Species abundance in floor vegetation of managed coppice and abandoned forest

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ABSTRACT

The species abundance in floor vegetation was compared among three developmental stages (early, middle and late) of managed coppices and two types of abandoned forest (broadleaved and pine). The studied coppices, which mainly consisted of *Quercus acutissima*, were maintained to produce charcoal, and had been cut periodically about once every decade. The abandoned forests appeared to have been left for at least 30 years. A hierarchical Bayesian model was constructed to estimate the probability distributions of presence for each species and each condition (forest type, management, stand age, and floor cleaning). The results showed that species abundance was higher in the managed coppices than in the abandoned forests and higher before floor cleaning (early and middle stages) than after clearing (late stages) within the coppices. In the coppices, a number of deciduous shrub, grass and herbaceous species were highly likely to be present while evergreen understory and shrub species were likely to be present in the abandoned forests. A simulation using the results of the model was conducted to estimate which management plan would maintain the abundance of floor species in coppices. The simulation showed that keeping a mosaic structure consisting of at least two levels of stand age would maintain a stable and rich abundance of species.

1. Introduction

Japanese rural landscape known as 'satoyama' is reevaluated from the viewpoint of sustainable land-use as holding rich species diversity under interactions between human and nature (Fukamachi et al., 2001; Washitani, 2001; Takeuchi, 2003, 2010; Kobori and Primack, 2003; Katoh et al., 2009). *Satoyama* is an ambiguous word and defined in many different ways (Takeuchi, 2003, 2010; Kobori and Primack, 2003; Katoh et al., 2009). Based on Takeuchi (2010), it narrowly denotes secondary woodlands and grasslands near human settlements used as coppices and meadows, while more broadly, it encompasses farm fields, paddies, irrigation canals and ponds, and settlements. The term *satoyama landscape* has been used to distinguish the broader meaning from the narrower one. The area comprising *satoyama landscape* is estimated to be approximately 60,000–90,000 km^2, or 20% of Japan's land mass (Tsunekawa, 2003). Similar traditional landscape or land-use systems are found in Korea, China, Indonesia, Spain and southern Africa (Takeuchi, 2010). Park et al. (2006) studied Korean village groves called *mae-ulsoop* or *bibosoop*, that provide habitats for cavity nesting birds.

Kumar and Takeuchi (2009) compared agroforestry in western India and *satoyama* in Japan. Rackham (1986) described the history of sustainably used English woodland. Bélair et al. (2010) compiled examples of sustainable land use systems worldwide. Mason and MacDonald (2002) studied the responses of ground flora to coppice management, and discussed which management system was preferable.

Typical *satoyama* landscapes comprise various components as described above, often including coppices (Washitani, 2001), from which it is possible to produce wood fuel or charcoal, or crop sprouts as fertilizer. Litter on the coppice floor also often serves as fertilizer. This usage of coppice is presumed to function as an intermediate disturbance (Connell, 1978), and to promote the rich species diversity of *satoyama* (Washitani, 2001; Katoh et al., 2009).

However, *satoyama* has not always been sustainably maintained. It is known that overuse impaired the sustainability in many rural areas during the 19th century (Takeuchi, 2010). Conversely, nowadays, abandonment has affected the biodiversity of the *satoyama* landscape (Washitani, 2001; Ichikawa et al., 2006). As the use of woody fuel and charcoal was replaced by the use of fossil fuels in the 1960s and 1970s, almost all coppices and pine forests were abandoned, and the latter were severely damaged by pine wilt disease. Nowadays, management activities are very rarely sustained in Japan despite traditional coppice management, which has allowed the growth of various light-demand plants on the forest floor (Nakagawa, 2003). Evergreen broadleaved shrub

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or tree species have colonized the abandoned forests, which has exacerbated the light condition of the forest floor. Changes in environment quality, declines in species and changes in habitat status due to reduced or discontinued human intervention is known as "the second crisis" (Japanese Government, 2007). The first crisis refers to these types of changes as a result of reduction or loss of habitat from human activities such as overuse and development, while the third crisis pertains to disturbances from artificially introduced factors, such as alien species.

Few studies have shown what factors contributed to species diversity in coppice woodlands of *satoyama* landscapes based on actual data because almost all traditional coppices were abandoned as fossil fuels replaced woody fuel and charcoal.

In the area between Ôsaka and Hyôgo Prefectures, in western Japan, charcoal has been produced since the 15th century (Hattori et al., 2005), and coppices are still maintained to produce the necessary wood. Itô et al. (2010) showed that the managed coppices in these areas had more abundant floor species than those of abandoned forests around the coppices.

