Title: Hierarchical trait-based model reveals positive and negative effects of land abandonment on butterfly communities across climatic regions in Japan

Running title: Land abandonment and butterfly diversity

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## Abstract

Land abandonment may decrease biodiversity but also provides an opportunity for rewilding. It is therefore necessary to identify areas that may benefit from traditional land management practices and those that may benefit from a lack of human intervention. In this study, we conducted comparative field surveys of butterfly occurrence in abandoned and inhabited settlements in 18 regions of diverse climatic zones in Japan to test the hypotheses that species-specific responses to land abandonment correlate with their climatic niches and habitat preferences. Hierarchical models that unified species occurrence and their habitat characteristics revealed that negative responses to land abandonment were associated with species having cold climatic niches utilizing open habitats, suggesting that traditional land use by human had long mitigated climate warming since the last glacier maximum through creating non-forest open habitats. Maps representing species gains and losses due to land abandonment, which were created from the model estimates, showed similar geographic patterns, but some parts of areas exhibited high species losses relative to gains. A hierarchical trait-based approach presented here revealed to be useful for scaling up local-scale effect of land abandonment to a macro-scale assessment, which is crucial to developing spatial conservation strategies in the era of depopulation.

## Keywords

depopulation, hierarchical model, rewilding, ridge regression, butterfly, trait-based approach

## Introduction

Traditional agricultural landscapes, with high spatial heterogeneity and moderate levels of disturbance, harbor a variety of organisms worldwide [1]. However, recent social changes, such as depopulation, population aging, and population concentration in urban areas, have resulted in an increase in abandoned fields [2,3]. While land abandonment is expected to decrease biological diversity at the national scale [4,5], it may also provide an opportunity for rewilding by vegetation succession [6,7]. To establish a long-term, broad-scale strategy for biodiversity conservation, it is necessary to identify areas where restoration by human management is effective for enhancing biodiversity as well as areas where rewilding is more effective.

Many studies have examined the relationship between land abandonment and biodiversity, but most have targeted a particular region within a nation [8,9]. These results cannot necessarily be extrapolated to other regions with different climates and land cover types because species responses to environmental changes may differ in different climatic zones [10,11]. Moreover, it is generally not possible to predict the responses of species that are not included in a field survey. Meta-analysis may be a promising tool to evaluate the effect of land abandonment [12,13], but it has shortcomings of heterogeneity in study design and inconsistent outcomes [14].

A practical approach to resolve these issues is to collect biodiversity and landuse data that are relevant to the spatial scale of land abandonment, which are taken from multiple climate zones (ecoregions) with a standardized sampling strategy. This makes it possible to evaluate how habitat traits of organisms (i.e., typical habitat types inhabited by particular species) affect the relationship between land abandonment and species

occurrence. Historically, abandoned settlements (or deserted villages) have emerged ubiquitously due to variety of causes such as economic environmental changes and disasters [15–17], and they offer us unique opportunities to evaluate long-term effect of land abandonment and recovery of ecosystems and to compare them among different climate. Species-specific sensitivity to land abandonment is determined by ecological traits [18,19] related to habitat preferences. Such trait-based relationships can be used to estimate the effects of abandonment on species that are not included in census data.

Traditional agricultural landscapes have been altered in Japan, with the increases in both urbanization and land abandonment. For instance, semi-natural grasslands areas have decreased by 87% during the last century [20] and agricultural fields have decreased by 26% [21]. These trends will continue in the future; 30–50% of currently inhabited settlements in rural areas are expected to become uninhabited by 2050 [22]. Abandonment of agricultural landscapes consisting of various elements, such as paddy field, dry crop field and grassland, has been causing decline in species diversity of various taxa [13,23–26]. As a result, many organisms are expected to become endangered [27], and butterflies are a typical example. In particular, grassland butterfly species are decreasing substantially; they account for approximately 70% of all Red List species of butterflies in Japan [28]. These grassland species were common in the late Pleistocene, when the climate was much cooler than at present and natural grasslands were predominant [29,30]. Thus, the effect of land abandonment is expected to be more severe in northern Japan, since more grassland species are likely included in the regional species pool. Meanwhile, land abandonment may increase forest-inhabiting species during the process of vegetation succession. Although fewer butterfly species are designated as

endangered in forests in Japan, there appears to be a tradeoff in butterfly conservation strategies with respect to whether we should manage abandoned land to maintain open habitats by human intervention or let succession proceed. Thus, the effect of land abandonment should be evaluated for each species across regions, and spatially explicit planning is needed to optimize conservation strategies. For nation-wide evaluations, butterflies are suitable subjects owing to extensive studies of their geographical distributions, preferred habitats, and larval host plants [31].

The aim of this study was to clarify the effect of land abandonment on butterfly communities at a national scale, including different climatic regions, and to determine how responses to land abandonment differ among species with different habitat traits. Here, we chose both inhabited and abandoned settlements in each region across Japan to estimate the effect of land abandonment, defined by inhabitation. We focused on three land use types, dry crop field, paddy field and built-up area (i.e. houses and garden around them), because they can be identified from past terrain map and visual inspection in the field. The hypotheses addressed in this study are (1) species preferring colder temperatures are more likely to show negative responses to land abandonment, and (2) open habitat species (inhabiting grassland/agricultural lands) generally show negative responses to land abandonment, whereas forest-dwelling species exhibit positive responses. Based on parameters related to the responses to land abandonment in butterflies with different habitat traits, we created a nation-wide map for the risks and benefits of land abandonment for butterfly diversity; this map could provide a guideline for identifying regions that may benefit from continuous human intervention.

## Materials and methods

### *Study area*

We selected 18 regions that covered most parts of mainland Japan (Fig. 1), with various annual mean temperatures (Table S1). In each region, we selected both abandoned and nearby inhabited settlements of approximately equal numbers, with a total of 2–5 settlements, including both types. We selected abandoned settlements from the databases of abandoned settlements in Japan [32–34] by the following criteria; 1. Settlement was inhabited in the past while uninhabited at present, 2. agricultural land existed before abandonment, 3. The year of abandonment was determined, and 4. Settlement was not submerged by a dam. As a result, we surveyed 34 abandoned and 30 inhabited settlements across all regions in Japan. The time elapsed since abandonment varied among settlements, ranging from 8 to 53 years (Table S1). The mean areas (± standard error) of the abandoned and inhabited settlements were, respectively, 10.6 ± 3.1 ha and 12.2 ± 4.4 ha, and these areas did not differ significantly.

