of agricultural ecosystem services and farmland biodiversity assessed.

Category	Indicator	Proxy	Unit	Data Year	Data Scale
Provisioning	Rice production	Percent of rice fields in total land	(%)	2015	Municipality
	Other agricultural production	Percent of other agricultural fields in total land	(%)	2015	Municipality
Cultural	Landscape aesthetics	Percent of terraced fields in farmland	(%)	1998	Municipality
	Rural tourism	Percent of villages that promote rural tourism	(%)	2015	Municipality
Biodiversity	Forest edges	Density of forest edges per hectare of farmland	(m ha^{-1})	1998	Municipality
	Irrigation ponds	Density of irrigation ponds per hectare of rice fields	(ponds ha^{-1})	2014	Prefecture

Note. References for databases are provided in the main body text.

We used administrative units at the municipal level to evaluate the spatial variation of the selected indicators for ecosystem services and biodiversity across Japan. By choosing this administrative level for summarizing the information, we intended to generate results that can be used in existing decision-making structures and policy implementation mechanisms [43]. Data were collected for 1719 municipalities. Because data on irrigation ponds were available only at the prefectural level (n = 47), the same values were assigned to all municipalities within each prefecture; details are given below. Proxies were quantified using data for 2015 or as close as possible to this date, except for landscape aesthetics and forest edges that were based on land-cover data in 1998. Land-cover was derived from the vector dataset Actual Vegetation Map of Japan [44]. The Land Cover Classification System developed by the Food and Agriculture Organization [45] was applied to reclassify the 774 vegetation communities into 22 land-cover classes: namely, cropland, pasture, rice fields, tree crop, shrub crop, broad-leaved forest, mixed forest, coniferous forest, mangrove, bamboo, shrub, herbaceous, sparse vegetation, lichen/moss, water body, fresh and brackish water wetland, salt marsh, bare area, snow/ice, vegetated urban, urban, and unknown (Supplementary Material 1). Classification of vegetation communities was carried out in reference to the classification scheme proposed by Ogawa et al. [46]. Generation of spatial data was performed using ArcGIS® 9.3 (ESRI, http://www.esri.com/, accessed on 30 June 2017).

2.2.1. Provisioning Service: Rice Production

Rice plays a special role as the staple food in Japan. Following the approach of Raudsepp-Hearne et al. [33] and Maes et al. [47], the share of rice fields as a fraction of the total land area of each municipality was used to indicate how much land is dedicated to rice production. Rice production in municipality i was expressed as $Rice.production_{ij}$ $[\%] = A.rice_{ij}$ $[ha]/A.land_{ij}$ $[ha] \times 100$, where $A.rice_{ij}$ and $A.land_{ij}$ are the area of rice fields [48] and total land [49] of municipality i in prefecture j, respectively.

2.2.2. Provisioning Service: Other Agricultural Production

Production of agricultural commodities besides rice (i.e., non-rice arable fields, permanent crops, and pasture) was assessed using an estimation method similar to that which was applied to rice production. It was defined as $Other.agricultural.production_{ij}$ $[\%] = A.other_{ij}$ $[ha] / A.land_{ij}$ $[ha] \times 100$, where $A.other_{ij}$ and $A.land_{ij}$ are the area of other agricultural fields [48] and total land of municipality i in prefecture j, respectively. Pasture is often separated from crops as it is associated with livestock production [47]. In Japan, however, pasture occupies only 13.5% of total farmland, where the majority of pasture is found in the northernmost island Hokkaido (83.5% of pasture; [50]). As the category Area of Upland Fields did not differentiate between pasture and cropland at the municipal level, we also treated them in the same category in our analysis rather than making two separate categories.

2.2.3. Cultural Service: Landscape Aesthetics

Terraced fields are common agricultural landscapes in hilly and mountainous areas of Japan [51]. Terraced landscapes receive much attention as areas of high aesthetic value among different groups of people such as tourists [52,53], conservation activists [52], and local residents [54]. For their scenic beauty, rice terraces are one of the few agricultural features included in the Top 100 Selection series, which lists outstanding sites of a given theme across Japan [55]. Terraced landscapes are under pressure from abandonment because much of the agricultural work on steep slopes requires manual labor [54], and a large number of new policies have been enacted to conserve such cultural landscapes [51]. In the study, the share of terraced fields in farmland was used as an indicator for its aesthetic potential provided by agricultural landscapes. Areas with a high likelihood of containing terraced fields were delineated using two spatial datasets, namely, the Elevation, Degree of Slope Tertiary Mesh Data [56] and the land-cover dataset. The elevation dataset includes minimum and maximum degrees of slope on a 1 km^2 grid basis. We extracted grid cells with maximum degrees of slope ≥15°, because the Direct Payment for Hilly and Mountainous Areas, which supports farmers in managing fields on slopes, sets this value as a minimum threshold for supporting non-rice arable fields and grasslands on steep slopes [57]. The extracted grid cells were then overlaid with farmland polygons derived from the land-cover dataset (i.e., cropland, pasture, rice fields, tree crop, and shrub crop); we interpreted the overlapping areas as terraced fields. Terraced landscapes as an indicator for landscape aesthetics in municipality *i* in prefecture *j* was formulated as $Landscape.aesthetics_{ij}$ [%] = $A.terrace_{ij}$ [ha]/$A.farmpoly_{ij}$ [ha] × 100, where $A.terrace_{ij}$ and $A.farmpoly_{ij}$ are the area of terraced fields and farmland polygons, respectively.

2.2.4. Cultural Service: Rural Tourism

Rural tourism provides visitors with recreational opportunities using a variety of local resources [58,59]. It is largely supported by local industries, as the activities involve overnight stays, participation in hands-on learning programs offered by the locals, direct sales of local products, and cultural exchanges in farming, forestry, and fishing villages [60]. The percentage of villages involved in rural tourism indicates the degree of attractiveness of a municipality as a recreational destination for such activities. It was expressed as $Rural.tourism_{ij}$ [%] = $N.tourismvillages_{ij}$ [villages]/$N.totalvillages_{ij}$ [villages] × 100, where $N.tourismvillages_{ij}$ and $N.totalvillages_{ij}$ are the number of villages that promote rural tourism and the total number of villages in municipality *i* in prefecture *j*, respectively. The data are available from the Census of Agriculture and Forestry [61].

