1 Title: Positive and negative effects of land abandonment on butterfly communities
2 revealed by a hierarchical sampling design across climatic regions

3 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 climatic niches and habitat preferences. Hierarchical models that unified species occurrence and habitat preferences revealed that negative responses to land abandonment were associated with species that have cold climatic niches and utilize open habitats, suggesting that species negatively impacted by land abandonment will decline more due to future climate warming. Maps representing species gains and losses due to land abandonment, which were created from the model estimates, showed similar geographic patterns, but some areas exhibited high species losses relative to gains. Our hierarchical modelling approach was useful for scaling up local-scale effects 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, climate change adaptation

Introduction

Traditional agricultural landscapes, with high spatial heterogeneity and moderate levels of disturbance, harbour a variety of organisms worldwide [1]. However, recent social changes, such as depopulation and population ageing, 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, a common approach for testing the effect of land abandonment has been to analyse each species separately or analyse diversity metrics, but such approaches cannot predict the responses of species in a community that are not detected in a field survey. Meta-analysis may be a promising tool for evaluating 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 land-use data that are relevant to the spatial scale of land abandonment, with the data collected from multiple climate zones (ecoregions) using a standardized sampling

66 strategy. This makes it possible to evaluate how the climatic niches or habitat preferences
 67 of organisms (i.e. typical habitat types inhabited by particular species) affect the
 68 relationship between land abandonment and species occurrence. Historically, abandoned
 69 settlements (or deserted villages) have emerged globally due to a variety of causes such as
 70 economic and environmental changes and disasters [15–17], and they provide unique
 71 opportunities to evaluate the long-term effects of land abandonment and recovery of
 72 ecosystems and to compare the effects among different climates. Species-specific
 73 sensitivity to land abandonment is determined by ecological traits [18,19] related to
 74 habitat preferences. Thus, information on habitat preferences which can be easily
 75 obtained from the literature would be useful for estimating the effects of land
 76 abandonment on species that are not included in field survey data.

77 Traditional agricultural landscapes have been altered in Japan with urbanization
 78 and land abandonment, but land abandonment has become more serious in recent years
 79 because of the country's declining human population. For instance, semi-natural
 80 grasslands areas have decreased by 87% during the past century [20] and agricultural
 81 fields have decreased by 26% [21]. These trends will continue in the future; 30%–50% of
 82 currently inhabited settlements in rural areas are expected to become uninhabited by 2050
 83 [22]. The abandonment of agricultural landscapes with various characteristics, such as
 84 paddy fields, dry crop fields and grasslands, has caused declines in species diversity of
 85 various taxa [13,23–26]. As a result, many organisms are expected to become endangered
 86 [27], and butterflies are a typical example. In particular, grassland butterfly species are
 87 decreasing substantially; they account for approximately 70% of all Red List butterfly
 88 species in Japan [28]. These grassland species are elements of the eastern Eurasian

temperate steppe biome [29], which is located in a cooler region than the Mediterranean and European steppes [30]. These species were common in Japan in the late Pleistocene when the climate was much cooler than at present and natural grasslands were predominant [31,32]. Later, in the warm Holocene when forests became predominant, open lands maintained by human activity offered refugia for the Pleistocene relic grassland fauna. Thus, the effect of land abandonment is expected to be more severe for species that favour cold climates, since grassland species in eastern Eurasia are likely to be cold adapted. Meanwhile, land abandonment may increase forest-dwelling species during the process of vegetation succession. Although relatively few forest-dwelling butterfly species in Japan are designated as threatened, there appears to be a trade-off 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 [33].

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 preferences. 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, namely dry crop field, paddy field and built-up area (i.e. houses and gardens around them), because they can be identified from past terrain maps

and visual inspection in the field. The following hypotheses are addressed in this study:
 (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 the estimated coefficients of land abandonment for
 butterflies with different habitat preferences, we created a nation-wide map reflecting 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) and
 differed in terms of mean annual temperature (MAT) (Table S1). The range of MAT in the
 selected regions was 4.5°C-15.7°C, which covers most of the MAT range in areas
 inhabited by humans in mainland Japan (the range of MAT of all the meteorological
 stations except Mt. Fujiwas was 6.0°C-18.8°C) [34]. In each region, we selected both
 abandoned and nearby inhabited settlements in approximately equal number, with a total
 of 2–5 settlements, including both types. We selected abandoned settlements from
 databases of abandoned settlements in Japan [35–37] according to the following criteria:
 (1) the settlement was inhabited in the past but uninhabited at present; (2) agricultural
 land was present before abandonment; and (3) the year of abandonment was known. 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

134 years (Table S1). Pearson's correlation coefficient between years since abandonment and
135 MAT was -0.16 (95% CI: -0.39, 0.09), and the difference in MAT between abandoned and
136 inhabited settlements was not significant ($p = 0.44$, Student's t-test). The mean areas ($\pm$
137 standard error) of the abandoned and inhabited settlements were, respectively, 10.6 ± 3.1
138 ha and 12.2 ± 4.4 ha, and these areas did not differ significantly.

139

140 *Butterfly survey*

141 We visited each settlement during late May to early August in 2015 and in 2016.
142 To account for differences in butterfly phenology among regions with different
143 temperatures, the visits started in the southern region and ended in the northern region in
144 each year. In 2016, we revisited 16 settlements which we surveyed in 2015 to examine the
145 effect of survey season on butterfly communities. In each visit, we established 4 to 16
146 plots (each 100 m^2) for the butterfly survey, depending on the area of the settlements. The
147 survey plots were located at dry crop fields, paddy fields and built-up areas, and the land
148 use category at each plot was also recorded. All the survey plots in inhabited settlements
149 were under active land use; crop fields and paddy fields were cultivated, and houses were
150 occupied. In contrast, in the abandoned settlements, all human activity was absent and
151 some houses had even collapsed. The butterfly survey was conducted on sunny or slightly
152 cloudy days from 8:00 am to 12:30 pm. A 5-minute census was conducted from roads or
153 rural paths adjacent to the survey plots, and the presence/absence of all species of
154 butterflies found at the plot was recorded. As we did not capture individual butterflies, but
155 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) Hesperidae; and (4) three genera of the tribe Theclini (*Neozephyrus*, *Favonius* and *Chrysozephyrus*). We also excluded the non-native species *Pieris rapae* [38] and *P. brassicae*.