### *Butterfly survey*

We visited each settlement during late May to early August in 2015 and in 2016. Accounting for the difference in butterfly phenology among regions with different temperatures, the first visitations started in the southern region and ended in the northern region in each year. In 2016, we revisited 16 settlements which we surveyed in 2015 to examine the effect of survey season on butterfly communities. In each visitation, we established 4 to 16 spots (each 100 $m^2$) for the butterfly survey, depending on the area of

the settlements. The survey spots were located at dry crop field, paddy field and built-up area, and the land use category at each spot was also recorded. All the survey spots in inhabited settlements were under active land use; crop fields and paddy fields were cultivated, and houses were used by residents. In contrast, all these human activities were absent, and some houses were even collapsed. The area of each spot was about 100 $m^2$. The butterfly survey was conducted on sunny or slightly cloudy days from 8:00 am to 12:30 pm. A 5-minute census was conducted from roads or rural paths adjacent to the survey spots, and the presence/absence of all species of butterflies found at the plot was recorded. As we did not capture individual butterflies, but instead recorded individuals by sight, some groups of species were difficult to identify to the species level during flight. Thus, the following taxonomic groups were omitted from further analysis: (1) four species of *Papilio* (*P. protenor*, *P. macilentus*, *P. memnon*, and *P. helenus*), (2) six species of the tribe Argynnini (*Fabriciana adippe*, *Speyeria aglaja*, *Nephargynnis anadyomene*, *Argynnis paphia*, *Argyreus hyperbius*, and *Damora sagana*), (3) Hesperiidae, and (4) three genera of the tribe Theclini (*Neozephyrus*, *Favonius*, and *Chrysozephyrus*). We also excluded nonnative species, *Pieris rapae* [35] and *P. brassicae*.

The habitat traits for each butterfly species were determined based on the habitat categorization established by the Japan Butterfly Conservation Society [31]. The categorization consists of the following 11 types: forests, forest edges, open forests, grasslands, crop fields, gardens, built-up areas, rivers, wetland, alpine, and rocky habitats. The habitat trait of a species often comprised several habitat types (Table S1).

*Statistical analysis*

We applied the three statistical approaches to (1) evaluate the correlation between species-specific responses to temperature and land abandonment, (2) evaluate the relationship between habitat traits of species and susceptibility to land abandonment, and (3) develop a predictive model for species-specific responses to land abandonment based on habitat traits. We incorporated region- and settlement-level random effects into the analyses because of the spatially clustered sampling design. These models were implemented by a hierarchical Bayesian approach.

(1) Correlation between the species-specific response to temperature and land abandonment

We applied generalized linear mixed models (GLMM) [36], incorporating heterogeneous responses to environmental properties among species as a random effect to determine whether species that prefer colder temperatures are more likely to respond negatively to land abandonment. The presence and absence of *i*th species at *j*th survey spot, $Y_{ij}$, was assumed to follow a Berunoulli distribution, Bernoulli($Y_{ij}$; $p_{ij}$), where $p_{ij}$ is the probability of occurrence. The parameter $p_{ij}$ was assumed to be expressed by a logistic regression model. We used land abandonment ($ABAN_j$) and mean annual temperature ($TEMP_j$) as explanatory variables. We also included month surveyed ($MONTH_j$) and categorical variable of three land use types (paddy field, dry field and built-up area, $LU_j$) as confounding factors. $TEMP_j$ was obtained from the Climate Mesh Data 2000 [37]. $MONTH_j$ and $LU_j$ were confounding factors controlling the possible

influence of seasonality and land use type at each survey spot on the other parameters, respectively. We also considered region- and settlement-level random effects, $\varepsilon_{reg(j)}$ and $\varepsilon_{set(j)}$, following normal prior with mean zero and variance $\sigma_r^2$ and $\sigma_s^2$, respectively. Overall, $p_{ij}$ was modeled as follows:

$$\text{logit}(p_{ij}) = \beta_{0i} + \beta_{1i}ABAN_j + \beta_{2i}TEMP_j + \beta_{3i}MONTH_j + \beta_{4i}I(LU_j = \text{“dry field”}) + \beta_{5i}I(LU_j = \text{“built-up area”}) + \varepsilon_{reg(j)} + \varepsilon_{set(j)}, \quad \text{Eqn. 1}$$

where $\beta_{0i}$ is an intercept, and $\beta_{1i}$, $\beta_{2i}$, $\beta_{3i}$, $\beta_{4i}$ and $\beta_{5i}$ are regression coefficients for the *i*th species. $I()$ is an indicator function indicating dummy variables for $\text{LU}_j$.

To infer species-specific effects of land abandonment and the correlation with their suitable temperature, a GLMM with a random slope was applied to estimate regression coefficients for each species. In a random slope model, regression coefficients of species are treated as random effects subject to the same prior distribution. As a prior distribution of $\boldsymbol{\beta}_i = (\beta_{1i}, \beta_{2i})$, the bivariate normal distribution $\text{MVN}(\boldsymbol{\beta}_i;\ \boldsymbol{\mu}_\beta,\ \boldsymbol{\Sigma}_\beta)$ was applied. $\boldsymbol{\mu}_\beta = (\mu_{\beta 1}, \mu_{\beta 2})$ and $\boldsymbol{\Sigma}_\beta$ are the mean vector and covariance matrix, respectively. Covariance matrix was decomposed to standard deviations and Pearson's correlation coefficient as follows:

$$\boldsymbol{\Sigma}_\beta = \begin{bmatrix} \sigma_{\beta 1}^2 & \rho\sigma_{\beta 1}\sigma_{\beta 2} \\ \rho\sigma_{\beta 1}\sigma_{\beta 2} & \sigma_{\beta 2}^2 \end{bmatrix}$$

The $\rho$ is Pearson's correlation coefficient of $\beta_{1i}$ and $\beta_{2i}$; a positive value indicates that a species preferring cooler temperatures is more likely to be negatively impacted by land abandonment. The priors of regression coefficients of confounding factors, $\beta_{3i}$, $\beta_{4i}$ and $\beta_{5i}$ were normal distributions with mean $\mu_{\beta 3}$, $\mu_{\beta 4}$ and $\mu_{\beta 5}$, variance $\sigma_{\beta 3}$, $\sigma_{\beta 4}$ and $\sigma_{\beta 5}$, respectively.