2.2.5. Biodiversity: Forest Edges

Forest edges are one of the key features influencing biodiversity in agricultural landscapes of Japan [39]. The length of forest edges per unit area tends to be long in those regions where the topography has facilitated the development of typical land-use patterns of satoyama; flat land at the bottom of valleys is used for rice production, while the hillsides are covered by forests, forming complex landscapes with long boundaries of forests and rice fields [11]. Having both habitats closely connected enhances habitat quality for organisms that require them at different stages of their life cycle [11]. Examples include amphibian species that inhabit forests and breed in aquatic habitats in agricultural areas (e.g., *Hynobius nebulosus* and *Rana ornativentris*; [62,63]) and umbrella species of birds that use forests for breeding and farmland and grassland for feeding (e.g., *Butastur indicus* and *Accipiter gentilis*; [64,65]). Strips of grassland maintained along the boundaries are known to support many plant species typical for open habitats [66]. We used the length of forest edges per unit area in farmland to indicate the availability of borders that support important aspects of farmland biodiversity in Japan. The length of forest edges where farmland polygons are adjacent to forest polygons (i.e., broad-leaved forest, mixed forest, coniferous forest, and mangrove) was calculated based on the land-cover dataset. Forest edges were estimated by $Forest.edges_{ij}$ [$m\ ha^{-1}$] = $L.forestedges_{ij}$ [m]/$A.farmpoly_{ij}$ [ha], where $L.forestedges_{ij}$ and $A.farmpoly_{ij}$ are the length of forest edges and the area of farmland polygons in municipality *i* in prefecture *j*, respectively.

2.2.6. Biodiversity: Irrigation Ponds

Irrigation ponds are part of rice farming systems in regions where water resources are scarce (i.e., low-rainfall areas and/or areas with catchments of limited size in hilly and mountainous areas), and approximately 70% of them were constructed more than 150 years ago [67]. Habitats under irrigation regimes contribute to spatial and temporal heterogeneity and are home to many aquatic plants and animals [13]. For example, irrigation ponds serve as stepping stones for birds [68] and Odonata species [69], and are also refuges for some aquatic insects when fields are drained [70]. The dredging of bottom sediment establishes vegetation at different succession stages in shallow water, providing a range of micro-habitats to aquatic animals [69]. We used the density of irrigation ponds to express the availability of permanent aquatic habitats in agricultural landscapes. It was defined as $Irrigation.ponds_j$ [ponds ha^{-1}] = $N.ponds_j$ [ponds]/$A.rice14_j$ [ha], where $N.ponds_j$ and $A.rice14_j$ are the number of irrigation ponds [67] and the area of rice fields [71] in prefecture *j*, respectively. Both data were taken in 2014. The prefectural values were assigned to municipalities that belong to the same prefecture ($Irrigation.ponds_{ij}$ = $Irrigation.ponds_j$).

2.3. Agricultural Data

There are two types of publicly available data related to agriculture in Japan: Crop Statistics and the Census of Agriculture and Forestry (hereafter addressed as Census Statistics). The former generally surveys all agricultural fields, but there is no information on the area of abandoned fields at the municipal level. The latter includes a special category 'Area of Abandoned Fields,' but it does not cover all fields; only land owners with ≥0.05 ha agricultural land are included, and land owners who don't live locally are not part of the survey. Here, an abandoned field is defined as an agricultural field that has not been cultivated for more than a year and is not considered for production in the next several years [61]. We used Crop Statistics [48] and Census Statistics [61] to obtain information on the area of cultivated and abandoned fields in 2015. Municipalities for which information on abandonment was not available were excluded, leaving 1651 municipalities covering 99.3% of the total area of abandoned fields for analysis.

2.4. Statistical Analysis

Non-normally distributed indicators were transformed ($Rice.production_{ij}^{0.1}$, $Other.agricultural.production_{ij}^{-0.2}$, $Landscape.aesthetics_{ij}^{0.3}$, $Rural.tourism_{ij}^{0.1}$, $Forest.edges_{ij}^{0.5}$, $Irrigation.ponds_{ij}^{-0.1}$) using the Box–Cox transformation function of the "MASS" package in R [72]. Other agricultural production and irrigation ponds were additionally multiplied by −1, so higher indicator values correspond to greater provision of respective services. Normality of the resulting frequency distributions was confirmed by the skewness measure available in R package "e1071" ($|S| < 0.5$; [73]). Pearson's correlation analysis was performed to assess pairwise relations between the proxies (r_p), and significance levels for r_p were corrected for spatial autocorrelation by adjusting the degree of freedom using Dutilleul's method [74]. We evaluated the degree of spatial clustering for each service using Moran's I available from the "spdep" package in R [75].

A two-step approach was taken to analyze if ecosystem services and biodiversity co-vary, i.e., whether they repeatedly occur together and form 'bundles'. Applying the sequence used by Turner et al. [76] and Schirpke et al. [77], we first used a principal component analysis (PCA) to extract the main multivariate interrelationships among the variables. Using principal components for cluster analysis can provide a more robust clustering, as removing features with low variance acts as a filter to characterize the non-random structure in the data [78]. Following the Kaiser–Guttman criterion (eigenvalue >1; [79]), PCA yielded two main axes for describing the spatial patterns of ecosystem services and biodiversity. In a second step, cluster analysis was applied to identify groups of municipalities according to the first two principal component scores. In line with earlier works [33,34,76,77], we used K-means clustering in R package "cluster," which minimizes within-group variability [80]. The optimal number of clusters was determined by examining scree plots, and the number of iterations was set at 10,000 to stabilize clustering. The spatial clustering of ecosystem bundles was assessed by using Moran's I. We tested differences in the values of ecosystem service and biodiversity proxies among the bundles by using Kruskal–Wallis tests and between pairs of bundles by using the Mann–Whitney U test. The mean values of ecosystem service and biodiversity proxies were calculated for each bundle. They were then standardized by the respective largest mean values among the bundles, and were visualized using star plots to show differences in the level of service provision. We used ArcGIS® 9.3 (ESRI, http://www.esri.com/, accessed on 30 June 2017) for mapping ecosystem services and biodiversity as well as the identified ecosystem service bundles.

The share of ecosystem services and biodiversity as a fraction of the respective total amounts in Japan was calculated to examine how much of service provision each bundle accounts for. We used the values at the municipal level taken from public statistics or spatial data. If data were only available at the prefectural level (i.e., irrigation ponds), then municipal values were estimated by redistributing the prefectural amounts to their affiliating municipalities. The number of irrigation ponds at the municipal level was estimated by redistributing the number at the prefectural level based on the density of irrigation ponds in prefecture *j* ($Irrigation.ponds_j$) and the area of rice fields in 2014 in municipality *i* that belonged to the prefecture ($A.rice14_{ij}$, [71]). It was expressed as $N.ponds_{ij}$ $[ponds] = Irrigation.ponds_j\ [ponds\ ha^{-1}] \times A.rice14_{ij}\ [ha]$. The municipal values were summed across Japan and according to the bundles to calculate the share.

The area of cultivated and abandoned fields was compared among the ecosystem service bundles using 1651 municipalities with abandonment data. The Kruskal–Wallis test was used to test differences among the bundles, and the Mann–Whitney U test was then carried out to test differences between pairs of bundles.

Statistical analyses were conducted using R-3.2.4 [81].