The habitat preferences for each butterfly species were determined based on the habitat categorization established by the Japan Butterfly Conservation Society [33]. 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 preferences of a species often comprised several habitat types (Table S1).

Statistical analysis

We applied three statistical approaches: (1) evaluating the correlation between species-specific responses to temperature and land abandonment; (2) evaluating the relationship between habitat preferences of species and susceptibility to land abandonment; and (3) developing a predictive model for species-specific responses to land abandonment based on habitat preferences. Our dataset had a hierarchical structure in which settlements were nested within a region, and a settlement contained multiple land-use types. Survey plots with the same land-use type were generally spatially aggregated in a settlement. Therefore, we incorporated region-, settlement- and land-use-type-level random effects into the analyses to accommodate the spatially

178 hierarchical sampling design. Then, we treated the presence/absence of a species in a
179 plot as the unit of analysis. These models were implemented by a hierarchical Bayesian
180 approach.

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

183 We applied generalized linear mixed models (GLMM) [39], incorporating
184 heterogeneous responses to environmental properties among species as a random slope
185 to determine whether species that prefer colder temperatures are more likely to respond
186 negatively to land abandonment. The presence and absence of the i th species at the j th
187 survey plot, Y_{ij} , was assumed to follow a Bernoulli distribution, $\text{Bernoulli}(Y_{ij}; p_{ij})$, where
188 p_{ij} is the probability of occurrence. The parameter p_{ij} was assumed to be expressed by a
189 logistic regression model. We used land abandonment ($ABAN_j$) and mean annual
190 temperature ($TEMP_j$) as explanatory variables. We also included month surveyed
191 ($MONTH_j$) and a categorical variable of three land-use types (LU_j : dry field, built-up
192 area and paddy field [baseline category]) as confounding factors. $TEMP_j$ was obtained
193 from the Climate Mesh Data 2000 [40]. $MONTH_j$ and LU_j were confounding factors
194 controlling for the possible influence on the other parameters of seasonality and
195 land-use type at each survey plot, respectively. We also considered region-, settlement-
196 and land-use-type-level random effects, namely $\varepsilon_{reg(j)}$, $\varepsilon_{set(j)}$ and $\varepsilon_{lu(j)}$, following normal
197 priors with mean zero and variance σ_r^2 , σ_s^2 and σ_l^2 , respectively, to accommodate the
198 hierarchical sampling scheme with unbalanced sample size [41]. Overall, p_{ij} was

199 modelled as follows:

$$\begin{aligned} 200 \quad \text{logit}(p_{ij}) = & \beta_{0i} + \beta_{1i}ABAN_j + \beta_{2i}TEMP_j + \beta_{3i}MONTH_j + \beta_{4i}I(LU_j = \text{“dry field”}) + \\ 201 \quad & \beta_{5i}I(LU_j = \text{“built-up area”}) + \varepsilon_{reg(j)} + \varepsilon_{set(j)} + \varepsilon_{lu(j)}, \quad \text{Eqn. 1} \end{aligned}$$

202 where β_{0i} is a species-specific fixed intercept, and β_{1i} , β_{2i} , β_{3i} , β_{4i} and β_{5i} are regression
203 coefficients for the i th species. $I()$ is an indicator function for the dummy variable LU_j .

204 To infer species-specific effects of land abandonment and the correlation with
205 their preferred temperature, a GLMM with a random slope was applied to estimate
206 regression coefficients for each species. In a random slope model, regression
207 coefficients of species are treated as random effects subject to the same prior
208 distribution. As a prior distribution of $\beta_i = (\beta_{1i}, \beta_{2i})$, the bivariate normal distribution
209 $MVN(\beta_i; \mu_\beta, \Sigma_\beta)$ was applied. $\mu_\beta = (\mu_{\beta 1}, \mu_{\beta 2})$ and Σ_β are the mean vector and
210 covariance matrix, respectively. The covariance matrix was decomposed to standard
211 deviations and Pearson’s correlation coefficient as follows:

$$\Sigma_\beta = \begin{bmatrix} \sigma_{\beta 1}^2 & \rho \sigma_{\beta 1} \sigma_{\beta 2} \\ \rho \sigma_{\beta 1} \sigma_{\beta 2} & \sigma_{\beta 2}^2 \end{bmatrix}$$

212 Here, ρ is Pearson’s correlation coefficient between β_{1i} and β_{2i} ; a positive value indicates
213 that a species preferring cooler temperatures is more likely to be negatively impacted by
214 land abandonment. The priors of regression coefficients of confounding factors, namely
215 β_{3i} , β_{4i} and β_{5i} , followed normal distributions with mean $\mu_{\beta 3}$, $\mu_{\beta 4}$ and $\mu_{\beta 5}$ and variance $\sigma_{\beta 3}$,
216 $\sigma_{\beta 4}$ and $\sigma_{\beta 5}$, respectively.

217 We calculated posterior distributions of the model by the Bayesian method
218 using vague or weakly informative priors for the hyperparameters of the model. For β_{0i} ,
219 $\mu_{\beta 1}$, $\mu_{\beta 2}$, $\mu_{\beta 3}$, $\mu_{\beta 4}$ and $\mu_{\beta 5}$, a normal prior with mean 0 and variance 100 was used. A

220 half-Cauchy distribution with a scale parameter set to 5 was used as a weakly
 221 informative prior for the standard deviations: σ_r , σ_s , $\sigma_{\beta 1}$, $\sigma_{\beta 2}$, $\sigma_{\beta 3}$, $\sigma_{\beta 4}$ and $\sigma_{\beta 5}$ [42,43]. A
 222 uniform distribution with range (-1, 1) was used for the prior of the correlation
 223 coefficient, ρ . Samples from the posterior distribution were obtained using the
 224 No-U-Turn Sampler implemented in RStan 2.21.1 [44] (three chains, 1000 iterations
 225 after 1000 burn-in iterations with no thinning). We obtained 3000 posterior samples.
 226 Convergence of the Markov chain Monte Carlo (MCMC) algorithm was evaluated
 227 using $\hat{R}$ [45], and we adopted $\hat{R} < 1.1$ as a threshold of successful convergence [46].
 228 We also evaluated the goodness of fit by using the posterior predictive p -value [47] with
 229 the following summary statistics: (1) proportion of presence observations over the
 230 dataset; (2) proportion of presence observations at abandoned settlements; (3)
 231 proportion of presence observations at inhabited settlements; (4) the Gini coefficient of
 232 the proportion of presence observations among the settlements; and (5) the Gini
 233 coefficient of the proportion of presence observations among species.