In this paper, we will discuss these points: (1) Why the managed coppice had more abundant floor species. (2) Which management plan can effectively maintain the abundance of floor species.

2. Methods

2.1. Study site

The study site was located in Inagawa Town, Hyôgo Prefecture, in western Japan (34.927°N, 135.397°E). The altitude of the study site ranged from 200 to 300 m a.s.l. Some of the areas of the study site were maintained coppices, mainly consisting of *Quercus acutissima* and others were covered in abandoned forest. The coppice was cleared every decade or so to obtain charcoal materials used in the Japanese tea ceremony. Clear cutting took place there in winter (mainly January and February). The area cut at a time was, at most, a few hectares. Not only *Q. acutissima* stems but also all stems of other species and floor vegetation were cleared.

There were two types of abandoned forest; one derived from broadleaved forest that mainly comprised deciduous oak (*Quercus serrata*), and the other derived from pine (*Pinus densiflora*) while most pine trees died out due to pine wilt disease after the 1970s or 1980s. Both seemed to have been left unmanaged for at least 30 years, as suggested by aerial photographs and the number of tree rings.

2.2. Data collection

In 2006, we set up 12 quadrats 10 × 10 m in size in the study site and added an additional three identical quadrats in 2007 (Table 1). They contained six coppices (early stage: CE1–CE2, middle stage: CM1–CM2, late stage: CL1–CL2), three abandoned broadleaved forests (AB1–AB3), and six abandoned pine forests (AP1–AP6). The CL quadrats had floor cleaning in 2005; grasses, herbs and shrubs on the floor were cut. The basal areas of the coppice (CE–CL) varied from 0.30 to 13.06 m^2 ha^{-1}, while those of AB ranged from 23.94 to 42.59 m^2 ha^{-1} and those of AP from 42.82 m^2 ha^{-1} (Itô et al., 2010). *Q. acutissima* was dominant in the managed coppices (CE–CL) while *Q. serrata* was dominant in the abandoned broadleaved forests (AB1–AB3). In the abandoned pine forests, *Ilex pedunculosa* (AP1, AP3), *Quercus glauca* (AP2), *P. densiflora* (AP4) and *Clethra barbinervis* (AP5, AP6) were dominant.

Each quadrat was divided into four squares (5 × 5 m), whereupon two diagonal squares were chosen for each quadrat as subquadrats to observe the floor vegetation; total subquadrats numbered 24 in 2006 and 30 in 2007 and 2008, respectively. The

subquadrats in a quadrat were treated as a replication. Observation was conducted three times (spring, summer and autumn) yearly, from 2006 to 2008. We listed the vascular plant species observed on the floor of each subquadrat (including seedlings and saplings of woody plants less than 1.3 m in height). The presence/absence data for the three observations during the year were compiled into a yearly record.

We observed 181 species throughout the observation period. The entire list is shown in the report by Itô et al. (2010). In CE quadrats, 39–56 vascular plant species were observed on the floor, 43–63 species were in CM and 34–56 species were in CL. Conversely, only 12–29 and 7–12 floor species were found in AB and AP, respectively (Itô et al., 2010). We used 135 of 181 species which appeared at least twice during the entire observation (species that appeared in two years or in two subquadrats were included) for the subsequent analysis to reduce the effect of rarely observed species on the performance of the calculation.

2.3. Statistical analysis

We constructed a hierarchical Bayesian model to explain the presence/absence of species by environmental factors. There were 11340 records in total: 12 quadrats × 2 subquadrats × 135 species (2006) + 15 quadrats × 2 subquadrats × 135 species × 2 years (2007 and 2008). The presence/absence of species in the i-th record (a_i) was stochastically determined with the probability of presence (p_i).

$$a_i \sim \text{Bernoulli}(p_i)$$

The parameter p_i was deterministically defined as follows.

$$\text{logit}(p_i) = \beta + \varepsilon_{Ss_i} + \varepsilon_{Qq_i} + \beta_7 y_{7i} + \beta_8 y_{8i} + (\beta_T + \varepsilon_{Ts_i})t_i + (\beta_M + \varepsilon_{Ms_i})m_i + (\beta_G + \varepsilon_{Gs_i})m_i(1 - c_i)(5 - g_i) + (\beta_C + \varepsilon_{Cs_i})m_i c_i$$

where β denoted the intercept, ε_{Ss_i} denoted the random effect made by differences of species on the intercept, s_i denoted the species of the i-th record, ε_{Qq_i} denoted the random effect which differences of the quadrat made on the intercept, q_i denoted the quadrat of the i-th record, and the prior distributions of the random effects were assumed to be normally distributed with mean = 0. The hyperparameters σ_S and σ_Q constrained the probability distributions of ε_S and ε_Q, respectively.