3. Results

3.1. Spatial Patterns and Interactions of Ecosystem Services and Biodiversity

Agricultural ecosystem services and farmland biodiversity showed distinct spatial patterns (Figure 1). The spatial distributions of landscape aesthetics and forest edges were positively correlated (r = 0.70; SM2), and were conjointly found in the mountain ranges (Figure 1). These two 'mountain indicators' showed contrasting patterns with provisioning services (SM2). Rice and other agricultural production shared areas of high concentration, but there were also cases in which they were spatially segregated (e.g., rice production close to alluvial plains vs. other agricultural production in Hokkaido and near the Tokyo Metropolis; Figure 1), resulting in a weak correlation (r = 0.12; SM2). Rural tourism was found throughout Japan (Figure 1), and was weakly but positively associated with landscape aesthetics and irrigation ponds (r = 0.10 and 0.14, respectively; SM2). Irrigation ponds were most commonly observed in the western part of Japan (Figure 1), and showed a weak positive and a moderate negative correlation with rice and other agricultural production, respectively (SM2).

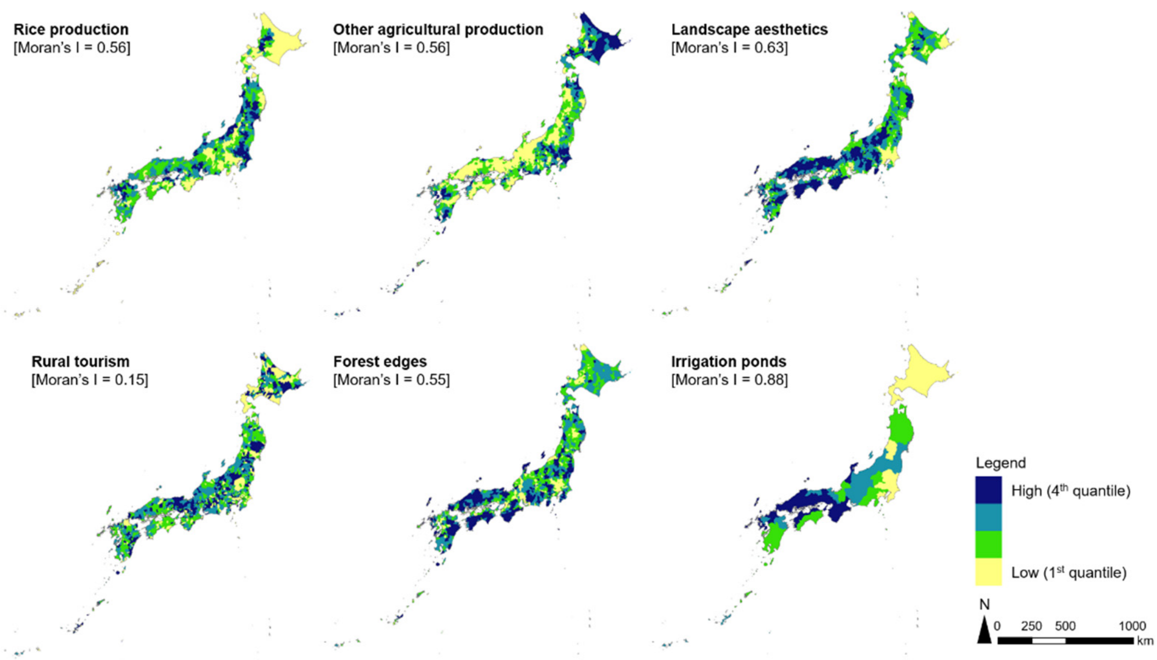

Figure 1. Spatial distributions of agricultural ecosystem services and farmland biodiversity in Japan at the municipal or prefectural level. Values are classified in quantiles. Moran's I is all $p < 0.001$.

3.2. Ecosystem Service Bundles

PCA was used prior to cluster analysis, and the first two axes accounted for 60.6% of the total variance in ecosystem services and biodiversity (Table 2). The first principal component explained 38.9% of the variation, and contrasted areas surrounded by forests (negative loadings; landscape aesthetics and forest edges) with food production areas (positive loadings; rice and other agricultural production). The second component accounted for an additional 21.7% of the variation, and separated rice production-related services (rice production and irrigation ponds) and other agricultural production.

Table 2. Principal component analysis of agricultural ecosystem services and farmland biodiversity at the national level in Japan (n = 1719). Results show PC loadings, eigenvalues, and the proportion of variance explained. Values in bold are the variables with the greatest weight in defining the two ordination axes.

	PC1	PC2
Rice production	**0.397**	**0.467**
Other agricultural production	**0.410**	**−0.377**
Landscape aesthetics	**−0.586**	−0.014
Rural tourism	−0.079	0.309
Forest edges	**−0.543**	−0.197
Irrigation ponds	−0.171	**0.711**
Eigenvalue	1.528	1.142
% variance explained	38.9	21.7

The 1719 municipalities were clustered into four ecosystem service bundles according to the two principal components. They were namely: non-irrigated agriculture (hereafter addressed as Non-Rice, n = 400), irrigated agriculture on flat land (Rice, n = 361), agriculture in hilly areas (Hill, n = 474), and agriculture in mountainous areas (Mountain, n = 484).

The four ecosystem service bundles showed geographical clustering (Moran's I = 0.58, $p < 0.001$; Figure 2), each representing distinct patterns in the distribution of ecosystem services and biodiversity (SM3, Kruskal–Wallis test, all $p < 0.001$). For example, the first two bundles (i.e., Non-Rice and Rice) comprised municipalities whose land was dedicated to food production. Municipalities in the Non-Rice bundle were mainly distributed in Hokkaido and some in the Greater Tokyo Area. This bundle showed the highest level of other agricultural production and the lowest level of rice production and irrigation ponds. Many of the municipalities in the Rice bundle were found on large alluvial plains and had the highest mean rice production. Levels of cultural services and biodiversity were generally low in this bundle. By contrast, the latter two bundles (i.e., Hill and Mountain) were linked to cultural services and biodiversity. Municipalities in the Hill bundle were found almost all over Japan and were often located between the Rice and Mountain bundles. Here, in agricultural landscapes with moderate food production, moderate to high levels of cultural services and biodiversity were also observed. Municipalities in the Mountain bundle were distributed near mountain ranges. They had the highest landscape aesthetics, and despite its having the lowest food production, moderate to high levels of all other farmland resources were observed.

The share of ecosystem services and biodiversity in their respective total amounts in Japan was summarized for each bundle (Table 3; n = 1719). For instance, the Non-Rice bundle accounted for 59.8% of the total amount of other agricultural production in Japan. Similarly, the Rice bundle accounted for 28.9% of rice production. The Hill bundle held the largest share for many of the ecosystem services and biodiversity in Japan. They were not only responsible for food production (i.e., 43.9% rice production and 16.6% other agricultural production), but also had large quantities of cultural services and biodiversity such as landscape aesthetics (35.8%), rural tourism (46.6%), forest edges (30.7%), and irrigation ponds (62.5%). In addition, the Mountain bundle accounted for a moderate share such as landscape aesthetics (41.1%), rural tourism (30.2%), forest edges (32.9%), and irrigation ponds (24.8%) within remarkably small food production areas (12.3% of cultivated fields).