234 For the explanatory variable $ABAN_j$, we considered two candidate variables,
 235 “abandoned or not” and “years since abandonment”, because it is unknown whether the
 236 response is immediate or gradual. We compared the performance of models using
 237 “abandoned or not” and “years since abandonment” on the basis of the widely
 238 applicable Bayesian information criterion (WBIC) [48]. WBIC is a generalization of the
 239 Bayesian information criterion which is applicable to both regular and singular
 240 statistical models; it asymptotically approximates the negative logarithm of the marginal
 241 likelihood. The Bayes factor (the ratio of posterior probabilities of competing models)
 242 was calculated as the exponential of the difference in WBICs. The abandonment

243 variable with a higher WBIC was used for further analyses.

244 (2) Relationship between habitat preferences of species and responses to land
245 abandonment

246 To test whether species with different habitat preferences respond differently to
247 land abandonment, we applied a hierarchical model incorporating a hierarchy of habitat
248 type and species [49]. The model is an extension of the species-level model described in
249 section (1), in which the average effect of land abandonment $\mu_{\beta 1}$ was modelled by the
250 linear predictor of habitat preferences as follows:

$$251 \quad \mu_{\beta 1i} = \alpha_0 + \alpha_1 H_{ik}, \quad \text{Eqn. 2}$$

252 where H_{ik} is a binary variable indicating whether the i th species utilizes the k th ($k = 1, 2,$
253 $\dots, 11$) habitat type or not. α_0 is the intercept, and α_1 indicates the difference in the
254 average effects of land abandonment between habitat types, where positive and negative
255 values of α_1 indicate positive and negative effects for species utilizing the k th habitat
256 type relative to species utilizing other habitat types. The same structure was used to
257 determine the effect of $TEMP_j$; that is, $\mu_{\beta 2i} = \alpha_{T0} + \alpha_{T1} H_{ik}$. As in the model of section (1),
258 slopes for each species vary following a multivariate normal distribution with mean
259 vector $(\mu_{\beta 1i}, \mu_{\beta 2i})$.

260 We calculated posteriors of α_0 , α_1 , α_{T0} and α_{T1} separately for the 11 habitat
261 types. We used vague priors of a normal distribution with mean 0 and variance 1000 for
262 these parameters. Other prior settings were the same as those for the species-level model
263 (Section (1)). Samples from the posterior distribution were obtained using RStan 2.21.1
264 [44], with the same MCMC settings and posterior diagnostics as in Section (1).

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

266 A hierarchical modelling approach is a powerful tool for predicting
 267 species-specific responses to environmental changes [50], and allows us to evaluate the
 268 broad-scale distribution of a species. Here, we developed a predictive model based on
 269 the habitat preferences of a species. As most of the species inhabit several habitat types,
 270 the predictive model was a multivariate extension of Eqn. 2:

$$271 \mu_{\beta 1i} = \alpha_0 + \sum_k \alpha_k H_{ik}. \quad \text{Eqn. 3}$$

272 However, models that are too complex are vulnerable to overfitting and tend to
 273 have large prediction error. In such a situation, ridge regularization is useful to constrain
 274 overfitting and improve prediction accuracy [51]. In a Bayesian manner, ridge
 275 regularization can be simply implemented using the same normal prior, $N(0, \sigma_\alpha^2)$, for
 276 each regression coefficient. This prior works as a penalty for the divergence of squared
 277 regression coefficients from zero, and the standard deviation, σ_α , corresponds to the
 278 weight of the penalty. The prior of σ_α was set to a weakly informative prior,
 279 half-Cauchy(0, 5), and σ_α was determined by calculating the posterior distribution. The
 280 prior of α_0 was a normal distribution with mean 0 and variance 100. Samples from the
 281 posterior distribution were obtained using RStan 2.21.1 [44], with the same MCMC
 282 sampling settings and posterior diagnostics as in Sections (1) and (2).

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

$$CL_j = \sum_i^{N_{sp}} \delta_{ij} |\min(\mu_{\beta 1i}, 0)|,$$

286 and

$$CG_j = \sum_i^{N_{sp}} \delta_{ij} \max(\mu_{\beta 1i}, 0),$$

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

293 We used nation-wide range maps of 70 butterfly species in Japan (Table S3),
 294 which were projected by Kasada et al. [52] using distribution models (MaxEnt) from
 295 butterfly records obtained from the fourth and fifth National Surveys on the Natural
 296 Environment. Before calculating CL and CG, we excluded seven alpine butterflies,
 297 *Carterocephalus palaemon*, *Erebia neriene*, *E. ligea*, *Oeneis norna*, *Colias palaeno*,
 298 *Anthocharis cardamines* and *Aporia hippia*, because land abandonment is not relevant
 299 in their ranges. The range maps comprise presence and absence data for species in each
 300 grid cell of a “1 × 1 km mesh (the third mesh),” a Japanese national grid system whose
 301 unit cell size is 30'' in latitude and 45'' in longitude, approximately 1 × 1 km. We
 302 determined the expected coefficient of land abandonment, $\mu_{\beta 1}$, using Eqn. 3, for 70
 303 species. We then evaluated CL and CG separately for all species and for species
 304 classified as “near threatened (NT)”, “vulnerable (VU)”, “endangered (EN)” or

305 “critically endangered (CR)” in the Red List of Japan in 2019 [53]. Then, we calculated
306 CG – CL to evaluate whether loss of species richness due to land abandonment
307 outweighed the gain.