$$\varepsilon_{Ss_i} \sim N(0, \sigma_S^2), \quad s_i = 1, \ldots, N_S$$

$$\varepsilon_{Qq_i} \sim N(0, \sigma_Q^2), \quad q_i = 1, \ldots, N_Q$$

The parameters β_7 and β_8 were coefficients of y_{7i} and y_{8i}, respectively, which denoted i-th year of record (2006: $y_{7i} = 0$ and $y_{8i} = 0$, 2007: $y_{7i} = 1$ and $y_{8i} = 0$, 2008: $y_{7i} = 0$ and $y_{8i} = 1$). We modeled the yearly changes as fixed effects because the level of the variable (=3) was small. β_T was a coefficient of t_i, which denoted the forest type of i-th record (pine forest: $t_i = 0$, broadleaved or coppice: $t_i = 1$). β_M was a coefficient of m_i, which denoted the presence/absence of management (abandoned: $m_i = 0$, managed: $m_i = 1$). β_G was a coefficient of g_i, which denoted the stand age (the year clear cutting was done: $g_i = 0$). Because we supposed that floor vegetation was rather temporally stable from floor cleaning until clear cutting, the parameter g was valid only before floor cleaning, which was presumed to be done at 5-year-old stand, so the term $(\beta_G + \varepsilon_{Gs_i})m_i(1 - c_i)(5 - g_i)$ would be 0 if the stand was unmanaged ($m_i = 0$), the stand age was 5 ($g_i = 5$), or $c_i = 1$, where c_i denoted the floor cleaning status (before clearing: $c_i = 0$, after clearing: $c_i = 1$). The parameter β_C was a coefficient of c_i.

The parameters ε_{Ts_i}, ε_{Ms_i}, ε_{Gs_i} and ε_{Cs_i} denoted the random effects of species si on the coefficients β_T, β_M, β_G and β_C, respectively. The prior distributions of these random effects were also assumed to be

Table 1
Quadrats in the study site. The basal areas were measured in the first year of observation.

Quadrat	Stand type	Management	Observation term	Basal area (m² ha⁻¹)
CE1	Coppice (0–1 years)	Managed	2007–2008	0.30
CE2	Coppice (0–1 years)	Managed	2007–2008	0.38
CM1	Coppice (1–3 years)	Managed	2006–2008	2.82
CM2	Coppice (1–3 years)	Managed	2006–2008	4.50
CL1	Coppice (6–8 years)	Managed	2006–2008	10.90
CL2	Coppice (6–8 years)	Managed	2006–2008	13.06
AB1	Broadleaved	Abandoned	2006–2008	34.75
AB2	Broadleaved	Abandoned	2006–2008	23.94
AB3	Broadleaved	Abandoned	2007–2008	42.59
AP1	Pine	Abandoned	2006–2008	42.82
AP2	Pine	Abandoned	2006–2008	25.18
AP3	Pine	Abandoned	2006–2008	36.47
AP4	Pine	Abandoned	2006–2008	36.59
AP5	Pine	Abandoned	2006–2008	39.89
AP6	Pine	Abandoned	2006–2008	35.10

normally distributed with mean = 0. The hyperparameters σ_T, σ_M, σ_G and σ_C constrained the probability distributions of ε_T, ε_M, ε_G and ε_C, respectively.

$$\varepsilon_{Ts_i} \sim N(0, \sigma_T^2)$$

$$\varepsilon_{Ms_i} \sim N(0, \sigma_M^2)$$

$$\varepsilon_{Gs_i} \sim N(0, \sigma_G^2)$$

$$\varepsilon_{Cs_i} \sim N(0, \sigma_C^2)$$

All the variables and parameters are listed in Tables 2 and 3. While the parameters ε_T, ε_M, ε_G and ε_C were random effects, we evaluated these values to examine which species were strongly affected by factors t, m, g and c, respectively.

The posterior distributions of the parameters were estimated using the Markov Chain Monte Carlo (MCMC) method. We assigned non-informative prior distributions to the parameters: $N(0, 10^4)$ for the coefficients and the intercept, and $1/Gamma$ $(100, 100)$ for the variances. The posterior distributions were estimated from the samples taken from the three chains of 40,000 iterations with 40 intervals after 10,000 burn-ins, so that the sample size was 3000 ($3 \times 40,000/40$). The BUGS code used in the analysis is included in the electronic Supplementary data; the calculation was performed using JAGS version 2.2.0 (Plummer, 2010).