We calculated posterior distributions of the model by the Bayesian method using vague or weakly informative priors for the hyperparameters of the model. For $\beta_{0i}$, $\mu_{\beta 1}$, $\mu_{\beta 2}$, and $\mu_{\beta 3}$, $\mu_{\beta 4}$ and $\mu_{\beta 5}$, a normal prior with mean 0 and variance 100 was used. A half-Cauchy distribution with a scale parameter set to 5 was used for the standard deviations as a weakly informative prior; $\sigma_r$, $\sigma_s$, $\sigma_{\beta 1}$, $\sigma_{\beta 2}$, $\sigma_{\beta 3}$, $\sigma_{\beta 4}$ and $\sigma_{\beta 5}$ [38,39], was used. Uniform distribution with range (-1, 1) was used for the prior of correlation coefficient, $\rho$. Samples from the posterior distribution were obtained using No-U-Turn Sampler implemented in RStan 2.21.1 [40] (three chains, 1000 iterations after 1000 burn-in iterations).

For the explanatory variable $ABAN_j$, we considered two candidate variables, “abandoned or not” and “years since abandonment”, because it is unknown whether the response is immediate or gradual. We compared the performance of models using “abandoned or not” and “years since abandonment” on the basis of a widely applicable Bayesian information criterion (WBIC) [41]. WBIC is a generalization of Bayesian information criterion that is applicable to both regular and singular statistical models; it asymptotically approximates the minus logarithm of the marginal likelihood. A Bayes factor (the ratio of posterior probability of competing models) was calculated by the exponential of the difference in WBICs. The abandonment variable with a higher WBIC was used for further analyses.

(2) Relationship between habitat traits of species and responses to land abandonment

To test whether species with different habitat traits respond differently to

abandonment, we applied a hierarchical model incorporating a trait-species hierarchy [42]. The model is an extension of the species-level model described in section (1), in which the average effect of abandonment $\mu_{\beta 1}$ was replaced with the linear predictor of habitat traits as follows:

$$\mu_{\beta 1i} = \alpha_0 + \alpha_1 H_{ik}, \qquad \text{Eqn. 2}$$

where $H_{ik}$ is a binary variable indicating whether the $i$th species utilizes the $k$th ($k$ = 1, 2, …, 11) habitat type or not. $\alpha_0$ is intercept, and $\alpha_1$ indicates the difference in the average effects of abandonment between habitat types, where positive and negative values of $\alpha_1$ indicate positive and negative effects of abandonment for species utilizing the $k$th habitat type relative to species utilizing other habitat types. The same structure was used to determine the effect of $TEMP_j$; that is, $\mu_{\beta 2i} = \alpha_{T0} + \alpha_{T1} H_{ik}$. As in the model of section (1), slopes of each species vary following Multivariate normal distribution with mean vector of ($\mu_{\beta 1i}$, $\mu_{\beta 2i}$).

We calculated posteriors of $\alpha_0$, $\alpha_1$, $\alpha_{T0}$, and $\alpha_{T1}$ separately for the 11 habitat types. We used vague priors of a normal distribution with mean 0 and variance 1000 for these parameters. Other prior settings were the same as those for the species-level model (Section (1)). Samples from the posterior distribution were obtained using RStan 2.21.1 [40], with the same settings as in Section (1).

### (3) Predictive model of species-specific responses to land abandonment

A trait-based approach is a powerful tool to predict species-specific responses to environmental changes [43], and allows us to evaluate the broad-scale distribution of a species. Here, we developed a predictive model based on the habitat trait of a species.

As most of the species have a habitat trait comprising multiple habitat types (i.e., they inhabit several habitat types), the predictive model was a multivariate extension of Eqn. 2:

$$\mu_{\beta 1i} = \alpha_0 + \Sigma_k \alpha_k H_{ik}. \qquad \text{Eqn. 3}$$

However, models that are too complex can lead to overfitting and tend to have a large predictive error. In such a situation, ridge regularization is useful to constrain overfitting and improve predictive accuracy [44]. In a Bayesian manner, ridge regularization can be simply implemented using the same normal prior, N(0, $\sigma_\alpha^2$), for each regression coefficient. This prior works as a penalty for the divergence of squared regression coefficients from zero, and the standard deviation, $\sigma_\alpha$, corresponds to the weight of the penalty. The prior of $\sigma_\alpha$ was set to a weakly informative prior, half-Cauchy(0, 5), and $\sigma_\alpha$ was determined by calculating the posterior distribution. The prior of $\alpha_0$ was a normal distribution with mean 0 and variance 100. Samples from the posterior distribution were obtained by RStan 2.21.1 [40], with the same MCMC sampling settings as in Sections (1) and (2).

To make projection maps for the effect of land abandonment on butterfly assemblages, we defined the loss (CL) and gain (CG) in butterfly species due to land abandonment as follows:

$$\mathrm{CL}_j = \sum_i^{N_{sp}} \delta_{ij} \left| min\left(\mu_{\beta 1i}, 0\right) \right|,$$

and

$$\mathrm{CG}_j = \sum_i^{N_{sp}} \delta_{ij} max\left(\mu_{\beta 1i}, 0\right),$$

where $N_{sp}$ is the number of species, and $\delta_{ij}$ is a binary indicator of whether the *i*th species is present in the *j*th grid cell. Operators $min(\mu_{\beta 1i}, 0)$ and $max(\mu_{\beta 1i}, 0)$ are filters to identify species affected negatively and positively, respectively. CL and CG can be interpreted as log-odds ratios of occurrence probabilities across species after land abandonment. Large values of CL or CG indicate a large loss or gain in species in the local butterfly assemblage due to land abandonment, respectively.