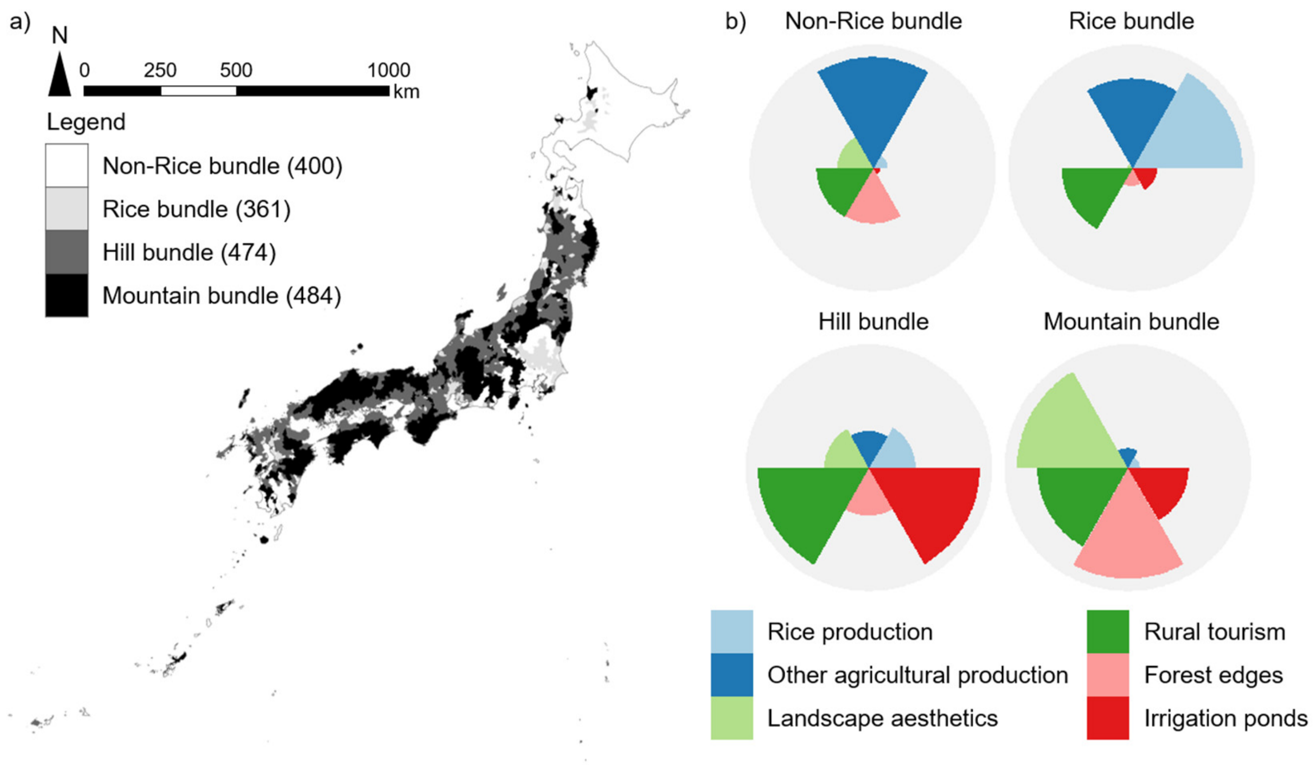

Figure 2. Results of cluster analysis showing: (**a**) spatial distributions of ecosystem service bundles and (**b**) average values of ecosystem services and biodiversity found within each bundle represented in flower diagrams. The number of municipalities per bundle is shown in parentheses next to the bundle names.

Table 3. Percent share of ecosystem services and biodiversity in total for each ecosystem service bundle.

Bundles	Non-Rice	Rice	Hill	Mountain
Number of municipalities	400	361	474	484
Rice production [1]	12.9	28.9	43.9	14.3
Other agricultural production [1]	59.8	13.6	16.6	10.0
Landscape aesthetics [3]	20.6	2.5	35.8	41.1
Rural tourism [1]	11.4	11.7	46.6	30.2
Forest edges [3]	29.1	7.3	30.7	32.9
Irrigation ponds [2]	1.8	10.9	62.5	24.8

Values derived from [1] 2015, [2] 2014, and [3] 1998 data.

3.3. Farmland Abandonment

Different distribution patterns of abandoned fields were observed among the ecosystem service bundles (n = 1651; Figure 3; Kruskal–Wallis Test, all $p < 0.001$). The Hill bundle had the largest area of abandoned fields (Figure 3b), although that of cultivated fields did not significantly differ from those of the Non-Rice and Rice bundles (Figure 3a). The Mountain bundle had a markedly large area of abandoned fields (Figure 3b), given its smallest cultivated area (Figure 3a). In total, the Non-Rice, Rice, Hill, and Mountain bundles comprised 34.3%, 21.9%, 31.5%, and 12.3% of 4,496,697 ha cultivated fields in 2015, respectively, and did 20.1%, 16.0%, 38.5%, and 25.4% of 419,978 ha abandoned fields, respectively. Farmland abandonment was observed all over Japan, with higher abandonment trends in the hilly and mountainous areas.