2.4. Simulation

We conducted a simple Monte Carlo simulation to predict which management would successfully retain species abundance on the coppice floor. We presumed 10 stands, each of which incorporated a quadrat sized 5×5 m. The species abundance in the stand was represented by the number of species recorded in the quadrat. The procedure was as follows: (1) a set of parameters was chosen from the samples which had been obtained in the cal-

Table 2
Variables in the model.

| Variable	Description
a_i	Presence/absence of the species in the i-th record
p_i	Probability of presence in the i-th record
t_i	Forest type in the i-th record
m_i	Presence/absence of the management in the i-th record
g_i	Stand age in the i-th record
c_i	Before/after floor cleaning
y_{7i}	Dummy variable denoting the observation year
y_{8i}	Dummy variable denoting the observation year

Table 3
Parameters in the model.

Parameter	Description
β	Intercept
β_7	Coefficient of y_7
β_8	Coefficient of y_8
β_T	Coefficient of t
β_M	Coefficient of m
β_G	Coefficient of g
β_C	Coefficient of c
ε_S	Random effect of the species on the intercept
ε_Q	Random effect of the quadrat on the intercept
ε_T	Random effect of the species on the coefficient of t
ε_M	Random effect of the species on the coefficient of m
ε_G	Random effect of the species on the coefficient of g
ε_C	Random effect of the species on the coefficient of c
σ_S	Standard deviation of ε_S
σ_Q	Standard deviation of ε_Q
σ_T	Standard deviation of ε_T
σ_M	Standard deviation of ε_M
σ_G	Standard deviation of ε_G
σ_C	Standard deviation of ε_C

culation of MCMC to estimate the parameters. (2) The presence/absence was stochastically determined per species and per quadrat using the set of parameters; if $R \geqslant P$, the species would be present in the quadrat, and if $R < P$, the species would be absent in the quadrat, where R was an uniform random number ($0 \leqslant R \leqslant 1$) and P was the probability of presence of the species in the quadrat. (3) The number of present species was totaled per each quadrat; the number of species that were determined as present ($R \geqslant P$) in the quadrat was calculated. Steps (2) and (3) were repeated for the definite years. A decade was presumed as the cycle from sprouting to clear cutting for the managed coppices. For simplicity, we did not incorporate yearly fluctuations in the probability of presence; the parameters β_7 and β_8 were set to 0 in the simulation.

We presumed three scenarios with differing cutting patterns: (A) 1 of 10 stands were cleared each year, (B) 10 of 10 stands were simultaneously cleared every decade, and (C) 5 of 10 stands were cleared every 5 years. An additional scenario which corresponded to heavy use was presumed: (D) 10 of 10 stands were cleared each year. Each stand of two types of abandoned forest was also simulated: (E) abandoned broadleaved forest left unmanaged, and (F) abandoned pine forest left unmanaged.