We used nation-wide range maps of 70 butterfly species in Japan (Table S3), which were projected by Kasada et al. [45] using distribution models (MaxEnt) from butterfly records obtained from the fourth and fifth National Surveys on the Natural Environment. Prior to calculate CL and CG, we excluded seven alpine butterflies, *Carterocephalus palaemon*, *Erebia neriene*, *E. ligea*, *Oeneis norna*, *Colias palaeno*, *Anthocharis cardamines* and *Aporia hippia*, because their ranges are irrelevant to land abandonment. The range maps comprise presence and absence data for species in each grid cell of a "1 × 1 km mesh (the third mesh)," a Japanese national grid system whose unit cell size is 30″ in latitude and 45″ in longitude, approximately 1 × 1 km. We determined the expected coefficient of land abandonment, $\mu_{\beta 1}$, using Eqn. 3, for 70 species. We then separately evaluated CL and CG for all the species and for species ranked "near threatened (NT)", "vulnerable (VU)", "endangered (EN)" or "critically endangered (CR)" in the red list of Japan in 2019 (https://www.env.go.jp/press/files/jp/110615.pdf, visited 10/19/2020). Losses and gains of species were estimated separately, rather than as a combined gain-minus-loss, because separate estimation is more informative for decisions regarding conservation practices.

## Results

A total of 49 butterfly species were recorded during our field surveys (Table S2). The top 10 species with the highest average occurrence (i.e., number of presence spots/total number of spots) were *Pieris melete*, *Colias erate*, *Celastrina argiolus*, *Ypthima argus*, *Libythea celtis*, *Plebejus argus*, *Lycaena phlaeas*, *Eurema mandarina*, *Papilio machaon* and *Apatura metis*, in decreasing order, and they represented 73.4% of the total occurrence records.

The model selection by WBIC indicated that the model including "abandoned or not" (WBIC = 3575.77) outperformed the model for "years since abandonment" (WBIC =3608.51), suggesting relatively immediate responses to land abandonment. The Bayes factor for the former model against the latter was $1.65 \times 10^{14}$. Among 49 species of butterflies analyzed, 12 showed a significant negative response (i.e., the 95% CI of the regression coefficient of "abandoned or not" was less than zero), while 3 species showed a positive response (Table S4). *Lycaena phlaeas*, *Papilio machaon* and *Papilio xuthus* exhibited the largest negative effect of abandonment. The three species that showed positive response were *Limenitis camilla*, *Cyrestis thyodamas* and *Graphium sarpedon*. Effects of abandonment and temperature were positively correlated (Fig. 2); Pearson's correlation coefficient for the effect of land abandonment and annual mean temperature was 0.402 with a 95% CI of (0.0414, 0.678).

There was a significant relationship between habitat types of species and responses to land abandonment for four habitat types; species utilizing farmland, grassland and built-up areas responded negatively, while those utilizing forest responded positively (Fig. 3, Table S5).

Using a hierarchical model with ridge regularization, we obtained the following predictive model for the effect of land abandonment based on the habitat trait of each species:

[predicted effect of land abandonment]

= –0.44 – 0.39 × [built-up area] – 0.99 × [grassland] – 0.40 × [garden]

– 0.74 × [farmland] – 0.38 × [alpine area] – 0.36 × [rocky area] + 0.34 × [wetland]

+ 0.06 × [riverside] + 0.54 × [open forest] + 0.58 × [forest edge]

+ 0.56 × [forest]. Eqn. 4

By applying this model, 37 of 70 species showed negative responses. Using the predicted values thus obtained, we drew maps of CL (Fig. 4a) and CG (Fig.4b) of species throughout Japan's mainland. The geographic distributions of loss and gain were similar in a coarse scale and the Pearson's correlation coefficient was 0.56; that is, larger values of both CL and CG were found in inland middle Kyushu, inland western Honshu, inland middle Honshu, northern Honshu and Hokkaido, while smaller values were found in high elevation areas. However, there was some contrast between CL and CG in lowland where small CG relative to CL was found. Standard deviations of CL and CG (Fig. S1ab) were almost proportional to the CL and CG themselves (Pearson's correlation coefficient was 0.86 and 0.99, respectively).

The 10 and 4 red list species were evaluated as victims and beneficiaries to land abandonment, respectively. Distribution patterns of CL and CG for red list species of Japan were shown in Fig. 4cd. The correlation between CL and CG for red list species was weaker than that of all the species (Pearson's correlation coefficient = 0.36), and their spatial patterns are different in a coarse scale. For instance, CL was small

while CG was large in northern Honshu. On the contrary, CL was large but CG was small in eastern Hokkaido. Similar to the maps for all the species, standard deviations (Fig. S1cd) were almost proportional to the CL and CG themselves (Pearson's correlation coefficient was 0.95 and 0.99, respectively).

## Discussion

As expected, the responses of butterflies to land abandonment were associated with climatic niches and habitat traits of species. Our study approach that compared community assemblages between inhabited and abandoned areas using a standard survey protocol enabled us to estimate the effects of land abandonment over broad range of climatic condition. In combination with trait-based approach, we were able to draw nation-wide potential maps of loss and gain of species richness through land abandonment.

Legacy of past climate and land use can affect current functional species composition within regional species pool [46,47], and different functional compositions among region can result in different community-level responses to current environmental change [48]. Such a difference would also reflect historical background of organisms inhabiting seminatural environments in Japan. Grassland was more abundant in Pleistocene due to cold and dry climate than at present [30]. After the last glacier period, open lands created by human activity have offered refugia for the Pleistocene relics [49], and such refugia become unlikely to be sustainable if they are abandoned [50]. Our results also raise a conservational concern that species declined by land abandonment will decline more due to climate warming in the future, because the species susceptible to

land abandonment tend to prefer low temperatures (Fig.2). In turn, this means that continuing land management in rural areas will be an effective measure of climate change adaptation for biodiversity conservation in Japan.