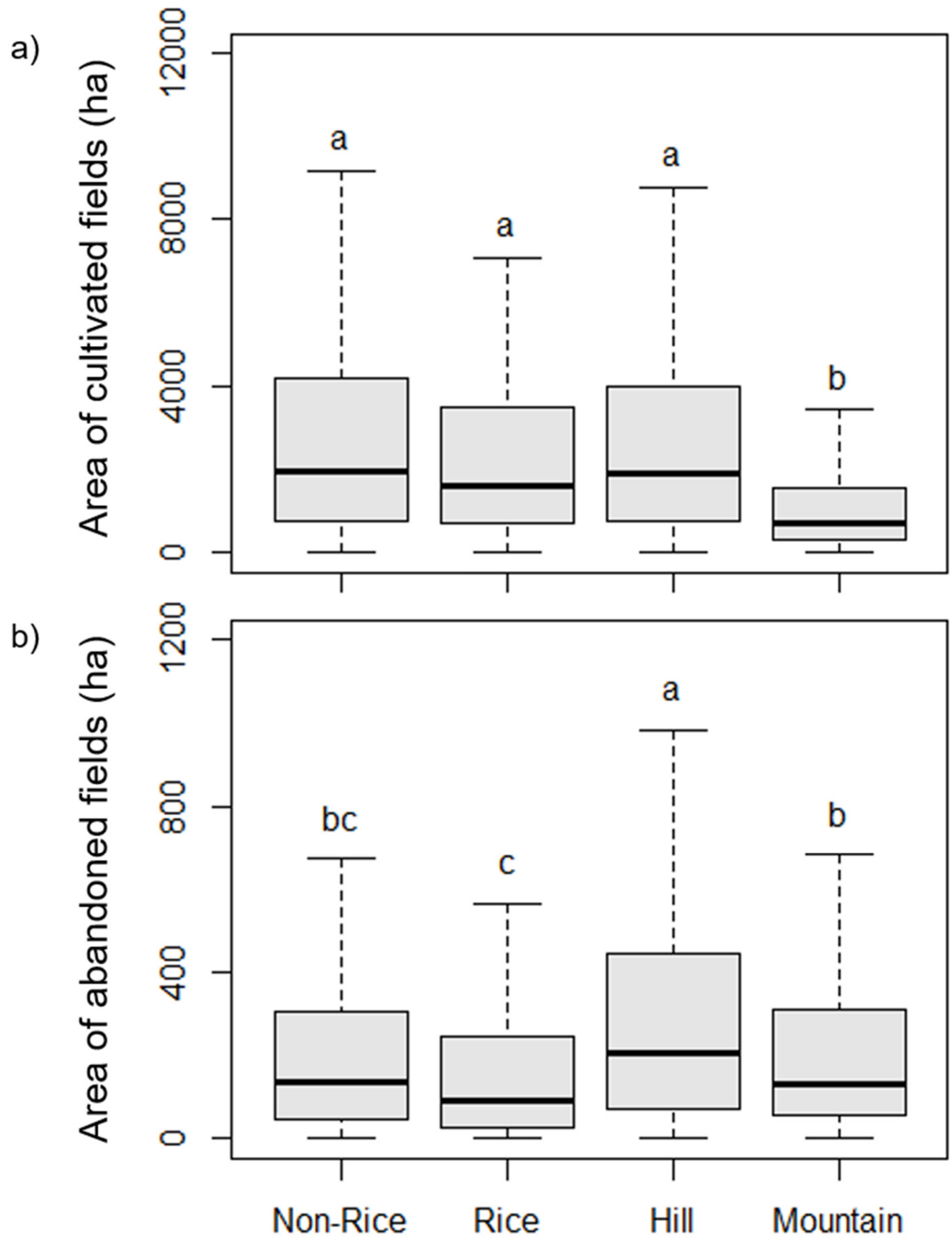

Figure 3. Boxplots comparing the area of (**a**) cultivated fields, and (**b**) abandoned fields in 2015. Significant differences were observed among the bundles (Kruskal–Wallis test all $p < 0.001$). Different letters indicate significant differences between pairs of bundles (Mann–Whitney U test $p < 0.05$) and are in descending order.

4. Discussion

Our study demonstrated that ecosystem services and biodiversity linked to agroecosystems are spatially aggregated and form hotspots in hilly and mountainous regions in Japan. The ecosystem service and biodiversity hotspots coincided with areas with high proportions of abandoned fields, suggesting that ecosystem services and biodiversity established by long-term human–nature interrelationships are at risk. We structure the discussion into three sections: (1) the relationships among ecosystem services in agricultural landscapes in Japan, the resulting spatial patterns of ecosystem services (ecosystem service bundles), and the possible mechanisms that underlie these patterns; (2) the processes leading to farmland abandonment and the feedback effects on agricultural ecosystem services; and (3) the implications for the management of agricultural landscapes in Japan.

4.1. Bundles of Agricultural Ecosystem Services and Biodiversity

The first principal component that separated municipalities according to a forest–agriculture gradient was related to topography. Japan is predominantly covered by forests due to the steepness of its slopes, which limits their suitability for agriculture. In municipalities in flat and easily accessible areas (i.e., the Non-Rice and Rice bundles), relatively large tracts of land were dedicated to agricultural uses, while in municipalities on slopes (i.e., the Hill and Mountain bundles), agriculture was practiced at a smaller scale. The second principal component was linked to a rice–other agricultural production gradient. Three types of agricultural landscapes were distinguished along this axis. The first type corresponded to the Rice bundle represented by high proportions of rice fields on alluvial plains. Biophysical factors such as stable water supply through access to groundwater and surface water and fertile soils created by a long history of sedimentation are responsible for the establishment of the major rice production areas [82]. The second type was associated with the opposite end of the gradient, namely, the Non-Rice bundle. It was found in regions characterized by special conditions; both socioeconomic and ecological factors played a significant role in allocating land for non-rice and dairy farming. For example, the boreal climate in much of Hokkaido is not suited to growing rice, restricting its production to the alluvial plain in the western part of the northernmost island. Dairy farming was promoted by the Japanese government in the second half of the 19th century, contributing to the dominance of this type of agriculture. The Greater Tokyo Area, another region where the Non-Rice bundle is widespread, is focused on producing vegetables and fruits due to its proximity to the capital [83]. The third type was related to the Hill and Mountain bundles characterized by a mixture of rice and other agricultural production. In these regions, rice paddy cultivation occurs on valley bottoms or on terraced fields, whereas other arable fields and grasslands are distributed on the uplands [84]. Irrigation ponds were also an important variable correlated to the second principal component. The majority were found in the western part of the main island Honshu where the Hill and Mountain bundles were dominant.

In the Non-Rice and Rice bundles, food provisioning services were pronounced, but cultural services and biodiversity were relatively low. The contrasting spatial patterns of food production with landscape aesthetics and irrigation ponds were most likely due to the differences in locations where flat farmland and these services are distributed (i.e., terraced fields on slopes and irrigation ponds in areas where water availability is scarce). On the other hand, high levels of food production and low levels of forest edges and rural tourism have possibly occurred due to land being diverted to agriculture. Productive and easily accessible land is generally prone to agricultural intensification. Simple landscapes resulting from intensified farming practices might explain the low participation rate of villages in hosting rural tourism in these bundles, as landscape homogenization can lower landscape appreciation of the countryside [85,86]. Our results suggest that prioritizing provisioning services not only induces trade-offs with regulating and cultural services provided by a total landscape (i.e., across land use/land cover types) as reported by previous studies [18,33,35,76,77,87–91], but can also degrade cultural services and biodiversity that are supported by traditional agriculture.

The Hill and Mountain bundles, in contrast, showed a joint supply of cultural services and farmland habitat features in space and have been identified as hotspots for agriculture-related ecosystem services and biodiversity in today's modern society. Areas with moderate to high proportions of landscape aesthetics coincided with areas where the extent of agricultural activities was constrained due to their topographic conditions. The Hill and Mountain bundles also revealed a high potential for biodiversity support, as shown by moderate to high levels of forest edges and irrigation ponds. Our finding is in line with previous studies, which reported that high nature value farmlands in Japan distribute in hilly and terraced landscapes where a mosaic of landscape elements occur within a limited area [11,13]. In Japan, a significant portion of farmland biodiversity has been lost due to land consolidation [40]. Traditional agricultural land which remains unconsolidated is most likely to occur in hilly and mountainous areas, as steep slopes impede modernization of agriculture. In addition, the two bundles showed the highest participation rate of villages in promoting rural tourism. Traditional rural landscapes like terraced fields and coppice woodlands are strongly linked to people's emotional attachment in Japan [52] and are considered to be the key source of rural tourism [58,59]. High occurrence of these landscape elements in areas of active rural tourism found in our study supports people's preference for such landscapes.