We simulated changes of species abundance over 20 years in the simulation model (Fig. 1). The mean and the 95% quantile of the number of species that appeared in all 10 quadrats each year were calculated with 2000 iterations. The simulation was over-simplistic to estimate the real changes in the stands, but allowed rough predictions.
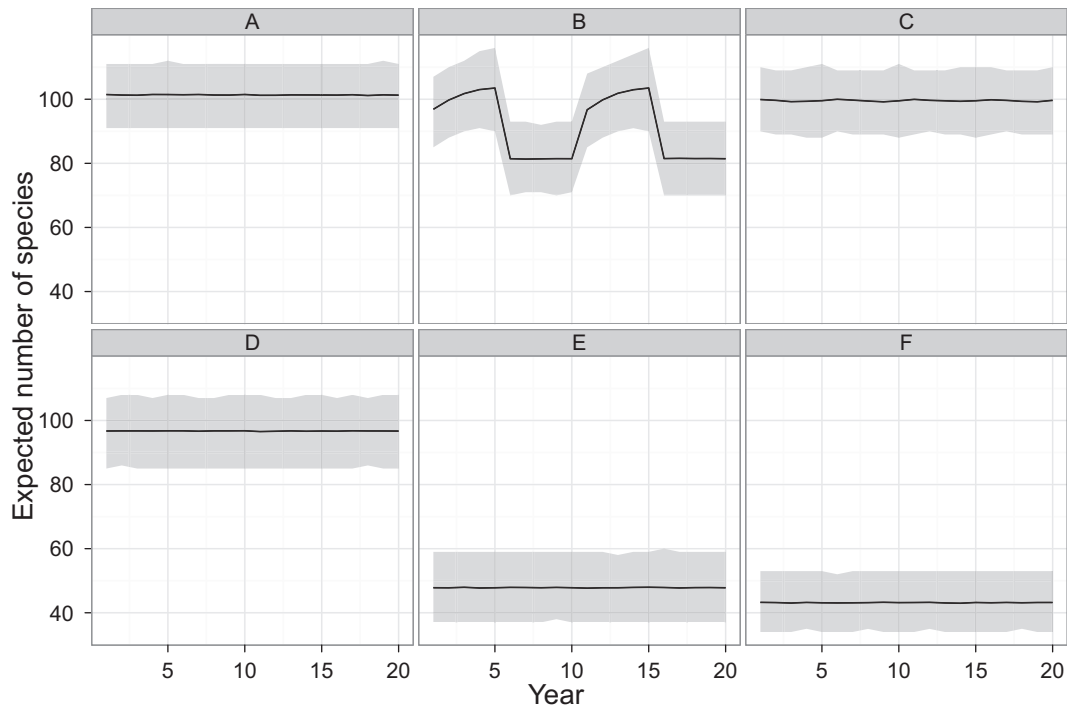
Fig. 1. Changes in the expected number of species in the 10 stands for each scenario. Curves denote expected values, and gray areas denote 95% prediction intervals. (A) managed coppice: clear 1 of 10 stands every year, (B) managed coppice: clear 10 of 10 stands every decade (C) managed coppice: clear 5 of 10 stands every 5 years, (D) managed coppice: clear 10 of 10 stands every year, (E) abandoned broadleaved forest: unmanaged, (F) abandoned pine forest: unmanaged.

3. Results

The calculation of MCMC was successfully converged; the Gelman–Rubin's diagnostic statistics (Gelman and Rubin, 1992; Brooks and Gelman, 1998) were less than 1.02 for all parameters. In addition, the three chains were well mixed in their trajectories for each parameter. Considering correlations between the parameters in the posterior samples, 4 of 21 combinations of the 7 parameters had absolute values of correlation coefficients greater than 0.5: $\beta_7 - \beta_8$ (0.621), $\beta_G - \beta_C$ (0.554), $\beta_M - \beta_G$ (−0.524) and $\beta_M - \beta_C$ (−0.504). The combination $\beta_7 - \beta_8$ might be due to a temporal autocorrelation, and the others might be due to the model definitions; e.g. stand age was valid only before floor cleaning in the managed stands.

The mean of the posterior distribution of the intercept β was −4.02, and β was always negative in the 95% credible interval (Table 4). The mean value of β suggested that overall probability of presence would be low (0.018 = 1/(1 + exp(4.02))), if the other terms were zero. The

mean of the posterior distribution of β_M was 3.33 and always positive in the 95% credible interval (Table 4), meaning the probability of presence of the species was overall higher in the managed coppice than in the abandoned forest. The probability of presence would be improved to 0.334 (=1/(1 + exp(4.02−3.33))) in the condition of managed coppice. The mean of the posterior distribution of β_C was −1.35, and β_C was negative in its 95% credible intervals. This suggested that floor cleaning would decrease the number of floor species, but the magnitude of the effect seemed to be smaller than that of β_M (the mean of $\beta_M + \beta_C$ was 1.98 and 95% credible interval was 0.89–3.09). The posterior distribution of β_8 was always positive in the 95% credible interval while that of β_7 contained 0. The value of β_8 suggested that the overall probability of presence was slightly higher in 2008 than that in 2006, while the reason was unclear; some environmental factors, such as weather might have affected it. The mean of the posterior of β_T was positive and the mean of the posterior of β_G was negative, but their 95% credible intervals contained 0.

The random effects by species on the coefficients (ε_T, ε_M, ε_G and ε_C) are shown in Tables 5–8. For simplicity, the values are shown only for species whose 95% credible intervals did not contain 0. There were no species whose 95% credible interval was always negative in ε_C (Table 8). The tables showing statistics of all the random effects are included in the Electronic supplementary material.

Positive values of ε_T indicate that the species showed higher probabilities of presence in broadleaved forests (AB) or coppices (CE, CM and CL) than in pine forests (AP), while negative values indicate species that tended to be found in pine forests (AP). Similarly, positive values of ε_M indicate species with higher probabilities of presence in managed coppices than in abandoned forests. Positive values of ε_G indicate that the species would be more abundant in younger coppices just after clear cutting, while positive values of ε_C indicate that the species would be more abundant in coppices after floor cleaning (CL).