308 Results

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

315 The parameters of all models successfully converged ($\hat{R} < 1.1$). In posterior
316 predictive checking, no summary statistics of the observed data showed significant
317 divergence from the posterior predictive distributions generated from all estimated
318 models (Table S4). Model selection using the WBIC indicated that the model including
319 “abandoned or not” (WBIC = 3577.68) outperformed the model for “years since
320 abandonment” (WBIC = 3611.28), suggesting relatively immediate responses to land
321 abandonment. The Bayes factor for the former model against the latter was 3.89×10^{14} .
322 Among the 49 butterfly species analysed, 13 showed a significant negative response (i.e.
323 the upper 95% CI of the regression coefficient of “abandoned or not” was less than
324 zero), while 3 species showed a positive response (Table S5). *Lycaena phlaeas*, *Papilio*
325 *machaon* and *Papilio xuthus* exhibited the largest negative effect of land abandonment.
326 The three species that showed positive responses were *Limenitis camilla*, *Cyrestis*

327 *thyodamas* and *Graphium sarpedon*. Effects of land abandonment and temperature were
328 positively correlated (Fig. 2); Pearson's correlation coefficient between the effect of
329 land abandonment and annual mean temperature was 0.4 with a 95% CI of (0.07, 0.7).

330 There was a significant relationship between habitat types of species and
331 responses to land abandonment for four habitat types; species utilizing farmland,
332 grassland and built-up areas responded negatively. Although those utilizing forest
333 showed a significant difference from the other habitat types, the 95% CI of the average
334 response to land abandonment overlapped with zero (Fig. 3, Table S6).

335 Using a hierarchical model with ridge regularization, we obtained the
336 predictive model for the effect of land abandonment based on the habitat preferences of
337 each species (Table S7). Although the parameter uncertainty of each regression
338 coefficient obtained by ridge regression was large due to the correlation between habitat
339 preferences, the model retained discriminative ability for species which respond
340 negatively to land abandonment (Fig. S1). By applying this model, posterior means of
341 37 and 33 species were negative and positive, respectively, and the upper 95% CIs of 7
342 species were negative. Using the predicted values thus obtained, we drew maps of CL
343 (Fig. 4a) and CG (Fig.4b) of species throughout Japan's mainland. The geographic
344 distributions of loss and gain were similar on a coarse scale and the Pearson's
345 correlation coefficient was 0.55; specifically, larger values of both CL and CG were
346 found in inland central Kyushu, inland western Honshu, inland central Honshu, northern
347 Honshu and Hokkaido, while smaller values were found in high elevation areas.
348 However, CL outweighed CG in 99.6% of grid cells (358045 of 359429) and CL tended
349 to be higher in lowlands (Fig. 4c,d,e). Standard deviations of CL and CG and the

350 proportion of CG (Fig. S2a,b,d) were almost directly proportional to their posterior
351 means (Pearson's correlation coefficient $r = 0.86, 0.99$ and 0.96 , respectively). The
352 standard deviations of the proportion of CL and CG – CL (Fig. S2c,e) had stronger
353 positive correlations with CG ($r = 0.87$ and 0.95 , respectively) than did their posterior
354 means ($r = -0.96$ and 0.51), reflecting the large uncertainty of CG.

355 Of the Red List species, 10 were evaluated as victims of land abandonment and
356 4 were evaluated as beneficiaries. Distribution patterns of CL and CG for Red List
357 species of Japan are shown in Fig. 5a,b. The correlation between CL and CG was
358 weaker for Red List species than for all species ($r = 0.36$), and their spatial patterns
359 were different on a coarse scale. For instance, CL was small while CG was large in
360 northern Honshu. Conversely, CL was large but CG was small in eastern Hokkaido (Fig.
361 5c,d,e). Similar to the maps for all species, the standard deviations of the CL and CG
362 and the proportion of CG (Fig. S3a,b,d) were almost directly proportional to their
363 posterior means ($r = 0.95, 0.99$ and 0.92 , respectively), and the standard deviations of
364 the proportion of CL and CG – CL, rather than their posterior means, were correlated
365 with CG (Fig. S3c,e).

366 Discussion

367 As expected, the responses of butterflies to land abandonment were associated
368 with the climatic niches and habitat preferences of species. Through our approach in this
369 study, which compared community assemblages between inhabited and abandoned areas
370 using a standard survey protocol, we were able to estimate the effects of land
371 abandonment over a broad range of climatic condition. In combination with the

372 hierarchical modelling approach, we were able to draw nation-wide potential maps of the
373 loss and gain of species richness through land abandonment.

374 The legacies of the past climate and past land use can affect current functional
375 species compositions within regional species pools [54,55], and different functional
376 compositions among regions can result in different community-level responses to
377 current environmental changes [56]. Such a difference would also reflect the historical
378 background of organisms inhabiting seminatural environments in Japan. Grassland was
379 more abundant in the Pleistocene because the climate was colder and drier than at
380 present [32]. After the last glacial period, open lands created by human activity have
381 offered refugia for the Pleistocene relics [57], and such refugia are unlikely to be
382 sustainable if they are abandoned [58]. Our results also raise a conservational concern
383 that species negatively impacted by land abandonment will decline more due to climate
384 warming in the future, because the species susceptible to land abandonment tend to
385 prefer low temperatures (Fig. 2). This means that continuing land management in rural
386 areas would be an effective measure of climate change adaptation for biodiversity
387 conservation in Japan.

388 Habitat degradation for openland butterflies due to land abandonment occurred
389 quickly, whereas forest butterflies would require a longer period of time to experience a
390 positive effect. We suggest that land abandonment resulted in a decrease in the richness
391 of herbaceous plant species [23], leading to the loss or decline of host plants for open
392 habitat butterflies (grassland, crop field, and residential species). Indeed, we often
393 observed tall grasses, such as *Miscanthus sinensis*, as predominant species in abandoned
394 paddy, dry fields, and built-up area in uninhabited settlements. The monodominance of

395 wind-pollinated *Miscanthus* would decrease the abundance and diversity of
 396 nectar-producing flowers that are important for adult butterflies. In contrast, forest
 397 species tended to increase in response to land abandonment, although the proportion of
 398 such species was low. Development of old-growth forest in Japan requires
 399 approximately 150 years [59], and some tree species require more than a hundred years to
 400 recover [60]; accordingly, recovery of forest butterfly species that depend on such trees
 401 would also require very long time as well.

