

LETTER

A macro-scale perspective on within-farm management: how climate and topography alter the effect of farming practices

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Abstract

Organic farming has the potential to reverse biodiversity loss in farmland and benefit agriculture by enhancing ecosystem services. Although the mixed success of organic farming in enhancing biodiversity has been attributed to differences in taxa and landscape context, no studies have focused on the effect of macro-scale factors such as climate and topography. This study provides the first assessment of the impact of macro-scale factors on the effectiveness of within-farm management on biodiversity, using spiders in Japan as an example. A multilevel modelling approach revealed that reducing pesticide applications increases spider abundance, particularly in areas with high precipitation, which were also associated with high potential spider abundance. Using the model we identified areas throughout Japan that can potentially benefit from organic farming. The alteration of local habitat-abundance relations by macro-scale factors could explain the reported low spatial generality in the effects of organic farming and patterns of habitat association.

Keywords

Agricultural intensification, agri-environment schemes, ecosystem services, macroecology, model transferability, organic farming, pest control, pesticides, *Tetragnatha*, wildlife-friendly farming.

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INTRODUCTION

Agriculture is now among the most serious threats to biodiversity across the globe (Krebs *et al.* 1999; Tilman *et al.* 2001). Continuous growth in human population poses a critical challenge to the maintenance of sustainable food supply for the human society with minimal loss of global biodiversity. One promising approach to this challenge is to maximise the benefits of ecosystem services provided by farmland biodiversity, such as the control of pest populations by predators (Bianchi *et al.* 2006).

Wildlife-friendly farming, defined as farming practices that aim to avoid negative impacts on organisms, and organic farming, which usually uses no pesticides or chemical fertilisers, have a potential to not only reverse biodiversity loss in farmland but also benefit agricultural production through the enhancement of ecosystem services (Bengtsson *et al.* 2005; Hole *et al.* 2005; Letourneau & Bothwell 2008). Consequently, in recent decades, there has been increasing emphasis and expenditure on such farming methods. For instance, at the end of 2003, organic land area worldwide was estimated at *c.* 26.5 million ha, or 69% higher than in 1998 (European Commission 2005). Given this expansion in organic farming, it has become an important challenge to investigate what factors determine the impact of organic farming on ecosystem services and biodiversity conservation in farmland.

Earlier studies have reported mixed success for organic farming in delivering biodiversity benefits (Bengtsson *et al.* 2005; Hole *et al.* 2005) and most studies have attributed such mixed benefits of organic

farming to varied responses in different taxa (Fuller *et al.* 2005; Hole *et al.* 2005) and surrounding landscape context (Tscharntke *et al.* 2005; Batáry *et al.* 2011). However, other important factors with a potential impact on the effect of farming practices that have been overlooked are climate and topography. Both climate and topography can be an influential factor, particularly at a large spatial scale, given the well-known importance of those factors as drivers of biodiversity dynamics at national, continental and global scales (Hawkins *et al.* 2003; Davies *et al.* 2007). Quantifying the impact of climate and topography on the effect of farming practices on biodiversity would also enable predicting the potential benefits of organic farming under different climatic and geographical conditions. This should help identify the highest priority areas for agri-environment schemes and predict the impact of climate change on the effectiveness of organic farming. The former is particularly policy relevant because organic farming is often subsidised through agri-environment schemes (Kleijn *et al.* 2006) and an efficient allocation of subsidies to areas most likely to benefit from organic farming is a critical issue. Nevertheless, to our knowledge, no studies to date have explored how such macro-scale factors alter the effect of within-farm agricultural practices on biodiversity.

Revealing the interacting effect of macro- and local-scale factors on organisms could also provide an explanation for well-known regional variations in habitat associations of organisms. The low spatial generality in habitat associations has repeatedly been reported without the underlying mechanisms being specified, making local-scale species distribution models non-transferable between different regions

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(Whittingham *et al.* 2007; McAlpine *et al.* 2008). Macro-scale factors as drivers of regional variations in habitat associations can be a solution to the contingent nature of those models and help promote a generalised understanding of habitat associations of organisms at a large spatial scale.

Given the possible interacting impact of macro-scale factors, landscape context and within-farm management, it is crucial to take into account all the relevant factors and their interaction pathways explicitly when evaluating the effect of farming practices (Hole *et al.* 2005). The present study tackles this issue with a multilevel modelling approach (Gelman & Hill 2007; McMahan & Diez 2007; Qian *et al.* 2010). Multilevel models, also known as hierarchical linear models, use nested regression equations to investigate associations between variables at multiple hierarchies or, equivalently, scales (McMahan & Diez 2007). This makes multilevel modelling a promising approach for simultaneously evaluating the impact of multiple factors on biodiversity itself and on the effect of farming practices.

Japan provides an excellent study system for investigating the impact of climate and topography on the effect of farming practices for the following two reasons. First, largely due to its vast north–south length of 3000 km, Japan has a varied climate, ranging from the subarctic to subtropical, and active tectonics around the country has produced elevational heterogeneity. Therefore, wildlife-friendly farming including organic farming has been adopted in fields with a wide range of climatic and topographic conditions, allowing an easy assessment of the impact of such macro-scale factors. Second, few studies to date have investigated the effect of farming practices on ecosystem services in rice-paddy areas, which cover *c.* 11% of the world's arable land [calculated from FAO (2008)] and supply 20% of total calories consumed worldwide, including 30% in Asia (IRRI 2007). Although rice-paddy areas provide important habitats for farmland biodiversity across the globe (Lawler 2001; Bambaradeniya & Amarasinghe 2003), biodiversity conservation in rice-paddy areas remains a relatively new and unexplored field globally, and in particular information on ecosystem services provided by biodiversity in rice fields is scarce. Thus, studies in Japan, where rice fields cover over 54% of cultivated land (MAFF 2005), should provide useful insights that can be applied to many parts of the world.