The species highly likely to be present in managed coppice (CE, CM and CL) included deciduous understory and shrub species (*Rosa*

Table 4
Statistics of the posterior distributions of the parameters excluding random factors.

Parameter	Mean	SD	2.5%	97.5%
β	−4.02	0.32	−4.69	−3.40
β_T	0.24	0.39	−0.55	0.98
β_M	3.33	0.58	2.19	4.49
β_G	−0.17	0.10	−0.36	0.02
β_C	−1.35	0.55	−2.47	−0.28
β_7	0.16	0.09	−0.02	0.34
β_8	0.23	0.10	0.03	0.43
σ_S	2.48	0.22	2.10	2.95
σ_Q	0.42	0.11	0.25	0.68
σ_T	1.91	0.22	1.52	2.38
σ_M	3.06	0.30	2.51	3.67
σ_G	0.45	0.06	0.33	0.58
σ_C	1.91	0.31	1.37	2.55

Table 5
Statistics of the posterior distributions of parameters. Species whose 95% credible intervals did not include 0 are shown. Positive values denote that the species are more likely to be present in the broadleaved forest or coppice, and negative values denote that they are more likely to be present in the pine forest. Proportion of the species listed in the table is 20.0% (27/135).

Sign	Species	Mean	SD	2.5%	97.5%
Positive	*Pertya scandens*	3.77	0.98	2.07	5.82
	Rhododendron macrosepalum	3.76	0.84	2.19	5.49
	Viburnum erosum	2.76	1.11	0.80	5.07
	Lindera obtusiloba	2.7	0.75	1.30	4.22
	Smilax china	2.65	1.24	0.56	5.31
	Dioscorea japonica	2.57	0.91	0.93	4.51
	Viola ovato-oblonga	2.49	1.11	0.43	4.80
	Cymbidium goeringii	2.44	1.12	0.42	4.83
	Styrax japonica	2.32	0.75	0.95	3.89
	Quercus serrata	2.22	0.75	0.83	3.75
	Fraxinus sieboldiana	2.18	0.75	0.84	3.74
	Viburnum dilatatum	2.07	0.72	0.73	3.57
	Acer crataegifolium	1.94	0.96	0.23	3.93
	Lindera glauca	1.89	0.98	0.06	3.91
	Callicarpa mollis	1.75	0.68	0.45	3.15
Negative	*Camellia japonica*	−3.34	1.11	−5.73	−1.42
	Clethra barbinervis	−2.89	0.79	−4.57	−1.44
	Neolitsea sericea	−2.87	1.3	−5.68	−0.61
	Illicium anisatum	−2.76	1.37	−5.75	−0.32
	Wisteria japonica	−2.69	1.09	−5.08	−0.82
	Ilex macropoda	−2.63	1.39	−5.77	−0.24
	Cleyera japonica	−2.62	1.39	−5.68	−0.27
	Platanthera minor	−2.61	1.36	−5.61	−0.26
	Osmanthus heterophyllus	−2.4	1.2	−4.94	−0.32
	Torreya nucifera	−2.37	1.29	−5.25	−0.13
	Quercus glauca	−2.16	0.92	−4.06	−0.39
	Wisteria floribunda	−1.38	0.74	−2.95	−0.03

Table 6
Statistics of the posterior distributions of the parameter. Species whose 95% credible intervals do not include 0 are shown. Positive values denote that the species are more likely to be present in the managed coppice, and negative values denote that they are more likely to be present in the abandoned forest. Proportion of the species listed in the table is 21.5% (29/135).