Decrease in open habitat species (grassland, crop field, and residential species) (Figure 4) would be related to the decreased species richness of herbaceous plants [23], leading to the loss or decline of host plants for these butterflies. Indeed, we often observed tall grasses, such as *Miscanthus sinensis*, as predominant species in abandoned paddy, dry fields, and built-up area in uninhabited settlements. The monodominance of wind-pollinated *Miscanthus* would also decrease abundance and diversity of nectaring flowers that are important for adult butterflies. In contrast, forest species tended to increase in response to abandonment, although the proportion of such species was low. Development of old-growth forest in Japan requires approximately 150 years [51], and some tree species require more than a hundred years to recover [52]; accordingly, recovery of forest butterfly species depending on such trees would also require very long time as well.

Comparing with land abandonment and temperature, local land use (paddy field, dry crop field and built-up area) had minor impact on butterfly occurrences. This is probably due to our focus on adult butterflies which were often affected by landscape-scale effect of land use [53]. In our study, the effect of landscape scale abandonment was actually more prominent than local factors.

It should be noted that there was a positive correlation between losses and gains in butterfly richness both for all species and for red list species due to land abandonment at the level of grid cells, indicating a tradeoff between the benefits of the active

management of abandoned sites and letting succession proceed. As endangered butterflies in Japan include more grassland species than forest species, human intervention should be prioritized, in principle, to conserve such species, but deliberate decision-making is required for areas where the benefit of abandonment is high. Our results indicated that conservation of butterflies by active management is desirable in lowland and eastern Hokkaido, in which loss of species preferring abandoned landscape is small by such management. The identification of highly cost-effective areas for habitat management based on species ranges and habitat preferences, with a high resolution, is necessary, because maintaining secondary natural environments is generally labor-intensive [54]. It is of course necessary to conduct similar analyses using taxonomic groups other than butterflies to enable more comprehensive assessments as effect of abandonment differs among taxonomic groups [13].

Here, we evaluated the risks and benefits of land abandonment using butterfly occurrence data; however, it is also important to clarify how the abundance of larval host plants and adult nectar plants change over time after abandonment. Previous studies have shown that many grassland species are still found even 10 years after abandonment [55], indicating the presence of host and nectar plants during that period. In our study, the effects of abandonment did not show a clear increase over time, as the model with a dichotomous variable (inhabited vs. abandoned settlements) outperformed the model with a continuous variable (years since abandonment). As Japan has a monsoon climate with a relatively high temperature and rainfall in comparison with Europe, vegetation succession may proceed within a few years, resulting in a rapid response to abandonment. This suggests the necessity to restore habitats as early as possible after abandonment. The

potential maps of effect of abandonment will contribute to prioritize habitat management plans in areas where settlement abandonment is expected in the immediate future and a large decrease in biodiversity after abandonment.

A major contribution of our study was the ability to apply the estimated relationship between habitat traits and responses to land abandonment to butterfly species that were not observed in the field survey. The utility of such a trait-based approach is widely recognized [56], but there are some caveats, as responses of habitat generalists may be difficult to predict. To resolve this problem, models incorporating responses of host plants to abandonment and resultant butterfly responses should be explicitly constructed, as has been demonstrated in climate change prediction models [57].

In conclusion, we demonstrated that a hierarchical trait-based approach proves to be useful to scale up the results of comparative field studies to a macro-scale evaluation of species losses and gains by land abandonment. Land abandonment had both positive and negative effects on different functional groups of butterflies in Japan, and our approach could be used to identify areas exhibiting high species losses relative to gains after land abandonment. We believe this approach is promising for large-scale and comprehensive biodiversity assessments regarding the risks and benefits of land abandonment, which are urgently needed in view of ongoing depopulation in developed countries.

## Ethics

Our field survey was conducted from roads and rural paths, and no permission was required in compliance with Japanese law. All information of site locations is coarse enough to protect landowners' privacy. To avoid negative consequences on conservation,

we kept specific records of endangered species closed.

## Data accessibility

The datasets and program codes are available from the Dryad Digital Repository at https://datadryad.org/stash/share/8u3_mEXi3SsWzm_ZElaD7iq7wWB8FSQ45czwu8u_V24, except specific records of endangered species.

## Author contributions

NS, KF, and TM conceived the ideas; NS conducted the field study; AA prepared part of the data for the analysis; MK and MM prepared the projected national distribution maps of butterflies; NS and KF conducted the analysis; and NS, KF, and TM wrote the manuscript with input from AA, MK and MM.

## Competing interest

We have no competing interest.

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Fig. 1 Location of study sites. Each site contained both rural abandoned villages and inhabited villages.