Overall, our broad analysis showed that the Hill and Mountain bundles are key to sustaining food security, cultural values, and farmland biodiversity, as these two bundles together accounted for two to three quarters of agricultural ecosystem services and biodiversity in Japan. One should note, however, that the study did not consider regulating services provided by agroecosystems, as many of them would either increase along with secondary succession or are not quantifiable at the national level due to their dependence on site-specific conditions and management intensity. Examples for the latter case include pollination and pest control for crops and mitigation of hazards such as landslides and floods. Mitigation of landslide damages is often optimized according to local ecological knowledge, where people for instance allocate grassland on slopes of thin-layer volcanic soil to keep the biomass or potential mass flows small [92]. In some parts of Japan, the locals utilize agricultural land as a retarding basin by the use of traditional open levees and mitigate flood damages at the site and downstream [93]. For ecosystem services optimized at the local level, suitable proxies were not available for all municipalities in Japan, and regional scales are suited to studies that investigate where and to what extent services are maintained by agricultural management. Since cultural diversity and biological diversity are the long-term outcomes of social–ecological systems [10,15,16,19], we think that the analysis of the selected indicators nevertheless provides useful insights into the challenges and opportunities involved in the maintenance and conservation of goods and services that are linked to agroecosystems in Japan.

Other limitations of the study are related to the use of an ecosystem service bundles approach. First, ecosystem service bundles delineated by cluster analysis are dependent on the variables used [87]. It is possible that different sets of ecosystem services and their indicators produce different cluster solutions, but we consider that overall clustering patterns would not be too deviated from the one presented here. This is because, in a country like Japan, where there is a clear contrast between areas of flat land and steep slopes, we would expect variables selected for agriculture-related ecosystem services and habitat features to reflect the topographic gradient to some extent. Variables would also be influenced by the gradient of rice and non-rice farming systems, which determines the types of agricultural infrastructure maintained as well as associated ecosystem services and biodiversity [13]. It is likely that cluster solutions fit somewhere along the two gradients, unless there are region-specific services that would override the influences of the gradients. Second, we assumed all services and biodiversity to be of equal weight. We did so because we do not have the a priori knowledge necessary for assigning different values. Their valuation can also vary considerably among different groups of people, even for the same service in the same region [94]. Instead of 'valuing' the bundles by giving them different weights, we considered them as a measure of ecosystem service diversity representing the number of services and the intensity with which they are delivered, as in the previous study done by Rodriguez-Loinaz et al. [95].

4.2. Ecosystem Service and Biodiversity Hotspots at Risk of Farmland Abandonment

Hotspots of agricultural ecosystem services and farmland biodiversity and areas of high abandonment trends overlapped spatially, as the largest area of abandoned fields was found in the Hill bundle and the second largest in the Mountain bundle, given its smallest agricultural area. This spatial coincidence is probably associated with shared drivers inherent in hilly and mountainous regions. For instance, the conversion of traditional landscapes to more simplified landscapes has occurred in regions where biophysical and structural conditions for agriculture are favorable [96]. Traditional farming systems on marginal land have thereby avoided landscape homogenization processes. Agricultural intensification can, however, occur alongside abandonment of less productive land [97], meaning that it indirectly induces farmland abandonment to take place in hilly and mountainous regions where ecosystem service hotspots persist. Natural disadvantages such as steep slopes and difficult access are themselves the geo-physical causes of farmland abandonment [5].

Succession on abandoned fields generally leads to communities dominated by trees and replaces agricultural ecosystem services by forest ecosystem services over time. In Japan, adding scrub and trees onto abandoned fields, which comprise 10% of the total farmland areas in 2015 [41], would only contribute to a 1.7% increase in forest area. One of the main negative impacts is clearly the loss of agricultural production potential. The loss is likely to become permanent, because it is increasingly difficult to restart agricultural use once the land has been abandoned [41]. Approximately two thirds of farmland abandonment have occurred in the Hill and Mountain bundles, and these two bundles were responsible for 58% of rice production and 27% of other agricultural production in Japan. As they constitute a large part of food security in the country, measures need to be taken to avoid a permanent loss of agricultural production potential from these special locations.

Previous studies revealed that farmland abandonment occurs at the expense of cultural heritage and aesthetic landscape values [2,23,98]. In our study, the Hill and Mountain bundles were shown to be responsible for more than three quarters of landscape aesthetics and rural tourism, meaning that these cultural values retained in rural Japan are likely be lost due to the cessation of farming practices that is happening at a higher rate across the country. The loss of character or identity unique to traditional farming systems might weaken the emotional bonds that people have established to these places [99]. Such character loss also implies that municipalities active in rural tourism (i.e., those in hilly and mountainous areas) might lose the opportunity to explore economic alternatives, which would hinder rural development in these regions. Degradation of cultural services on top of declining agricultural economy due to farmland loss puts pressure on the maintenance of viability in rural areas.

Another issue is the loss of biological diversity uniquely established in social–ecological systems [16]. First of all, forest expansion is likely to put open-landscape specialists at risk of local and regional extinction due to the small area of their habitats available in Japan [100]. With regard to paddy fields, a meta-analysis by Koshida and Katayama [101] revealed that abandonment effects on multiple groups of taxa were negative overall, and implied that abandonment is not necessarily followed by ecological restoration in cases where farming practices support high levels of biodiversity. The loss of secondary wetland habitats (i.e., paddy fields) and associated landscape elements (e.g., field margins, irrigation channels, ponds, and forest edges) is found to have deteriorating effects on farmland biodiversity in many cases [11,13,101]. In our study, the Hill and Mountain bundles accounted for 64% of forest edges and 87% of irrigation ponds, contributing largely to supporting farmland biodiversity in Japan. Threatened plant species that depend on certain farming practices were also found to be in areas of high abandonment trends according to studies conducted in Japan [22,102]. High probabilities of farmland abandonment taking place in areas with high biodiversity potential have also been reported elsewhere. In Europe, areas at risk of abandonment were found to occur in areas with a large proportion of high nature value (HNV) farmland, which includes a range of semi-natural habitats and associated species of nature conservation importance [7,21,103]. There, projections even suggest that abandonment could further take place in HNV farmland areas, leading to a decline in farmland biodiversity [98,104]. Japan is likely to follow spatial trends similar to Europe, as farmland abandonment is expected to occur on marginal land [39], where high amounts of farmland habitat features are maintained.

4.3. Management Implications

Management schemes that aim to maintain agricultural ecosystem services and farmland biodiversity provided by agroecosystems should target locations where abandonment pressure is likely severest [22], i.e., hilly and mountainous areas, as their hotspots were shown to be at risk of disappearance due to farmland abandonment.