This study provides the first rigorous assessment of the impact of macro-scale factors, climate and topography, on the effect of farming practices on biodiversity. *Tetragnatha* spiders are used as the target species, as they are known to deliver ecosystem services through pest control in farmland (Riechert & Lockley 1984) and be vulnerable to pesticides in rice fields (Ito *et al.* 1962; Oyama & Kidokoro 2003a). Reducing pesticide applications is expected to increase the abundance of spiders particularly in areas with high temperature, high precipitation and low elevation, where, based on the species-energy theory (Wright 1983; Evans *et al.* 2005), large sizes and/or fast growth of regional populations are expected through increased energy availability. The effect of macro-scale factors, quantified with a multilevel modelling approach, is then used to identify rice-paddy areas throughout Japan that are most likely to benefit significantly from organic farming.

MATERIAL AND METHODS

Field surveys

Two hundred and thirty rice fields, 128 of which are understood to be farmed with reduced levels of pesticides, were selected for field

surveys in 12 prefectures throughout Japan (Table S1 and Figure S1). Details of the field selection were described in Appendix S1.

In Japanese rice fields, three types of pesticides are expected to affect invertebrates, such as spiders and dragonfly larvae (Oyama & Kidokoro 2003a,b): insecticides applied directly to fields after seedling transplanting, insecticides applied to nursery boxes before seedling transplanting and herbicides applied directly to fields after seedling transplanting. Fungicides are also frequently used for rice cultivation but have been reported to have little effect on aquatic invertebrates, such as larvae of libellulid dragonfly *Sympetrum eroticum eroticum* and the chironomid *Polypedilum nubifer* (Tanaka 2004). In each survey field, the number of (1) insecticide applications to fields, (2) insecticide applications to nursery boxes and (3) herbicide applications were investigated by interviewing farmers, and used as explanatory variables that represent within-farm management (Table S2).

This study focused specifically on *Tetragnatha* spiders, which construct horizontal orb webs between rice plants, as species in this genus are abundant generalist predators in rice fields, are expected to control pest populations and are known to be vulnerable to pesticides (Ito *et al.* 1962; Oyama & Kidokoro 2003a,b). For instance, *T. maxillosa* has 35–98% lower LC₅₀ for (i.e. is more susceptible to) four out of nine insecticides than *Nilaparvata lugens*, one of the main pest species in rice fields (Tanaka *et al.* 2000). In each survey field, sampling of spiders was conducted 2–10 times (6.2 on average) in 2008 and 2009 by a total of 13 organisations that specialise in invertebrate surveys (Table S1). Sampling was evenly distributed across the rice growing season (May–November). Surveys within a prefecture were conducted by the same organisation, following the same protocol, except for Shimane Prefecture, where two organisations participated to cover two relatively separated areas. In each survey, spiders were sampled during the daytime with 20–60 swings (30 on average) of a 36-cm diameter insect net that was swung at the upper part of rice plants with each pace while walking in the middle of the field. In the daytime, most *Tetragnatha* individuals settle above or below rice leaves or remain on the webs and thus, can be captured effectively by sweeping. Species were identified by each surveyor and the number of individuals was recorded.

Environmental data

To evaluate the impact of macro-scale factors on the effect of farming practices on spider abundance, three groups of explanatory variables (temperature, precipitation and elevation) were recorded for 41 squares, sized 100-km² each and including at least one survey field.

Three temperature (annual mean, monthly maximum and monthly minimum) and three precipitation (annual, summer and winter) variables were obtained from the Mesh Climate Value 2000 provided by the Meteorological Agency of Japan, which are 30-year (1971–2000) means of monthly/annual values within 1-km² squares spread through a contiguous nationwide grid. Two topography variables (mean elevation and range of elevation) were obtained from the Digital National Land Information project of the Japanese Ministry of Land, Infrastructure, Transport and Tourism. After checking the correlations among these variables (Appendix S2), annual mean temperature, summer precipitation and mean elevation were selected for the following analysis.

To investigate the effect of non-crop habitats in surrounding landscapes, the area of forest surrounding the survey fields, which is often associated with the presence of *Tetragnatha* species (Yoshida

1981), was also used as an explanatory variable. The area of surrounding forest was obtained from the Precise Land-Use, Land-Cover Map created by the Japan Aerospace Exploration Agency in 2010 (http://www.eorc.jaxa.jp/ALOS/lulc/lulc_jindex.htm). The map was based on satellite images obtained from AVNIR-2 on the Advanced Land Observing Satellite. Each 50 × 50 m square grid throughout Japan was classified into nine categories and the sum of those 50 × 50 m squares classified as deciduous forest and evergreen forest was defined as the area of forest. The area of forest was calculated within circles of 0.25, 0.5, 1.0, 2.0 and 3.0 km radius around the survey fields, which mostly cover the range of scales at which landscape elements affect the abundance of arable spiders (Schmidt *et al.* 2008). Tscharrntke *et al.* (2005) indicated that the effectiveness of wildlife-friendly farming varies between simple (< 20% non-crop habitat) and complex (> 20%) landscapes. The proportion of forest area surrounding the survey fields was almost evenly distributed between these two categories (e.g. 122 survey fields with < 20% forest within 0.25 km and 108 with > 20% forest).

Data analysis

Multilevel modelling

In order to simultaneously consider the impact of macro-scale and landscape-scale factors on spider abundance itself and on the effect of farming practices, hierarchical linear models were implemented within a Bayesian framework (McMahon & Diez 2007). In the model, the number of individuals $y_{i,t}$ that were recorded in all surveys in survey field i and year t is assumed to follow a Poisson distribution, $y_{i,t} \sim \text{Poisson}(\mu_{i,t})$, where $\mu_{i,t}$ is the expected mean count in survey field i and year t . The expected mean count is related to linear predictors via the log-link function as:

$$\log(\mu_{i,t}) = \alpha_i + \beta_{1,i} \cdot X_{i,t} + \beta_{2,i} \cdot Y_{i,t} + \beta_{3,i} \cdot Z_{i,t} + \gamma_{k(i),t} \\ + \log(\delta_{k(i),t}) + \log(\zeta_{k(i),t}) + \varepsilon_{i,t},$$