Sign	Species	Mean	SD	2.5%	97.5%
Positive	*Rosa paniculigera*	5.67	2.00	1.88	9.76
	Oplismenus undulatifolius	5.12	1.89	1.59	8.97
	Aster semiamplexicaulis	4.58	1.71	1.40	8.25
	Carex stenostachys	4.56	1.93	1.08	8.81
	Pourthiaea vilosa var. *laevis*	4.51	1.74	1.27	8.10
	Wisteria floribunda	4.27	1.99	0.85	8.50
	Rubus hirsutus	3.85	1.73	0.67	7.56
	Paederia scandens	3.78	1.67	0.68	7.20
	Deutzia crenata	3.58	1.72	0.51	7.12
	Miscanthus sinensis	3.27	1.70	0.19	6.76
	Reynoutria japonica	3.15	1.70	0.07	6.74
	Tylophora aristolochioides	2.87	1.49	0.00	5.83
Negative	*Eurya japonica*	−6.42	1.26	−8.99	−4.04
	Pieris japonica	−5.66	1.83	−9.65	−2.34
	Lyonia ovalifolia var. *elliptica*	−5.41	1.47	−8.39	−2.64
	Abelia spathulata	−5.39	1.40	−8.24	−2.75
	Rhododendron macrosepalum	−5.37	1.22	−7.82	−3.04
	Ilex pedunculosa	−5.24	1.37	−8.04	−2.62
	Fraxinus sieboldiana	−4.98	1.24	−7.50	−2.59
	Ilex crenata	−4.97	1.90	−9.03	−1.65
	Acer crataegifolium	−4.92	1.48	−7.97	−2.15
	Aphananthe aspera	−4.38	1.93	−8.47	−0.81
	Rhododendron reticulatum	−4.01	1.21	−6.47	−1.73
	Clethra barbinervis	−4.01	1.53	−7.19	−1.12
	Quercus variabilis	−3.53	1.45	−6.43	−0.77
	Celtis sinensis var. *japonica*	−3.27	1.25	−5.69	−0.82
	Diospyros kaki	−2.92	1.14	−5.12	−0.72
	Lindera umbellata	−2.49	1.12	−4.82	−0.36
	Cymbidium goeringii	−2.47	1.22	−4.89	−0.12

Table 7
Statistics of the posterior distributions of the parameter. Species whose 95% credible intervals did not include 0 are shown. Positive values denote that the species are more likely to be present in the younger coppice, and negative values denote that they are more likely to be present in the older coppice (before floor cleaning). Proportion of the species listed in the table is 3.0% (4/135).

Sign	Species	Mean	SD	2.5%	97.5%
Positive	*Weigela hortensis*	0.94	0.33	0.32	1.63
	Crassocephalum crepidioides	0.85	0.34	0.21	1.55
	Erechtites hieracifolia	0.79	0.30	0.24	1.42
Negative	*Lindera obtusiloba*	−0.96	0.33	−1.64	−0.35

Table 8
Statistics of the posterior distributions of the parameter. Species whose 95% credible intervals did not include 0 are shown. Positive values denote that the species are more likely to be present in the coppice after floor clearing. There were no species whose 95% credible intervals were entirely negative. Proportion of the species listed in the table is 5.9% (8/135).

Sign	Species	Mean	SD	2.5%	97.5%
Positive	*Callicarpa japonica*	3.63	1.40	1.03	6.54
	Quercus aliena	3.14	1.39	0.57	5.99
	Callicarpa mollis	3.07	1.43	0.45	6.11
	Rhododendron macrosepalum	2.60	1.15	0.44	4.94
	Camellia japonica	2.54	1.36	0.04	5.39
	Fraxinus sieboldiana	2.50	1.19	0.3	4.9
	Padus grayana	2.45	1.24	0.14	4.99
	Elaeagnus pungens	2.45	1.17	0.21	4.82

paniculigera, *Pourthiaea vilosa* var. *laevis* and *Rubus hirsutus*), herbaceous species (*Aster semiamplexicaulis*, *Reynoutria japonica*) and grass species (*Oplismenus undulatifolius*, *Carex stenostachys* and *Miscanthus sinensis*) (Table 6). In the youngest coppice, three species, *Weigela hortensis*, *Crassocephalum crepidioides* and *Erechtites hieracifolia*, were highly likely to be present (Table 7). *W. hortensis* is a deciduous shrub, which can grow quickly after clear cutting by sprouting. *C. crepidioides* and *E. hieracifolia* are herbaceous species of Asteraceae, and often dominate stands just after clear cutting. The coppices after the canopy had closed and the floor had been cleared (CL) had fewer species than CE and CM ($\beta_C < 0$, Table 4), but still retained much more abundant species than the abandoned forests (Itô et al., 2010). In CL, species such as *Callicarpa japonica*, *Quercus aliena* and *Callicarpa mollis* were more likely to be present (Table 8). However, in fact, we had only two quadrats of one stand for the coppice after floor cleaning (CL1 and CL2), meaning there might be a bias due to the small sample size. For example, *Q. aliena* was rarely found in the other stands and might be located in the stand by chance. The species abundance in CL compared to AB and AP might be attributable to the general abundance in managed coppices.

On the other hand, species present with high probability in abandoned pine forest (AP) included many evergreen tree or understory species such as *Camellia japonica*, *Neolitsea sericea*, *Illicium anisatum* and *Cleyera japonica* (Table 5). In abandoned forest (AP and AB), evergreen understory species such as *Eurya japonica*, *Pieris japonica*, *Ilex pedunculosa* and *I. crenata* were included in those frequently present (Table 6), while the understory species in the shrub layer would impair the floor light condition.