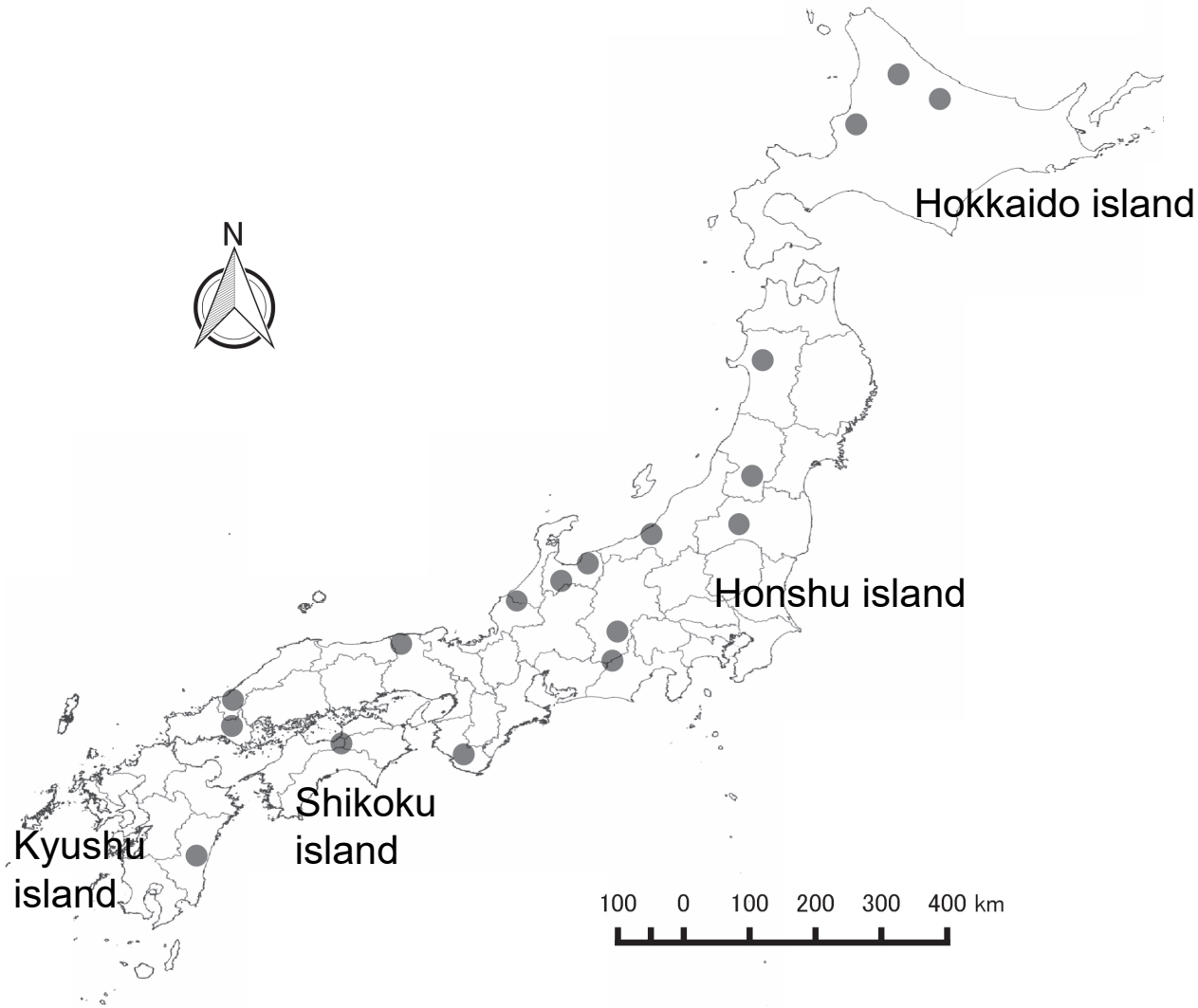

Fig. 2 Relationship between coefficients of mean annual temperature and land abandonment. Black dots and gray error bars indicate posterior means and 95% credible intervals of species, respectively. The dashed ellipsoid and line are 95% equiprobable ellipsoid and principal axis of coefficients.

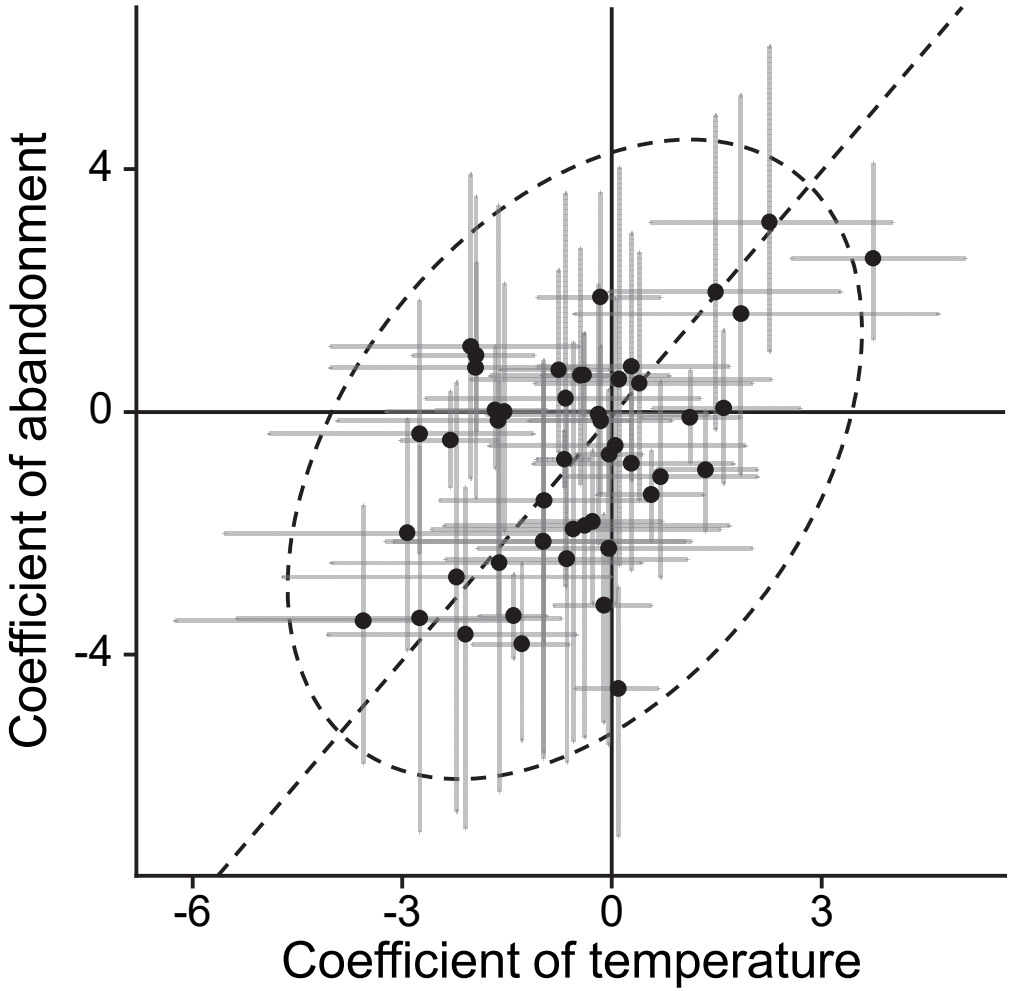

Fig. 3 Effects of land abandonment on the occurrence of butterflies with different habitat characteristics.The 1 and 0 of x axis indicate the species does and does not utilize the habitat type, respectively. Gray dots represent coefficients of abandonment ($\beta_{1i}$) for each species. Black dots and error bars represent posterior means and 95% credible interval (95% CI) of the expected value of the coefficient of abandonment ($\mu_{\beta 1i}$ in eqn. 1), respectively. Four habitat types with significant effect on $\mu_{\beta 1i}$ (i.e. 95% CI of $\alpha_1$ in eqn. 2 did not overlap 0) were shown.