where α_i is a site-specific intercept term, $\beta_{j,i}$ are site-specific regression coefficients and $X_{i,t}$, $Y_{i,t}$ and $Z_{i,t}$ are the number of insecticide applications to fields, to nursery boxes and herbicide applications respectively. The random effects $\gamma_{k(i),t}$ for organisation $k(i)$ and year t allow the model to account for random variations in counts among survey organisations and years. $k(i)$ indicates an organisation that investigated survey field i . $\gamma_{k(i),t}$ is assumed to follow a normal distribution as $\gamma_{k(i),t} \sim \text{Normal}(\gamma_{\text{global}}, \sigma_{\gamma}^2)$, where γ_{global} represents a global mean count. $\delta_{k(i),t}$ and $\zeta_{k(i),t}$ are the number of surveys per year and swings per survey respectively, which are taken into account as offset terms. $\varepsilon_{i,t}$ is a random effect that accounts for overdispersion (Kéry 2010) and is assumed to follow a normal distribution as $\varepsilon_{i,t} \sim \text{Normal}(0, \sigma_{\varepsilon}^2)$.

The site-specific intercepts are modelled by site-level covariates as follows:

$$\alpha_i = \alpha 1 \cdot TMP_i + \alpha 2 \cdot PPT_i + \alpha 3 \cdot ELV_i + \alpha 4 \cdot TMP_i \cdot PPT_i \\ + \alpha 5 \cdot TMP_i \cdot ELV_i + \alpha 6 \cdot PPT_i \cdot ELV_i + \alpha 7 \cdot FRT_i,$$

where $\alpha 1-7$ are regression coefficients for annual mean temperature TMP_i , summer precipitation PPT_i , mean elevation ELV_i , interaction terms of the three explanatory variables and area of surrounding forest FRT_i . A global intercept, which is common to all sites, was not included because it could be confounded with a global mean count γ_{global} . All the explanatory variables were centred before the analysis.

The site-specific regression coefficients $\beta_{j,i}$ are modelled as random effects drawn from a global distribution with a mean determined by a global coefficient $\beta 0_j$ and site-level covariates as follows:

$$\beta_{j,i} = \beta 0_j + \beta 1_j \cdot TMP_i + \beta 2_j \cdot PPT_i + \beta 3_j \cdot ELV_i + \beta 4_j \cdot FRT_i + \omega_{j,i},$$

where $\beta 1-4_j$ are regression coefficients for annual mean temperature, summer precipitation, mean elevation and area of surrounding forest. Interaction terms of these explanatory variables were not included in the site-specific regression coefficients to avoid model complexity caused by three-way interaction terms. Since all the explanatory variables were centred before the analysis, global coefficients $\beta 0_j$ indicate the effect of each pesticide application with mean values for all the explanatory variables. The error terms are normally distributed as $\omega_{j,i} \sim \text{Normal}(0, \sigma_{\omega_j}^2)$.

To investigate the effect of spatial autocorrelation, the model described above was first fitted to the data and regression residuals were calculated by subtracting observations from predictions. Moran's I calculated from the residuals showed that the peak of the autocorrelation in the regression residuals first appeared at a scale of 0.50 km but Moran's I at the scale was 0.24, indicating a relatively weak autocorrelation, and therefore, spatial autocorrelation was not considered explicitly in the model for the following analysis.

The model was fitted to the data with WinBUGS 1.4.3 (the script provided in Appendix S3) and a package R2WinBUGS (the script in Appendix S4) in R 2.13.0. Prior distributions of parameters were set as non-informatively as possible, so as to produce estimates similar to those generated by a maximum likelihood method. Normal distributions with mean of 0 and variance of 1000 were used as prior distributions for $\alpha 1-7$, $\beta 0-4_j$ and γ_{global} . Gamma distributions with mean of 1 and variance of 1000 were used as prior distributions for the inverses of σ_{γ}^2 , σ_{ε}^2 and $\sigma_{\omega_j}^2$. Each MCMC algorithm was run with three chains with different initial values for 200 000 iterations with the first 50 000 discarded as burn-in and the remainder thinned to one in every thirty iterations to save storage space. Model convergence was checked with R-hat values (Gelman *et al.* 2003) and trace plots of all the chains for sampling (Spiegelhalter *et al.* 2003).

The model was first performed for the area of surrounding forest at each of the five spatial scales, together with all the other variables, and the spatial scale at which the surrounding forest is relevant was determined by comparing the Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002). The final version of results for both this model and the model with the covariance matrix (described below) was then derived with the area of surrounding forest at the determined scale.

The goodness of fit of the model was assessed by posterior predictive checking (Gelman & Hill 2007; see Appendix S5 for more details). As the multilevel model incorporates multiple interactions, average predictive comparisons were also estimated for each input variable following Gelman & Pardoe (2007) (see Appendix S6 for more details).

Three explanatory variables, temperature, precipitation and elevation, were naturally correlated with each other while correlation coefficients for all the other combinations of explanatory variables were less than 0.5 (Table S3). Thus, to allow for covariance among the coefficients of the three explanatory variables, the covariance matrix of the distribution of coefficients was modelled in another model with the scaled inverse-Wishart distribution (Gelman & Hill 2007) and

results were compared with the model assuming independent coefficients. The details of the model are explained in Appendix S7 and scripts in Appendices S8, S9.

Predictions

The Bayesian framework allows us to obtain an entire posterior distribution and consequently, full inference regarding uncertainty, given the data and model (Gelfand *et al.* 2006). Thus, the effect of conducting organic farming in other rice-paddy areas throughout Japan, together with the associated uncertainties, were predicted in WinBUGS using the scripts provided in Appendix S3. Predictions were derived for all the 100-km² squares where annual mean temperature, summer precipitation and mean elevation fall within the range of values for the survey fields (i.e. temperature: 9.0–18.0 °C, precipitation: 360–1144 mm and elevation: 0–600 m). The values of the explanatory variables for the survey fields, which were used for model parameterisation, were evenly scattered across the variable space for the selected 100-km² squares (Figure S2), indicating that the developed model can be used effectively for the prediction.