402 It should be noted that there was a positive correlation between losses and gains
 403 in butterfly richness both for all species and for Red List species due to land abandonment
 404 at the level of grid cells, indicating a trade-off between the benefits of active management
 405 of abandoned sites and letting succession proceed. As threatened butterflies in Japan
 406 include more grassland species than forest species, human intervention should be
 407 prioritized, in principle, to conserve such species, but deliberate decision-making is
 408 required for areas where the benefit of land abandonment is high. Our results indicate that
 409 conservation of butterflies by active management is desirable in lowland and eastern
 410 Hokkaido, where the loss of species that prefer abandoned landscapes would small under
 411 such management. Highly cost-effective areas for habitat management based on species
 412 ranges and habitat preferences need to be identified with high resolution, because
 413 maintaining secondary natural environments is generally labour-intensive [61]. The maps
 414 of gain and loss of butterfly diversity presented in this study did not incorporate spatial
 415 heterogeneity in land abandonment and instead assumed that all locations in Japan were
 416 abandoned. In actuality, the current human population density and the speed of decline is
 417 spatially heterogeneous, which will create heterogeneous land-use patterns in the future

418 [62,63]. However, our predictions would still be useful for evaluating biodiversity loss
419 and gain in rural landscapes because human population decline is expected to be severe in
420 most of those areas.

421 Here, we evaluated the risks and benefits of land abandonment using butterfly
422 occurrence data; however, it is also important to clarify how the abundance of larval host
423 plants and adult nectar plants changes over time after abandonment. Previous studies
424 have shown that many grassland species are still found even 10 years after abandonment
425 [64], indicating the presence of host and nectar plants during that period. In our study, the
426 effects of land abandonment did not show a clear increase over time, as the model with a
427 dichotomous variable (inhabited vs. abandoned settlements) outperformed the model
428 with a continuous variable (years since abandonment). As Japan has a monsoon climate
429 with relatively high temperatures and rainfall in comparison with Europe, vegetation
430 succession may proceed within a few years, resulting in a rapid response to land
431 abandonment. This suggests the need to restore habitats as soon as possible after
432 abandonment. The potential maps of the effect of land abandonment will contribute to
433 prioritizing habitat management plans in areas where settlement abandonment in the
434 immediate future and a large decrease in biodiversity after abandonment are expected.

435 A major contribution of our study was the ability to apply the estimated
436 relationship between habitat preferences and responses to land abandonment to butterfly
437 species that were not observed in the field survey. Potential drawbacks of our survey
438 design are sparse occurrence records and low completeness of species in the dataset due
439 to the small amount of survey effort per sample. Hierarchical modelling could overcome
440 the problems of sparse data, such as model unidentifiability, by introducing a hierarchy of

441 superspecies that stabilize the species-level estimates [65]. With this hierarchical
 442 structure, we could predict the responses of butterfly communities even when not all
 443 species were detected in the field survey. The utility of such a hierarchical modelling
 444 approach is widely recognized [66], but there are some caveats, as responses of habitat
 445 generalists may be difficult to predict. To resolve this problem, models incorporating
 446 responses of host plants to land abandonment and resultant butterfly responses should be
 447 explicitly constructed, as has been done for climate change prediction models [67].

448 Our hierarchical modelling approach also allowed us to evaluate the correlation
 449 between susceptibility to climate warming and land abandonment, which could provide
 450 important information for the management of semi-natural habitats in order to ensure
 451 biodiversity under climate change. However, we should be cautious about extrapolating
 452 our results to other of in the world with different biogeographical factors. For example,
 453 some grassland butterflies in Europe have expanded their range northward in response to
 454 the warming climate [68], while such a range expansion is not expected in Japan. Such a
 455 difference would arise from the different latitudes of stable grassland biomes. Grassland
 456 butterflies in Japan have high commonality with Eurasian temperate steppe fauna ranging
 457 from eastern Eurasia to Mediterranean region, and seminatural grassland in Japan can be
 458 thought as the extrazonal remnant of the temperate stable grassland [29]. Interestingly,
 459 the climatic limit of eastern Eurasian steppe is much cooler than the Mediterranean region
 460 [30]. This is due to the difference in relative importance of coldness and dryness for the
 461 formation of stable grassland; in eastern Eurasia, the rainy season occurs in the growing
 462 season of plants and winter frost plays a more important role than in the Mediterranean
 463 steppe. Europe and Japan are respectively located in the northern and southern regions of

464 the outer part of the Eurasian temperate steppe. Thus, a northward biome shift due to
465 climate warming can help grassland butterflies in Europe, but not in Japan. A
466 continental-scale comparative study of the responses of grassland butterflies to climate
467 warming is a potential topic for future research to test the hypothesis.

468 Although we focused on the effect of land abandonment in this study, the
469 hierarchical modelling approach would be also applicable to predicting the response of
470 biological community to climate change if climatic niche information of species [69] is
471 available. A database of climatic niche information of butterflies in Japan has not yet been
472 developed due to the difficulty in collecting the distribution data of butterflies which are
473 widespread in Asia, and this should be a topic for further research.

474 In conclusion, a hierarchical modelling approach that incorporates the
475 relationship between the habitat preferences of species and their responses to land
476 abandonment was useful for scaling up the results of comparative field studies to a
477 macro-scale evaluation of species losses and gains due to land abandonment. Land
478 abandonment had both positive and negative effects on different functional groups of
479 butterflies in Japan, and our approach could be used to identify areas exhibiting high
480 species losses relative to gains after land abandonment. We believe this approach is
481 promising for large-scale and comprehensive biodiversity assessments regarding the risks
482 and benefits of land abandonment, which are urgently needed in view of ongoing
483 depopulation in developed countries.