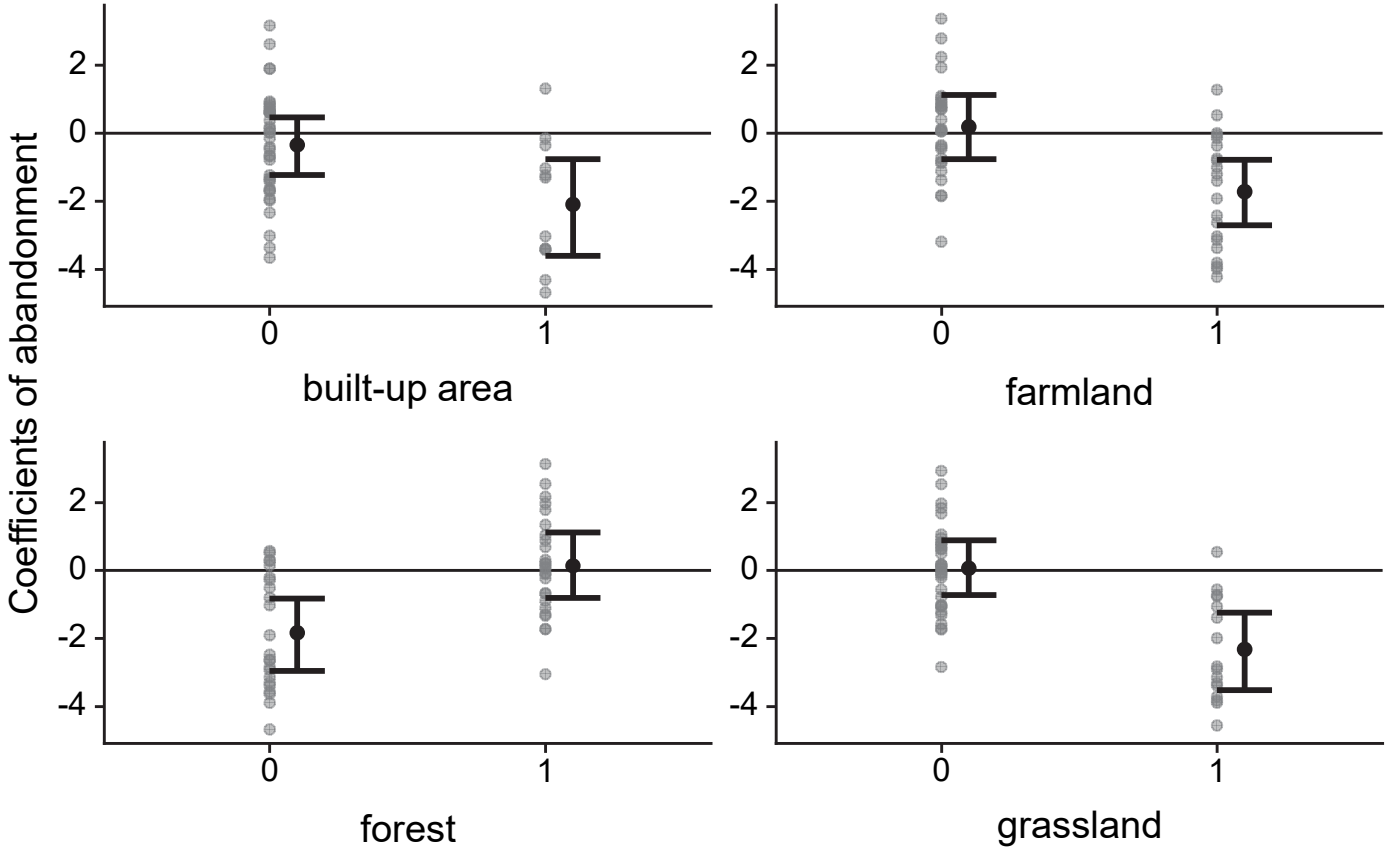

Fig. 4 Maps of cumulative loss (CL) and gain (CG) in butterfly species richness due to land abandonment for all the species(a and b, respectively) and for the Red List species (c and d, respectively). The boxed graphs are hexagonal binning plots showing their relationship with elevation.