RESULTS

One hundred and eighteen and 168 rice fields were surveyed 6.4 (range: 2–9) and 6.0 (range: 3–10) times on average between May and

November in 2008 and 2009 respectively. The *Tetragnatha* spiders recorded in the survey fields included nine species: *T. caudicula*, *T. extensa*, *T. maxillosa*, *T. nitens*, *T. pinicola*, *T. praedonia*, *T. squamata*, *T. vermiformis* and *T. yesoensis*. 0.17 and 0.22 individuals on average (range: 0.0–0.76 and 0.0–1.32) were recorded per swing of a sweep net in 2008 and 2009 respectively (9619 individuals in total).

Effects of macro-scale and landscape-scale factors

The optimal model based on the minimum DIC score included the area of surrounding forest within 0.25 km of survey fields (Figure S3), which was used in the following analysis. Posterior predictive check suggested that the sum of squared residuals calculated for the replicated data sets tended to be smaller than those for the actual data sets (Figure S4). However, the estimated Bayesian *P*-value, the proportion of times when the sum of squared residuals for the replicated data sets were greater than those for the actual data, was 0.147, not particularly close to 0 or 1, indicating that the fit of the model to the data was moderate.

Implementing the model with the covariance matrices for coefficients revealed that the estimated parameters (Figure S5) were virtually the same as those estimated with the model assuming independent coefficients (Fig. 1). Thus, for simplicity, the following results are based on the model assuming independent coefficients.

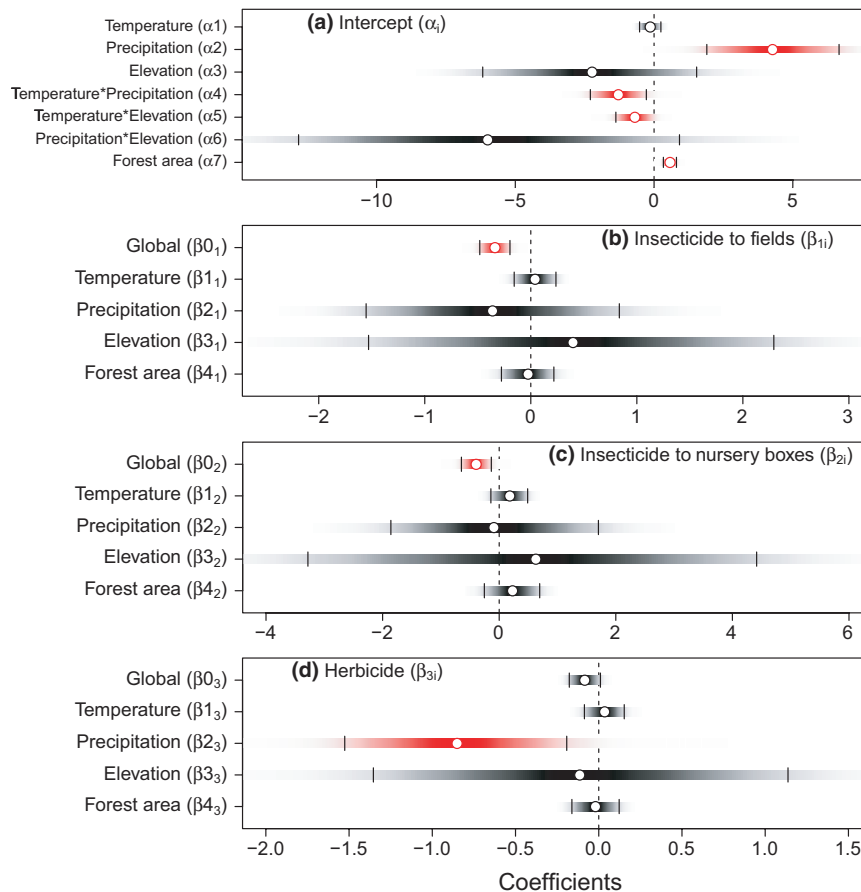


Figure 1 The estimated parameters for the hierarchical linear model assuming independent coefficients, fitted to the data on the abundance of *Tetragnatha*. Points represent the median estimates, bars are shaded in proportion to the posterior probability density and vertical lines mark the 95% credible intervals. Parameters for which 95% credible intervals did not include zero are shown in red.

Precipitation and forest area had a significant positive effect on the site-specific intercepts while the temperature–precipitation interaction and temperature–elevation interaction had a significant negative effect (Fig. 1a). The estimated 95% credible interval of the global coefficient for the number of insecticide applications to fields indicated a significant positive effect of reductions in insecticide application on the abundance of the *Tetragnatha* spiders (Figs 1b and 2). None of the four climatic and topographic variables had a significant impact on the relationship between spider abundance and the number of insecticide applications to fields (Fig. 1b). The estimated 95% credible interval of the global coefficient for the number of insecticide applications to nursery boxes indicated a significant positive effect of reduced insecticide applications on spider abundance (Figs 1c and 3). Although none of the four explanatory variables had a significant impact on this relationship in terms of the 95% credible intervals (Fig. 1c), low temperature seemed to enhance the benefit of reducing insecticide applications to nursery boxes (Fig. 3). Reducing herbicide applications also had a marginally significant positive effect on abundance (Figs 1d and 4). Precipitation affected the impact of herbicide applications significantly (Fig. 1d); high precipitation enhanced the benefit of reducing herbicide applications (Fig. 4).

The estimated average predictive comparisons revealed the overall contribution of each input variable to the abundance of *Tetragnatha*: precipitation and forest area had a particularly positive effect on abundance while the application of insecticide to fields and nursery boxes had a clear negative effect (Figure S6).

Predictions

Based on annual mean temperature, summer precipitation and mean elevation in the 100-km² squares throughout Japan (Figure S7), the effect of organic farming on the abundance of spiders was predicted using the estimated model with all the explanatory variables shown in Fig. 1. The area of surrounding forest did not have a significant impact on the effect of reduced pesticide usage, and thus, the mean value for the survey fields was assumed in all the 100-km² squares.