484 Ethics

485 Our field survey was conducted from public roads and rural paths, and no permission
486 was required in compliance with Japanese law. All information of site locations is

coarse enough to protect landowners' privacy. To avoid a negative impact on conservation due to specimen collection, we have not released specific records of endangered species.

Data accessibility

The datasets, program codes and model predictions shown in Fig.4, 5 and Supplementary Fig. S2, 3 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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References

1. Fischer J, Hartel T, Kuemmerle T. 2012 Conservation policy in traditional farming landscapes. *Conserv. Lett.* **5**, 167–175. (doi:10.1111/j.1755-263X.2012.00227.x)
2. Benayas JMR, Martins A, Nicolau JM, Schulz JJ. 2007 Abandonment of agricultural land: an overview of drivers and consequences. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* **2**, 1–14.
3. Fukamachi K, Oku H, Nakashizuka T. 2001 The change of a satoyama landscape and its causality in Kamiseya, Kyoto Prefecture, Japan between 1970 and 1995. *Landsc. Ecol.* **16**, 703–717.
4. Schmitt T, Rákossy L. 2007 Changes of traditional agrarian landscapes and their conservation implications: A case study of butterflies in Romania. *Divers. Distrib.* **13**, 855–862. (doi:10.1111/j.1472-4642.2007.00347.x)
5. Henle K *et al.* 2008 Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agric. Ecosyst. Environ.* **124**, 60–71.
6. Corlett RT. 2016 Restoration, Reintroduction, and Rewilding in a Changing World. *Trends Ecol. Evol.* **31**, 453–462. (doi:10.1016/j.tree.2016.02.017)
7. Svenning J-C *et al.* 2016 Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci.* **113**, 898–906. (doi:10.1073/pnas.1502556112)
8. Scozzafava S, De Sanctis A. 2006 Exploring the effects of land abandonment on habitat structures and on habitat suitability for three passerine species in a highland area of Central Italy. *Landsc. Urban Plan.* **75**, 23–33.

- 533 (doi:10.1016/j.landurbplan.2004.10.006)
- 534 9. Herrando S, Brotons L, Anton M, Paramo F, Villero D, Titeux N, Quesada J,
535 Stefamescu C. 2016 Assessing impacts of land abandonment on Mediterranean
536 biodiversity using indicators based on bird and butterfly monitoring data. *Environ.*
537 *Conserv. FirstView*, 1–10. (doi:doi:10.1017/S0376892915000260)
- 538 10. Randin CF, Dirnböck T, Dullinger S, Zimmermann NE, Zappa M, Guisan A. 2006
539 Are niche-based species distribution models transferable in space? *J. Biogeogr.* **33**,
540 1689–1703. (doi:10.1111/j.1365-2699.2006.01466.x)
- 541 11. Wenger SJ, Olden JD. 2012 Assessing transferability of ecological models: An
542 underappreciated aspect of statistical validation. *Methods Ecol. Evol.* **3**, 260–267.
543 (doi:10.1111/j.2041-210X.2011.00170.x)
- 544 12. Queiroz C, Beilin R, Folke C, Lindborg R. 2014 Farmland abandonment: Threat or
545 opportunity for biodiversity conservation? A global review. *Front. Ecol. Environ.*
546 **12**, 288–296. (doi:10.1890/120348)
- 547 13. Koshida C, Katayama N. 2018 Meta-analysis of the effects of rice-field
548 abandonment on biodiversity in Japan. *Conserv. Biol.* **32**, 1392–1402.
549 (doi:10.1111/cobi.13156)
- 550 14. Stewart G. 2010 Meta-analysis in applied ecology. *Biol. Lett.* **6**, 78–81.
551 (doi:10.1098/rsbl.2009.0546)
- 552 15. Fukasawa K, Mishima Y, Yoshioka A, Kumada N, Totsu K, Osawa T. 2016
553 Mammal assemblages recorded by camera traps inside and outside the evacuation
554 zone of the Fukushima Daiichi Nuclear Power Plant accident. *Ecol. Res.* **31**, 493.
555 (doi:10.1007/s11284-016-1366-7)

- 556 16. Dyer C, Jones R. 2010 *Deserted Villages Revisited*. University of Hertfordshire
557 Press. <https://books.google.co.jp/books?id=JLcfFqRel3MC>.
- 558 17. Webb RH, Wilshire HG. 1980 Recovery of soils and vegetation in a Mojave desert
559 ghost town, Nevada, U.S.A. *J. Arid Environ.* **3**, 291–303.
560 (doi:10.1016/s0140-1963(18)31634-3)
- 561 18. Ohwaki A, Ogawa H, Taketani K, Tomisawa A. 2014 Butterfly responses to
562 cultivated field abandonment are related with ecological traits in a temperate
563 Japanese agricultural landscape. *Landsc. Urban Plan.* **125**, 174–182.
564 (doi:10.1016/j.landurbplan.2014.02.024)
- 565 19. Slancarova J, Bartonova A, Zapletal M, Kotilinek M, Fric ZF, Micevski N, Kati V,
566 Konvicka M. 2016 Life history traits reflect changes in mediterranean butterfly
567 communities due to forest encroachment. *PLoS One* **11**, 1–18.
568 (doi:10.1371/journal.pone.0152026)
- 569 20. Ogura J. 2006 The transition of grassland area in Japan. *J. Kyoto Seika Univ.* **30**,
570 159–172.
- 571 21. Ministry of Agriculture, Forestry and Fisheries. 2016 On the present condition of
572 abandoned farmland and the countermeasures.
573 http://www.maff.go.jp/j/nousin/tikei/houkiti/pdf/2804_genjo.pdf (accessed on 16
574 February 2016).
- 575 22. Ministry of Land, Infrastructure, Transport and Tourism. 2014 On the estimation
576 of future population in Japan by 1 km² grid.
577 http://www.mlit.go.jp/kokudoseisaku/kokudoseisaku_tk3_000044.html (accessed
578 on 13 June 2017).