In 2000, the Japanese government introduced a direct payment scheme specifically targeted at hilly and mountainous areas [57]; it aims at preventing further farmland abandonment in these disadvantaged areas. It is an adaptation of the European Union's Less Favoured Areas (LFA) measure. As in the EU, the Japanese LFA payments are designed to ensure a continuation of farming through provision of an annual compensatory allowance for permanent natural disadvantages. The Japanese LFA differs from the European one in that payments are made to rural communities, not to individual farmers. The idea is that members use the payments to engage in community activities that contribute to maintaining agricultural production (e.g., prevention of abandoning fields, management of common pool resources such as irrigation facilities and farmland roads, and machine sharing; see [105] for further details). The payment scheme is widely accepted in Japan, where 72% of rural communities eligible to receive LFA payments took the opportunity in 2005 [106]. According to a survey conducted toward LFA participants [107], approximately 80% of rural communities evaluated the payments as positive for the prevention of farmland abandonment. Although modest, LFA payments were found to have positive effects on continued farming through the maintenance of farm households and their members [105]. The scheme also contributes to increased communication among community members, as it requires them to plan together and to take shared roles [107]. Its implementation has led to the development of another direct payment scheme, i.e., multifunctional payment, which provides support for community activities in a similar manner but to a broader audience working on agricultural land. It appears that the policy tools do contribute to the maintenance of agricultural production but are not sufficient enough to support rural areas, as agricultural land has increasingly been abandoned despite these efforts [40].

The FAO [108] recommends that issues of land abandonment should be taken with a broader approach, which contributes to the revitalization of marginal areas. They propose different policy options according to agronomic potential and population density of marginal areas: revitalization through nature, recreation, and economic development. Revitalization through nature applies to cases where both agronomic potential and population density are low, e.g., remote and mountainous areas. The standpoint of this approach is that agriculture produces public goods and services, and that positive externalities should be preserved and compensated for. Examples include public goods-based incentives established for terraced fields through the latest LFA payments, where the government compensates JPY (approximately 94.39 USD or 77.58 EUR on 25 February 2020) 0.1 ha^{-1} $year^{-1}$ for terraced landscape conservation [57]. Such agricultural support should also be applicable to agricultural areas of natural and cultural significance like FAO Globally Important Agricultural Heritage Systems (GIAHS). Moreover, agroecosystems represented by positive and sustained long-term outcomes that are taking place outside protected areas have the potential to contribute to the IUCN's 'other effective area-based conservation measures' [109]. Their integration in well-connected conservation systems will be important for ensuring a range of positive conservation outcomes as well as for the achievement of Aichi Target 11. The second approach, i.e., revitalization through recreation, is suggested for areas where agronomic potential is low and population density is medium to high. The main objective here is to maintain characteristic landscapes by utilizing available natural and human capitals, like off-farm activities such as rural tourism. Our study showed consistent results with this approach, as agricultural landscapes in the Hill bundle, which were characterized by cultural and biological diversity, benefited from rural tourism the most. In these areas, farmers have opportunities to explore incomes from direct selling, organic food, and branding and labelling of local products. The third approach, i.e., revitalization through economic development, is recommended when agronomic potential is high and population density is low. The primary concern is to maintain a satisfactory population base by transforming a primary sector-based economy into a highly diversified, secondary and tertiary sector-based rural economy. Not many rural areas fall under this category in a developed society where usable land is limited, but revitalization through agricultural development will be essential under depopulation conditions in Japan. At last, areas with high agronomic potential and high population density are mostly urban or peri-urban areas, where problems are more related to environmental pollution and landscape degradation. Revitalization policies are not required for these areas, but eco-friendly farming should be promoted in order to keep the environment healthy and sustainable.

In Japan, the population is expected to decline by 25% compared to its peak year 2008 by 2050, where population ages 65 and above will make up approximately 40% of the total population [110]. In addition to demographic issues, it is reported that almost a half of today's abandoned fields are owned by non-farmers [111], e.g., absentee landowners who live far away from land which they inherited from older generations. Such socio-economic structures make it difficult for the national government and regional authorities to reach landowners and prescribe appropriate measures with agricultural and rural development policies. Considering that not all communities are viable in the future due to depopulation problems, re-naturalization should also be seen as one land management option. Similar discussion exists for secondary forests, where it is stated that leaving land for natural processes may be wise if it is in a state close to natural forests [112]. In the case of farmland, active interventions such as afforestation and its maintenance at early development stages might be needed to foster succession and mitigate negative consequences of land abandonment like soil erosion. If agricultural land has to be abandoned completely, broadleaf species should be promoted for reforestation in order to keep land in good environmental condition.

5. Conclusions

Our study demonstrated that agricultural ecosystem services and farmland biodiversity in Japanese agroecosystems are spatially linked and form ecosystem service bundles. Trade-offs were found between provisioning services and cultural services as well as biodiversity indicators. Ecosystem service hotspots occurred in areas where farmland abandonment is pronounced, suggesting that existing support schemes for agriculture in marginal areas have not been sufficient to counteract the underlying socio-economic drivers. Large quantities of agricultural ecosystem services and farmland biodiversity may be lost if farmland abandonment continues to follow the recent spatial trends at the national level. We consider that regional studies addressing a wider range of indicators will help develop more comprehensive assessments of ecosystem services and biodiversity supported by agroecosystems. Contributions of agricultural land to regulating services as part of ecosystem-based disaster risk reduction (Eco-DRR) will be particularly important owing to the increasing frequency of extreme weather events associated with climate change. Integrated evaluation of the multiple functions of agricultural areas should be included in monitoring schemes to improve policies that aim to ensure sustainable development of rural areas in Japan.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/land10101031/s1, SM1 Classification table of 774 vegetation communities recorded in the Actual Vegetation Map of Japan into 22 land-cover types. Classification was done in reference to the work by Ogawa et al., and land-cover types used in this study were those suggested by FAO; SM2 Pearson correlation coefficients between pairs of indicators of agricultural ecosystem services and farmland biodiversity; SM3. Average values and standard deviations (mean ± SD) of agricultural ecosystem services and farmland biodiversity found within each bundle. Kruskal-Wallis test and Mann-Whitney's U test were performed to test the differences among and between the bundles, respectively.

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Electric supplementary material

Hotspots of agricultural ecosystem services and farmland biodiversity overlap with areas at risk of land abandonment in Japan

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SM1 Classification table of 774 vegetation communities recorded in the Actual Vegetation Map of Japan [1] into 22 land-cover types. Classification was done in reference to the work by Ogawa et al. [2], and land-cover types used in this study were those suggested by FAO [3].