The benefit of reducing insecticide applications to fields in increasing the abundance of *Tetragnatha* was predicted to be particularly high in low-temperature or high-precipitation areas (Figure S8a). The benefit of reducing insecticide applications to nursery boxes was predicted to be high in low-temperature areas (Figure S8b). The predicted benefit of reducing herbicide applications was high in high-precipitation areas (Figure S8c).

With conventional farming, where it is assumed that insecticides are applied once each to fields and nursery boxes and herbicides are applied three times, the abundance of *Tetragnatha* was predicted to be high in southern lowland (Fig. 5a). In contrast, with organic farming, where no pesticide application is assumed, high abundance was predicted mainly in high-precipitation parts of Japan (Fig. 5b). Consequently, the model predicted that the impact of organic farming (i.e. increase in the abundance of *Tetragnatha*) is largest in those areas although most other areas were also predicted to experience an increase in the abundance of *Tetragnatha* to some degree (Fig. 6). The

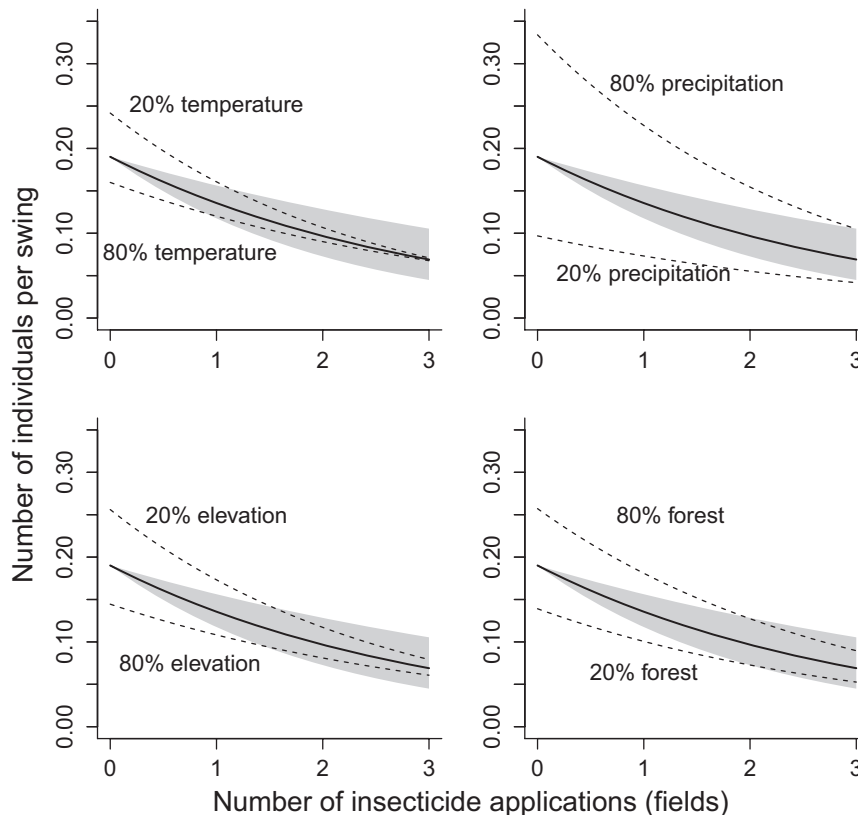


Figure 2 Predicted abundance of *Tetragnatha* per swing of a sweep net given different numbers of insecticide applications to fields. The abundance was predicted by the hierarchical linear model fitted to the data, using the actual range of values for the number of insecticide applications to fields. Solid lines with grey backgrounds show median predictions and associated 95% credible intervals with mean values for all four explanatory variables (i.e. annual mean temperature, summer precipitation, mean elevation and area of forest within 0.25 km). Dashed lines represent predictions with 20 and 80 percentiles of actual values for the explanatory variable of interest, and mean values for the other variables. Note that ‘20% forest’ does not mean that the proportion of surrounding forest is 20%, etc.

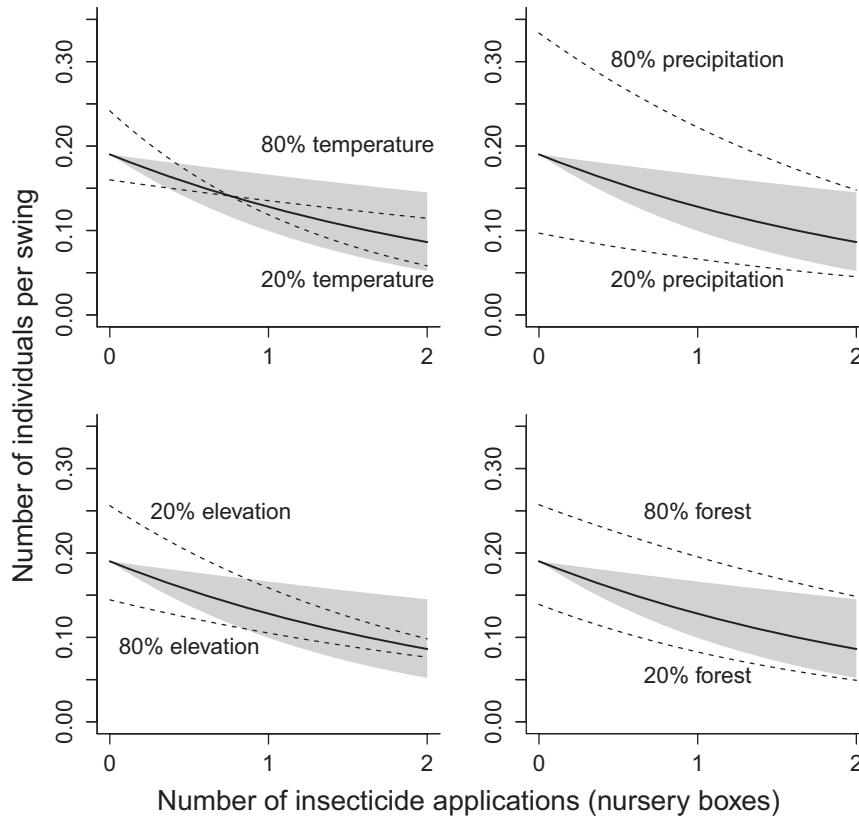


Figure 3 Predicted abundance of *Tetragnatha* per swing of a sweep net given different numbers of insecticide applications to nursery boxes. Lines and backgrounds are as defined in Figure 2.

uncertainties in these predictions were generally low with the coefficients of variations in most squares smaller than 80% (Figure S9).