- 579 23. Uchida K, Ushimaru A. 2014 Biodiversity declines due to abandonment and
580 intensification of agricultural lands: Patterns and mechanisms. *Ecol. Monogr.* **84**,
581 637–658. (doi:10.1890/13-2170.1)
- 582 24. Uchida K, Ushimaru A. 2015 Land abandonment and intensification diminish
583 spatial and temporal α -diversity of grassland plants and herbivorous insects
584 within paddy terraces. *J. Appl. Ecol.* **52**, 1033–1043.
585 (doi:10.1111/1365-2664.12443)
- 586 25. Uchida K, Takahashi S, Shinohara T, Ushimaru A. 2016 Threatened herbivorous
587 insects maintained by long-term traditional management practices in semi-natural
588 grasslands. *Agric. Ecosyst. Environ.* **221**, 156–162.
589 (doi:10.1016/j.agee.2016.01.036)
- 590 26. Uchida K, Koyanagi TF, Matsumura T, Koyama A. 2018 Patterns of plant
591 diversity loss and species turnover resulting from land abandonment and
592 intensification in semi-natural grasslands. *J. Environ. Manage.* **218**, 622–629.
593 (doi:10.1016/j.jenvman.2018.04.059)
- 594 27. Koyanagi TF, Furukawa T. 2013 Nation-wide agrarian depopulation threatens
595 semi-natural grassland species in Japan: Sub-national application of the Red List
596 Index. *Biol. Conserv.* **167**, 1–8. (doi:10.1016/j.biocon.2013.07.012)
- 597 28. Nakamura Y. 2011 Conservation of butterflies in Japan: Status, actions and
598 strategy. *J. Insect Conserv.* **15**, 5–22. (doi:10.1007/s10841-010-9299-x)
- 599 29. Ohwaki A. 2018 How should we view temperate semi-natural grasslands? Insights
600 from butterflies in Japan. *Glob. Ecol. Conserv.* **16**.
601 (doi:10.1016/J.GECCO.2018.E00482)

- 602 30. Wesche K, Ambarlı D, Kamp J, Török P, Treiber J, Dengler J. 2016 The
603 Palaearctic steppe biome: a new synthesis. *Biodivers. Conserv.* **25**, 2197–2231.
604 (doi:10.1007/s10531-016-1214-7)
- 605 31. Hiura I. 1971 An analysis of butterfly fauna of Japan from the standpoint of
606 historical biogeography. *Spec. Bull. Lepidopterol. Soc. Japan* **5**, 73–88.
- 607 32. Yamaura Y *et al.* 2019 Genomic reconstruction of 100 000-year grassland history
608 in a forested country: population dynamics of specialist forbs. *Biol. Lett.* **15**,
609 20180577. (doi:10.1098/rsbl.2018.0577)
- 610 33. Japan Butterfly Conservation Society. 2012 *Field guide of butterflies in Japan*.
611 Tokyo: Seibundo Shinko-sha.
- 612 34. Japan Meteorological Agency. 2021 Climatological Normals (1991–2020)
613 [Heinenchi Download].
614 <https://www.data.jma.go.jp/obd/stats/data/mdrr/normal/index.html> (accessed on
615 20 February 2021).
- 616 35. Asahara A. 2010 *Landscape of abandoned and depopulated settlements 4*.
617 Saitama: Heyaneko.
- 618 36. Asahara A. 2011 *Landscape of abandoned and depopulated settlements 5*.
619 Saitama: Heyaneko.
- 620 37. Murakage Y. 2009 Murakage Yataro’s travelogue of the villages [Murakage
621 Yataro no Shuraku Kikou]. <http://www.aikis.or.jp/~kage-kan/> (accessed on 27
622 February 2020).
- 623 38. Ryan SF *et al.* 2019 Global invasion history of the agricultural pest butterfly *Pieris*
624 *rapae* revealed with genomics and citizen science. *Proc. Natl. Acad. Sci. U. S. A.*

- 625 **116**, 20015–20024. (doi:10.1073/pnas.1907492116)
- 626 39. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White
627 J-SS. 2009 Generalized linear mixed models: a practical guide for ecology and
628 evolution. *Trends Ecol. Evol.* **24**, 127–135.
629 (doi:http://dx.doi.org/10.1016/j.tree.2008.10.008)
- 630 40. Japan Meteorological Business Support Center. 2002 *Mesh climatic data of Japan*.
631 Japan Meteorological Agency.
- 632 41. Schielzeth H *et al.* 2020 Robustness of linear mixed-effects models to violations of
633 distributional assumptions. *Methods Ecol. Evol.* **11**, 1141–1152.
634 (doi:10.1111/2041-210X.13434)
- 635 42. Gelman A. 2006 Prior distributions for variance parameters in hierarchical models.
636 *Bayesian Anal.* **1**, 515–534. (doi:10.1214/06-BA117A)
- 637 43. Van Dongen S. 2006 Prior specification in Bayesian statistics: Three cautionary
638 tales. *J. Theor. Biol.* **242**, 90–100. (doi:http://doi.org/10.1016/j.jtbi.2006.02.002)
- 639 44. Stan Development Team. 2016 RStan: the R interface to Stan. R package version
640 2.14.1.
- 641 45. Gelman A, Rubin DB. 1992 Inference from Iterative Simulation Using Multiple
642 Sequences. *Stat. Sci.* **7**, 457–472. (doi:10.1214/ss/1177011136)
- 643 46. Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., & Rubin DB.
644 2013 *Bayesian Data Analysis*. third edit. New York: Chapman and Hall/CRC.
645 (doi:10.1201/b16018)
- 646 47. Meng X-L. 1994 Posterior Predictive *p*-Values. *Ann. Stat.* **22**, 1142–1160.
647 (doi:10.1214/AOS/1176325622)