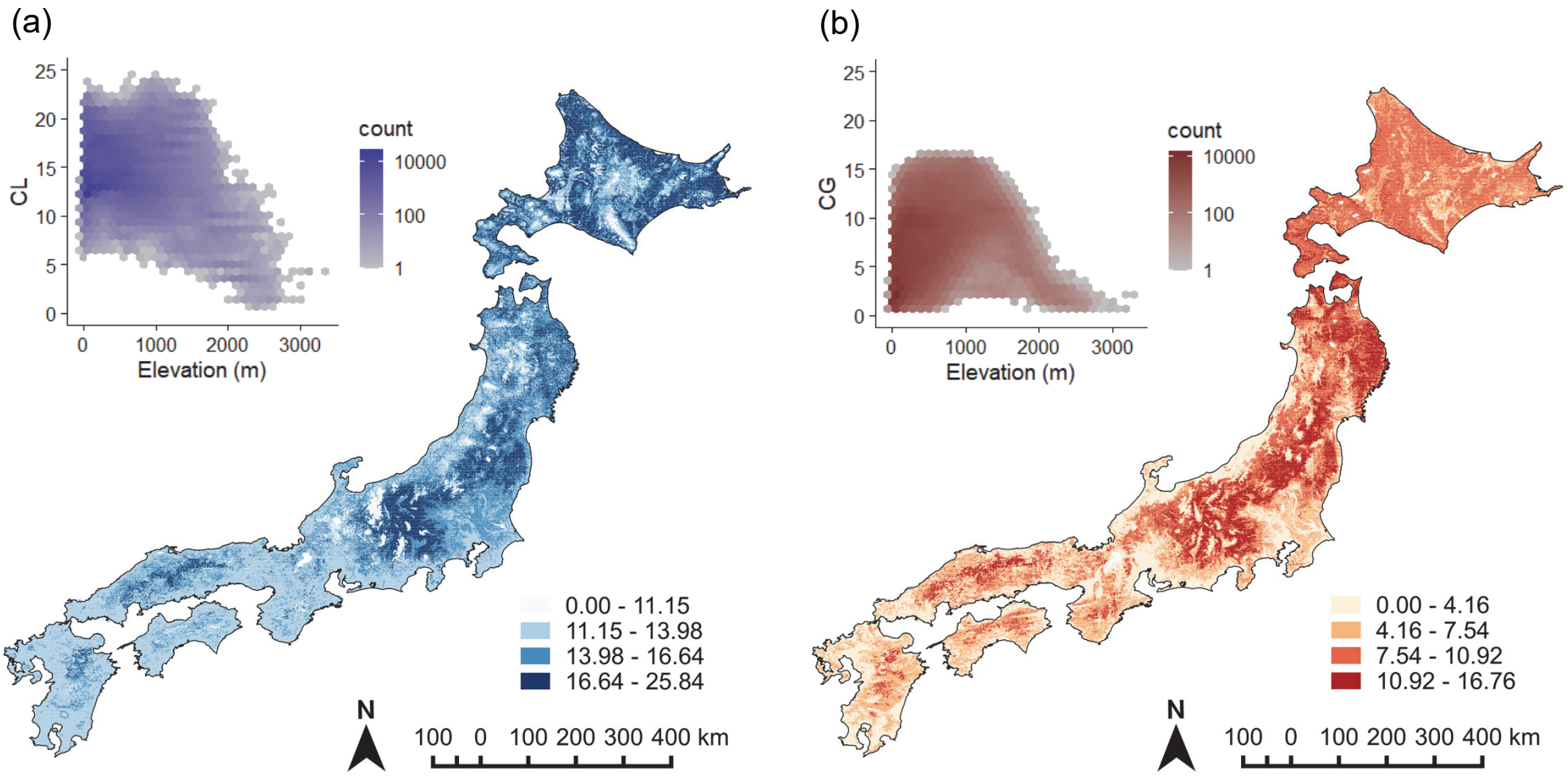
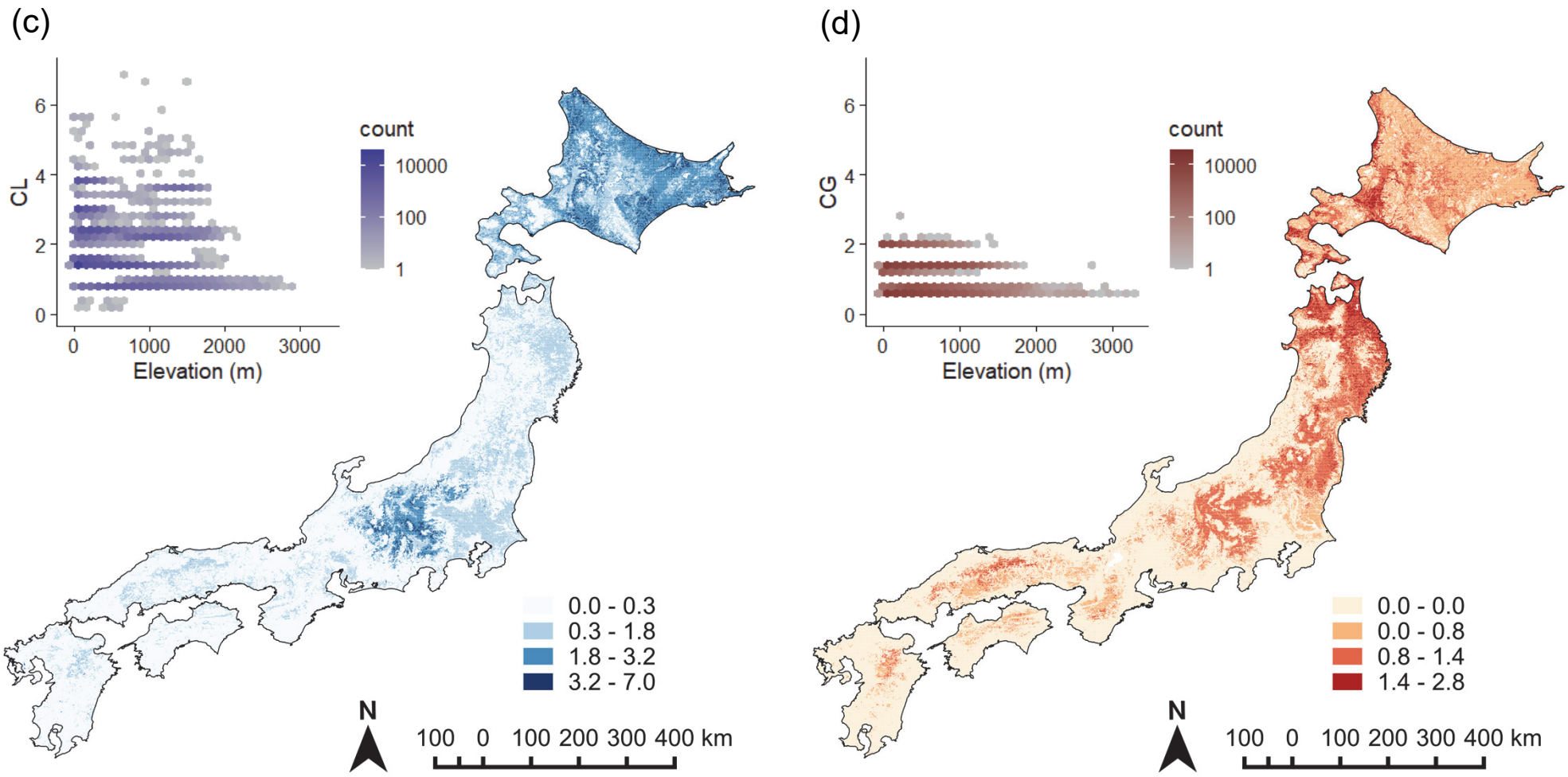
Fig. 4 *Continued.*