DISCUSSION

This study illustrated the importance of macro-scale factors, such as climate and topography, in regulating the impact of within-farm management on biodiversity, and possibly ecosystem services. Earlier studies have indicated that the effectiveness of organic farming varies considerably between regions (Clough *et al.* 2005; Gabriel *et al.* 2010) and countries (Kleijn *et al.* 2006). More broadly, patterns of habitat association in animals have repeatedly been shown to vary on a regional basis (e.g. Whittingham *et al.* 2007; McAlpine *et al.* 2008) although the underlying mechanism has rarely been specified to date. The alteration of local habitat-abundance relations by macro-scale factors revealed in the present study seems to provide a possible explanation to the reported low spatial generality in both the effect of organic farming and patterns of habitat association. This finding, although based on one spider genus, should provide a crucial and new starting point for future studies aiming to evaluate the effectiveness of local conservation measures including organic farming at a large spatial scale.

The results indicate that the benefit of organic farming in increasing the abundance of *Tetragnatha* is particularly high in areas with high precipitation, which were also associated with high potential spider abundance. This result supports the hypothesis that regions with high energy availability should benefit significantly from organic farming through increased sizes of regional populations. The apparent benefit

of reducing insecticide applications to nursery boxes in low-temperature areas seems counterintuitive given the well-known positive relationship between temperature and energy availability. This relationship may be due to a negative correlation between temperature and latitude because latitude is known to be positively correlated with abundance in a wide range of species (e.g. Gaston & Blackburn 1996; Johnson 1998). Selecting the appropriate metrics of energy availability for organisms is a complex process (Evans *et al.* 2005), and further studies are required to confirm the hypothesis that regions with high energy availability benefit more from organic farming.

The result that organic farming is highly effective in areas with high abundance differs from the findings of earlier studies in Europe, where simple, biodiversity-poor areas have been reported to benefit relatively more from organic farming (Tscharntke *et al.* 2005; Batáry *et al.* 2011). This disparity seems to be attributable to the difference in the relative influence of within-farm management and other (i.e. macro- and landscape-scale) factors in regulating the dynamics of target populations. In Japanese rice fields, pesticide applications seem to have a greater impact on spider abundance than other factors, causing the abundance to be virtually constant irrespective of other environmental factors when applied at a maximum (Figs 2–4). Contrarily, in most European cases, the species pool of the landscape from which local communities are drawn seems to be more important than the difference between organic and conventional farming, with complex landscapes compensating for the difference caused by management (Tscharntke *et al.* 2005). This difference deserves attention as a process to potentially explain the context-dependent benefits of organic farming.

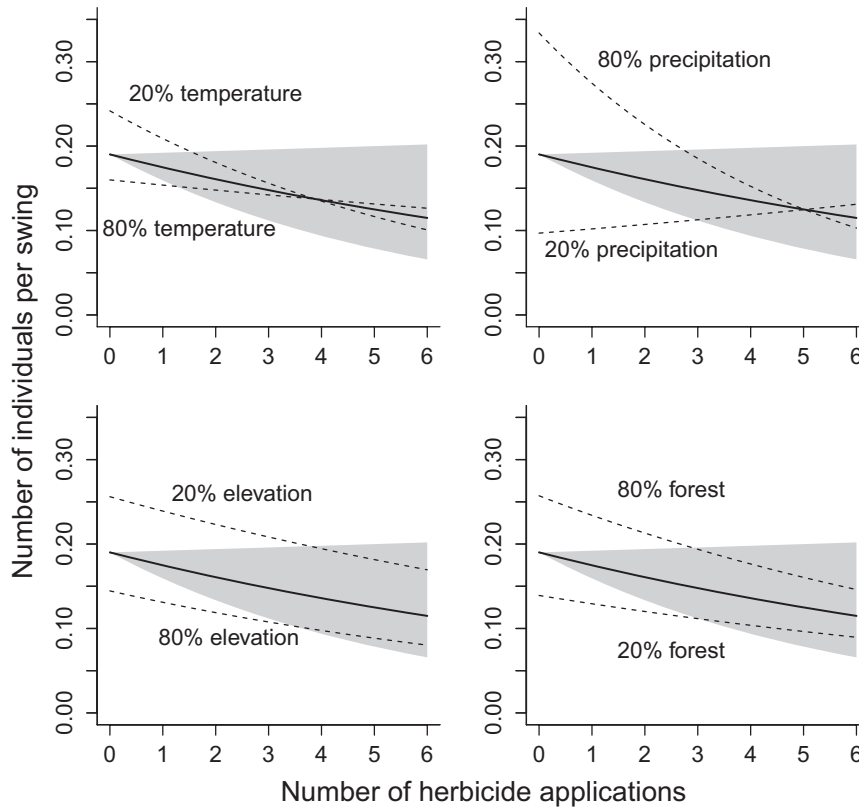


Figure 4 Predicted abundance of *Tetragnatha* per swing of a sweep net given different numbers of herbicide applications. Lines and backgrounds are as defined in Figure 2.