- 648 48. Watanabe S. 2013 A widely applicable Bayesian information criterion. *J. Mach.*
649 *Learn. Res.* **14**, 867–897.
- 650 49. Pollock LJ, Morris WK, Vesk PA. 2012 The role of functional traits in species
651 distributions revealed through a hierarchical model. *Ecography (Cop.)*. **35**,
652 716–725. (doi:10.1111/j.1600-0587.2011.07085.x)
- 653 50. Öckinger E *et al.* 2010 Life-history traits predict species responses to habitat area
654 and isolation: A cross-continental synthesis. *Ecol. Lett.* **13**, 969–979.
655 (doi:10.1111/j.1461-0248.2010.01487.x)
- 656 51. Hooten MB, Hobbs NT. 2015 A guide to Bayesian model selection for ecologists.
657 *Ecol. Monogr.* **85**, 3–28. (doi:10.1890/14-0661.1)
- 658 52. Kasada M, Matsuba M, Miyashita T. 2017 Human interest meets biodiversity
659 hotspots: A new systematic approach for urban ecosystem conservation. *PLoS One*
660 **12**, e0172670. (doi:10.1371/journal.pone.0172670)
- 661 53. Ministry of Environment. 2019 Red list of Japan 2019.
662 <https://www.env.go.jp/press/files/jp/110615.pdf> (accessed on 7 September 2021).
- 663 54. Blonder B *et al.* 2018 Late Quaternary climate legacies in contemporary plant
664 functional composition. *Glob. Chang. Biol.* **24**, 4827–4840.
665 (doi:10.1111/gcb.14375)
- 666 55. Perring MP, De Frenne P, Baeten L, Maes SL, Depauw L, Blondeel H, Carón MM,
667 Verheyen K. 2016 Global environmental change effects on ecosystems: the
668 importance of land-use legacies. *Glob. Chang. Biol.* **22**, 1361–1371.
669 (doi:10.1111/gcb.13146)
- 670 56. Svenning J-C, Normand S, Skov F. 2009 Plio-Pleistocene climate change and

- 671 geographic heterogeneity in plant diversity–environment relationships. *Ecography*
672 (*Cop.*). **32**, 13–21. (doi:10.1111/j.1600-0587.2008.05732.x)
- 673 57. Ushimaru A, Uchida K, Suka T. 2018 Grassland biodiversity in Japan: threats,
674 management and conservation. In *Grasslands of the world: diversity, management*
675 *and conservation* (eds VR Squires, J Dengler, L Hua, H Feng), pp. 197–218. Boca
676 Raton: CRC press. (doi:10.1201/9781315156125)
- 677 58. Fukasawa K, Akasaka T. 2019 Long-lasting effects of historical land use on the
678 current distribution of mammals revealed by ecological and archaeological
679 patterns. *Sci. Rep.* **9**, 1–11. (doi:10.1038/s41598-019-46809-1)
- 680 59. Yamaura Y, Lindenmayer D, Yamada Y, Gong H, Matsuura T, Mitsuda Y, Masaki
681 T. 2020 A spatially explicit empirical model of structural development processes
682 in natural forests based on climate and topography. *Conserv. Biol.* **34**, 194–206.
683 (doi:https://doi.org/10.1111/cobi.13370)
- 684 60. Ohtani S, Koike F, Townsend P. 2005 Implications of 19th century landscape
685 patterns for the recovery of *Fagus crenata* forests. *Appl. Veg. Sci.* **8**, 125–132.
686 (doi:10.1658/1402-2001(2005)008[0125:IOTCLP]2.0.CO;2)
- 687 61. Takeuchi K, Brown RD, Washitani I, Tsunekawa A, Yokohari M. 2012 *Satoyama:*
688 *the traditional rural landscape of Japan*. Springer Science & Business Media.
- 689 62. Ohashi H, Fukasawa K, Ariga T, Matsui T, Hijioka Y. 2019 High-resolution
690 national land use scenarios under a shrinking population in Japan. *Trans. GIS* **23**,
691 786–804. (doi:10.1111/TGIS.12525)
- 692 63. Fujita T, Ariga T, Ohashi H, Hijioka Y, Fukasawa K. 2019 Assessing the potential
693 impacts of climate and population change on land-use changes projected to 2100 in

- 694 Japan. *Clim. Res.* **79**, 139–149. (doi:10.3354/CR01580)
- 695 64. Krauss J *et al.* 2010 Habitat fragmentation causes immediate and time-delayed
696 biodiversity loss at different trophic levels. *Ecol. Lett.* **13**, 597–605.
697 (doi:10.1111/j.1461-0248.2010.01457.x)
- 698 65. Ovaskainen O, Tikhonov G, Norberg A, Blanchet FG, Duan L, Dunson D, Roslin
699 T, Abrego N. 2017 How to make more out of community data? A conceptual
700 framework and its implementation as models and software. *Ecol. Lett.* **20**, 561–576.
701 (doi:10.1111/ELE.12757)
- 702 66. Webb CT, Hoeting JA, Ames GM, Pyne MI, LeRoy Poff N. 2010 A structured and
703 dynamic framework to advance traits-based theory and prediction in ecology. *Ecol.*
704 *Lett.* **13**, 267–283. (doi:10.1111/j.1461-0248.2010.01444.x)
- 705 67. Araújo MB, Luoto M. 2007 The importance of biotic interactions for modelling
706 species distributions under climate change. *Glob. Ecol. Biogeogr.* **16**, 743–753.
707 (doi:10.1111/j.1466-8238.2007.00359.x)
- 708 68. Kudrna O, Harpke A, Lux K, Pennerstorfer J, Schweiger O, Settele J, Wiemers M.
709 2011 *Distribution Atlas of Butterflies in Europe*. Halle, Germany: Gesellschaft für
710 Schmetterlingsschutz.
- 711 69. Schweiger O, Harpke A, Wiemers M, Settele J. 2014 CLIMBER: Climatic niche
712 characteristics of the butterflies in Europe. *Zookeys* **367**, 65.
713 (doi:10.3897/ZOOKEYS.367.6185)

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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 grey 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. On the x axis, 0 indicates that the species does not utilize the habitat type and 1 indicates that it does. Gray dots represent coefficients of abandonment (β_{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 α_1 in eqn. 2 did not overlap 0) were shown.

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

Fig. 4 Continued.

Fig. 4 *Continued.*

(e)

Fig. 5 Maps of cumulative loss (CL, a), cumulative gain (CG, b), the proportions of CL (c) and CG (d) and the difference between CG and CL (CG - CL, e) in butterfly species richness due to land abandonment for Red List species. The boxed graphs are hexagonal binning plots showing their relationship with elevation.

Fig. 5 Continued.

Fig. 5 Continued.