Land-cover classification proposed by Ogawa et al. [2]			
coarse category	intermediate category	fine category	Land-cover classification used in this study (Land-cover types according to FAO [3])
grassland	natural grassland	alpine vegetation	herbaceous or shrub depending on vegetation communities
		snow patch community	snow/ice
		sand dune vegetation	herbaceous
		coastal cliff herb vegetation	herbaceous
		natural grassland	herbaceous
	secondary grassland	secondary grassland (high height)	herbaceous
		secondary grassland (low height)	herbaceous
	artificial grassland	artificial grassland (including golf courses)	vegetated urban
		artificial grassland (excluding golf courses)	pasture or vegetated urban depending on vegetation communities
	others	sasa grassland	herbaceous
forest	natural forest	evergreen conifer natural forest	coniferous forest
		deciduous conifer natural forest	coniferous forest
		evergreen broad-leaved natural forest	shrub or broad-leaved forest depending on vegetation communities
		deciduous broad-leaved natural forest	shrub or broad-leaved forest depending on vegetation communities
		evergreen conifer and evergreen broad-leaved natural forest	mixed forest
		evergreen conifer and deciduous broad-leaved natural forest	mixed forest

	secondary forest	evergreen conifer secondary forest	coniferous forest
		evergreen broad-leaved secondary forest	shrub or broad-leaved forest depending on vegetation communities
		deciduous broad-leaved secondary forest	shrub or broad-leaved forest depending on vegetation communities
		evergreen conifer and evergreen broad-leaved secondary forest	mixed forest
		evergreen conifer and deciduous broad-leaved secondary forest	mixed forest
	plantation	evergreen conifer plantation	coniferous forest
		deciduous conifer plantation	coniferous forest
		evergreen broad-leaved plantation	shrub or broad-leaved forest depending on vegetation communities
		deciduous broad-leaved plantation	shrub or broad-leaved forest depending on vegetation communities
	others	natural scrub	shrub
		coastal scrub	shrub
		bamboo forest	bamboo
wetland	wetland	salt marsh vegetation	salt marsh
		wetland vegetation	fresh and brackish water wetland
near water	near water	aquatic plant community	water body
		seaweed community	water body
		mangrove community	mangrove
special character	special character	natural bare land	bare area
		plant communities in limestone	herbaceous
		vegetation in volcanic desert, vegetation in solfatara formation	herbaceous or lichens/mosses depending on vegetation communities

		rocky vegetation	bare area
		plant community on raised coral-reef	sparse vegetation
	paddy	paddy-field weed communities	paddy
		weed communities in uncultivated paddy-field	herbaceous
	cropland	field weed communities	cropland
		weed communities in uncultivated field	herbaceous
	others	weed communities of the roadside	herbaceous
		Thea sinensis garden	shrub crop
		orchard	tree crop
urban	urban	urban and residential district with many trees	vegetated urban
		urban district with a few trees	urban
		land constructed for residence and factory	urban
water body	water body	water body	water body
unknown	unknown	unknown	unknown

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SM2 Pearson correlation coefficients between pairs of indicators of agricultural ecosystem services and farmland biodiversity. Significant correlations were shown by . $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Rice production	Other agricultural production	Landscape aesthetics	Rural tourism	Forest edges	Irrigation ponds
Rice production	1					
Other agricultural production	0.12.	1				
Landscape aesthetics	-0.43***	-0.47***	1			
Rural tourism	0.02	0.00	0.10***	1		
Forest edges	-0.45***	-0.30***	0.70***	0.06*	1	
Irrigation ponds	0.12**	-0.34*	0.18.	0.14***	0.04	1

SM3. Average values and standard deviations (mean±SD) of agricultural ecosystem services and farmland biodiversity found within each bundle. Kruskal-Wallis test and Mann-Whitney's U test were performed to test the differences among and between the bundles, respectively. Different letters indicate significant differences between the bundles (p<0.001) and are in descending order of average values.

Bundles	Non-Rice	Rice	Hill	Mountain	Kruskal-Wallis
Number of municipalities	400	361	474	484	test (p)
Rice production [%]	3.3±4.4[c]	24.2±13.8[a]	10.2±5.6[b]	2.6±2.4[d]	<0.001
Other agricultural production [%]	11.7±11.2[a]	9.4±7.3[a]	3.9±4.0[b]	2.1±2.6[c]	<0.001
Landscape aesthetics [%]	24.2±21.5[c]	2.9±5.9[d]	30.4±20.5[b]	75.8±21.7[a]	<0.001
Rural tourism [%]	6.4±11.4[b]	8.0±12.9[b]	12.6±15.3[a]	10.3±12.4[a]	<0.001
Forest edges [$m \cdot ha^{-1}$]	62.9±35.3[b]	20.4±21.3[c]	54.1±28.9[b]	125.6±44.5[a]	<0.001
Irrigation ponds [$ponds \cdot ha^{-1}$]	0.016±0.017[d]	0.051±0.109[c]	0.223±0.331[a]	0.123±0.178[b]	<0.001

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Publications

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Birkhofer, K., Diehl, E., Andersson, J., Ekroos, J., Früh-Müller, A., Machnikowski, F., Mader, V.L., Nilsson, L., **Sasaki, K.**, Rundlöf, M., Wolters, V., Smith, H.G., 2015. Ecosystem services—current challenges and opportunities for ecological research. Front. Ecol. Evol. 2, 87.

Hotes, S., **Sasaki, K.**, Jopp, F., Eigner, A., Wolters, V. 2013. Regional bio-diversity strategies in Europe – the German example. Landscape Research Japan 77(2), 114-118. (In Japanese)

Conference presentations

Sasaki, K., Hotes, S., Ichinose, T., Doko, T., Wolters, V., 2018. Future impacts of farmland abandonment on agricultural ecosystem services and biodiversity in Japan. The 48th Annual Conference of the Ecological Society of Germany, Austria and Switzerland. 2018 September 10. – Sep 14. Vienna, Austria (Poster)

Sasaki, K., Früh-Müller, A., Hotes, S., Eigner, A., Ichinose, T., Doko, T., Wolters, V., 2017. Farmland abandonment in Japan: potential effects on ecosystem services and policy responses. The 64th Annual Meeting of the Ecological Society of Japan. 2016 March 14. – March 18. Tokyo, Japan (Poster)

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Sasaki, K., Hotes, S., Wolters, V., Kadoya, T., Yoshioka, A., Aue, B., Jopp, F., 2015. The ecological role of landscape structure in agricultural landscapes of Japan and Germany: a comparative approach based on common indicators. The 45th Annual Conference of the Ecological Society of Germany, Austria and Switzerland. 2015 Aug 31 – Sep 4. Göttingen, Germany (Poster)

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Declaration

I declare that I have completed this dissertation single-handedly without the unauthorized help of a second party and only with the assistance acknowledged therein. I have appropriately acknowledged and cited all text passages that are derived verbatim from or are based on the content of published work of others, and all information relating to verbal communications. I consent to the use of an anti-plagiarism software to check my thesis. I have abided by the principles of good scientific conduct laid down in the charter of the Justus Liebig University Giessen „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" in carrying out the investigations described in the dissertation.

(Keiko Sasaki)	Place, date