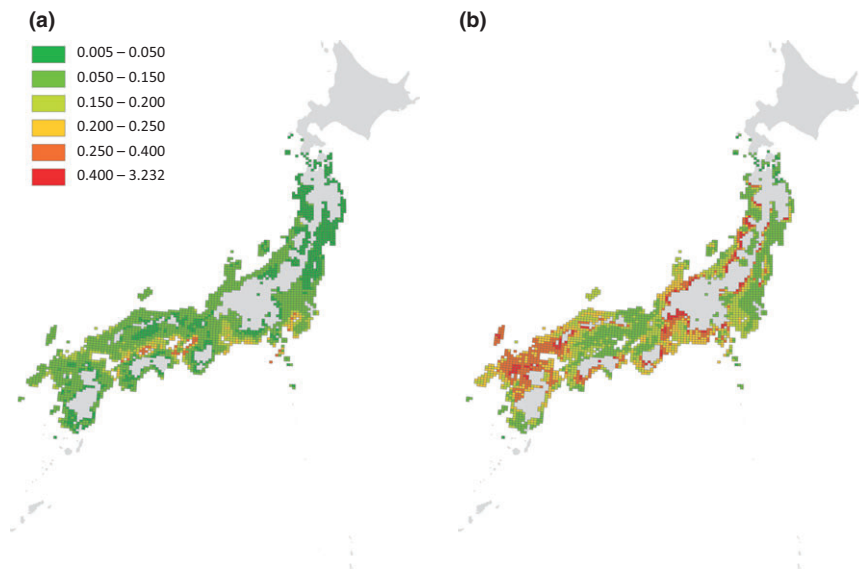


Figure 5 Predicted abundance of *Tetragnatha* per swing of a sweep net under (a) conventional farming (one insecticide application to fields and to nursery boxes and three herbicide applications) and (b) organic farming (no pesticides) scenarios. Medians of the estimated posterior distributions are shown. The abundance was predicted based on values for annual mean temperature, summer precipitation and mean elevation in all the 100-km² squares where values fall within the range of the survey fields (i.e. temperature: 9.0–18.0 °C, precipitation: 360–1144 mm and elevation: 0–600 m). The area of surrounding forest did not have a significant impact on effectiveness of pesticide reduction (see Figure 1) and thus, the mean value for the survey fields was assumed in all the 100-km² squares.

Another strength of our study is that the effect of each management method in organic farms was evaluated separately. For each of the three pesticide application methods, the effectiveness of pesticide reduction seemed to be affected by different macro-scale factors,

causing a large spatial variation in areas that benefit the most from pesticide reductions depending on the management method (Figure S8). This result indicates that it is more efficient to adopt different management methods in different regions than to apply the

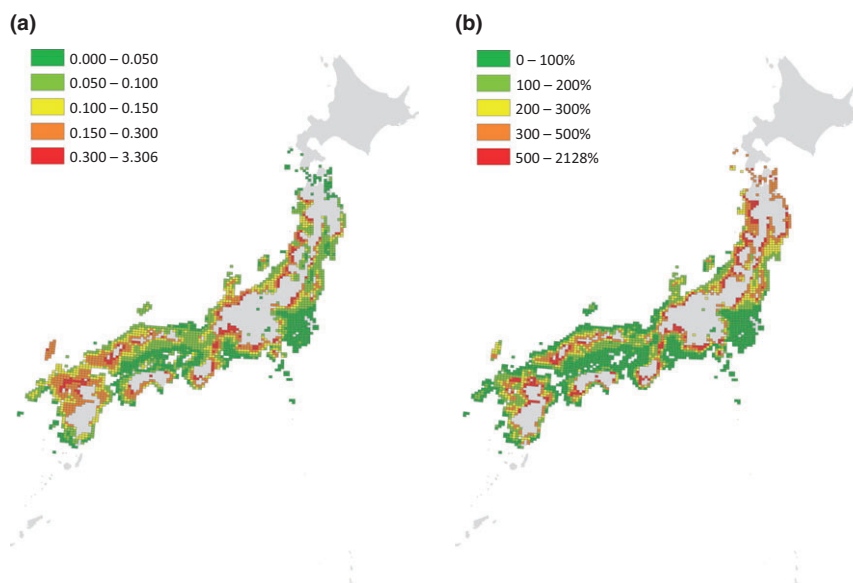


Figure 6 The predicted benefits of conducting organic farming in increasing the abundance of *Tetragnatha*, expressed as (a) the difference in abundance predicted under organic (Figure 5b) and conventional farming (Figure 5a) and (b) the percentage of increase. Medians of the estimated posterior distributions are shown.

same prescription to the whole country, for example, when introducing agri-environment schemes. To date, the benefits of organic farming have typically been investigated in the 'organic farming vs. conventional farming' context and the detailed effects of different farming methods, such as the type and amount of pesticides reduced, have often been neglected (but see Geiger *et al.* 2010). However, quantifying the relative benefits from different components of management, as shown above, would make the implementation of organic farming more effective and efficient. The revealed impact of temperature and precipitation would also be useful for predicting the impact of climate change on the effectiveness of organic farming in future. Thus, the approach in this study should be of help not only when introducing new agri-environment schemes and allocating subsidies efficiently at a large spatial scale but also when examining the cost-effectiveness of, and the impact of climate change on, existing schemes.

The difference in the interacting effect of macro-scale factors among different pesticides may be explained by different pathways through which each pesticide affects spider abundance. Both insecticide applications to nursery boxes and herbicide applications are usually performed in the early growing season while insecticide applications to fields are performed in the mid- to late-growing season. The colonisation and early-stage growth of generalist predator populations in rice fields seem to rely on aquatic invertebrates (Settle *et al.* 1996), and both insecticides applied to nursery boxes and herbicides are known to affect such aquatic invertebrates negatively (Oyama & Kidokoro 2003b; Tsuruta *et al.* 2009). Thus, both types of pesticides, particularly the herbicide in this study, seem to have a great impact on the establishment of spider populations irrespective of environmental conditions, leading to a strong interacting effect of environmental factors. Clearly, the mechanisms underlying different effects of macro-scale factors need to be explored in future to reinforce the findings of this study.

The average predictive comparisons revealed that precipitation and forest area had a relatively strong effect on spider abundance. At a macro scale, precipitation generally plays a prominent role in diversity patterns of a wide range of taxonomic groups including invertebrate

(Hawkins *et al.* 2003). For example, low precipitation is known to limit the distribution of spiders in southern Europe (Kumschick *et al.* 2009). *Tetragnatha* spiders particularly prefer wet environments as habitats (Yoshida 1981), which seems to be reflected in the strong effect of precipitation. Some species of *Tetragnatha* also prefer woodland area to open land as habitats (Yoshida 1981) and it has been indicated that terrestrial detritus from the forest enhances the emergence of aquatic insect prey for spiders including *Tetragnatha* (Kato *et al.* 2004). Thus, although the possibility that forest area is correlated with the area of other important habitats cannot be dismissed, forest surrounding rice fields may increase the abundance of *Tetragnatha* through direct immigration from source habitats and/or increased prey availability.

It should also be noted that the increase in the abundance of predatory spiders in organic farms, revealed in this study, may not necessarily translate to increased levels of pest control and ultimately benefits to farmers. As the next step, it will be necessary to investigate whether the macro-scale factors also affect pest pressure and consequent crop yields. Nevertheless, a growing body of evidence is accumulating in a wide range of geographical areas to show that pest pressure in organic farms is at least at the same level as, or even lower than, conventional farms (Bianchi *et al.* 2006; Letourneau & Bothwell 2008). Spiders, such as Tetragnathidae and Lycosidae, have also been shown to suppress the density of main pest species in rice fields (Ito *et al.* 1962; Oyama & Kidokoro 2003a). This suggests that the effect of organic farming on abundance of spiders evaluated in this study could be indicative of the effect of organic farming on ecosystem services.

The finding of the present study provides new insights into both basic and applied ecological studies. From the perspective of basic ecology, it was indicated that the relationship between species abundance and local-scale factors, such as habitat amount, habitat heterogeneity and various anthropogenic disturbances, can be affected by macro-scale drivers like climate and topography. Ecological theories usually suffer from a tradeoff between generality at a broad scale and realism at a local scale (Lawton 1999; Simberloff

2004) but exploring the interacting effects of macro- and local-scale factors on organisms would help generalise local habitat-abundance associations at a broad scale, possibly providing a solution to the contingent nature of ecological theories. From a more applied perspective, such macro-scale perspectives on local-scale drivers would improve the transferability of predictive models among regions and different climatic conditions, enabling more accurate spatial and temporal predictions of the impact of biodiversity drivers, including climate change and the effectiveness of conservation management. Consequently, the approach in this study should be of help in allocating conservation efforts efficiently at a large spatial scale and in the long term.

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T.A. performed analyses and wrote the paper. Y.K. and S.Y. collated and supplied the data and were involved in study design. H.O. performed analyses. K.T. devised the project, was involved in study design and conducted surveys. Y.G.B. and K.H. conducted surveys and were involved in study design. All authors discussed the results and commented on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed description of the selection of survey fields.

Appendix S2 Detailed description of the selection of explanatory variables.

Appendix S3 The WinBUGS script for specifying the hierarchical linear model that assumes independent coefficients among explanatory variables.

Appendix S4 The R script for running the hierarchical linear model that assumes independent coefficients among explanatory variables.

Appendix S5 Brief description of posterior predictive checking.

Appendix S6 Brief description of the calculation of average predictive comparisons.

Appendix S7 Brief description of the hierarchical linear model with covariance matrices for the coefficients of explanatory variables.

Appendix S8 The WinBUGS script for specifying the hierarchical linear model with the covariance matrices for the coefficients of explanatory variables.

Appendix S9 The R script for running the hierarchical linear model with the covariance matrices for the coefficients of explanatory variables.

Figure S1 Locations of the survey fields.

Figure S2 The range of annual mean temperature, summer precipitation and mean elevation for 100-km² squares used for predictions (black) and those including the survey fields (red).

Figure S3 DIC values of hierarchical linear models for the abundance of *Tetragnatha* with the area of forest surrounding the survey fields calculated at different spatial scales, and all the other explanatory variables.

Figure S4 Graphical posterior predictive check to assess the goodness-of-fit of the hierarchical model assuming independent coefficients. Dots show the sums of squares (SSQ) discrepancies (residuals) calculated from the actual vs. replicated data sets for 1000 MCMC samples. The line indicates the 1 : 1 line.

Figure S5 The estimated parameters for the hierarchical linear model with covariance matrices for the coefficients of explanatory variables, fitted to the data on the abundance of *Tetragnatha*. Points and bars are as defined in Figure 1.

Figure S6 Estimated average predictive comparisons for the abundance of *Tetragnatha* for each input variable in the hierarchical model assuming independent coefficients. Bars show ± 1 standard-error bounds.

Figure S7 (a) Annual mean temperature (°C), (b) summer (Jun–Aug) precipitation (mm) and (c) mean elevation (m) in the 100-km² square for predictions.

Figure S8 The predicted benefits of reducing (a) insecticide applications to fields, (b) insecticide applications to nursery boxes and (c) herbicide applications in increasing the abundance of *Tetragnatha*. The benefits were defined as the inverted site-specific regression coefficients against the number of pesticide applications, predicted for each 100-km² square.

Figure S9 The uncertainties (coefficients of variation) in the predicted abundance of *Tetragnatha* under (a) conventional farming (Figure 5a in the main text) and (b) organic farming (Figure 5b). Medians of the estimated posterior distributions are shown.

Table S1 Summary of data used for the analysis. Means and ranges (in parentheses) are shown.

Table S2 The number of replicates for each application level of three pesticide types. The number of pesticide applications was defined as the multiple of the total number of active ingredients in a pesticide and the number of times that pesticide was applied.

Table S3 Correlation coefficients among explanatory variables used for the hierarchical linear model. The number of sampling and the total number of swings (range: 40–540, mean \pm SE: 184.2 \pm 6.0) in each survey field were not strongly correlated with other explanatory variables ($|r| < 0.32$).

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