The results of the simulation are shown in Fig. 1. The curve of scenario B shows large fluctuation while that of scenario A maintains a stable number of species. The curve of scenario C, designed as the intermediate of A and B, also shows a stable number of species though the amount is expected to be slightly smaller than A. In addition, the curve of scenario D, designated as heavy use, is also stable, though the number of species is smaller than that of scenario A. Although there were some differences described above,

the prediction intervals of scenarios A–D widely overlapped. Scenarios E and F, in which no management was presumed, show stable curves though the expected numbers of present species are smaller than the other three scenarios in which management was presumed.

4. Discussion

The closed canopy and evergreen shrub layer in the abandoned forest should make it harder for species to survive on the floor except for shade-tolerant species. This would explain why abandoned forests had less abundant species on the floor ($\beta_M < 0$, Table 4). In addition, shade-tolerant but disturbance-intolerant species might have disappeared in this area due to long-term human disturbances. These suggested that periodical clear cutting would function as an intermediate disturbance to prevent dominance of evergreen understory species and would contribute to maintaining rich species abundance in the coppice. The floor cleaning seemed to have negative effects on the floor species abundance ($\beta_C < 0$, Table 4). Nevertheless, the total effect of the management and floor cleaning was positive. This suggested that the managed coppices after the floor cleaning still had larger numbers of species on the floor than the abandoned forests.

Washitani (2001) pointed out that seasonal fluctuation and spatial heterogeneity of microsite light availability were conspicuous features of patchy deciduous forests, and that this would enhance plant species coexistence in the understory layer. The floor of the managed coppices seemed to fit the condition as a whole; the light condition of the managed coppice fluctuated seasonally and changed with stand age (Itô, unpublished data). Washitani (2001) also pointed out that human disturbances worked to mimic natural disturbances, maintaining a shifting mosaic that helped retain diversity. The simulation suggested that cutting a small area every year (scenario A) would be the optimal management plan allowing the coppice to retain species abundance on the floor, but cutting half the stands by turns (scenario C) would also maintain stable species abundance. While the number was smaller than in scenario A, their prediction intervals widely overlapped. The management plan without a shifting mosaic structure (scenario B) showed unstable fluctuation of species abundance. The fluctuation would be driven by the variables g (stand age) and c (before/after floor cleaning), which depended on the year. In reality, simultaneous shrub layer growth might hamper the survival of light-demanding herbs. Under such circumstances, in the absence of seed sources of the species near the stands, the species may become locally extinct. Washitani (2003) pointed out that plants dependent on seed dispersal by ants found it difficult to recover once those plants have disappeared from the area. Such plants without shade-tolerance might be especially vulnerable to this management plan.

The management plan with heavy use (scenario D) showed stable species abundance though the number was slightly smaller than in scenarios A and B. However, scenario D would be inferior to the scenarios A–C from the viewpoint of the wood production. In 2008, 8 years after the regeneration of CL1 and CL2, basal areas of Q. acutissima were 8.8 and 10.1 m^2 ha^{-1}, respectively (Itô, unpublished data). This suggested that the management plan of scenarios A–C could produce about 10 m^2 ha^{-1} yield of Q. acutissima wood in a decade. Contrarily, basal areas of Q. acutissima in CE1 and CE2 were 0.21 and 0.37 m^2 ha^{-1}, respectively, at the 1st year after the regeneration (Itô et al., 2010). This suggested that the management plan of scenario D could produce about 4 m^2 ha^{-1} yield of Q. acutissima wood in a decade at most even if it assumed that the production would not decline in spite of overuse. One-year-old sprouts would be too small for use as charcoal woods, in the first place. In addition, most shrub and tree species would probably not survive annual clear cutting, hence the real species abundance might be poorer than that anticipated by the simulation.

All of these scenarios (A–D) predicted a larger number of species present in managed rather than unmanaged stands (scenarios E and F). In abandoned forests, in reality, some shade-tolerant species would be expected to colonize, whereupon the number of species may proliferate. However, it seemed to be very difficult for the abandoned forests to restore species abundance to the level of the managed coppices. Scenario D would not be preferable to scenarios A–C from the viewpoint of wood production, and scenario B would be inferior to scenarios A and C from the viewpoint of stability. Scenarios A and C, which would have at least two phases of stands in the region, would be expected to retain stable species abundance in floor vegetation. From the viewpoint of income from the coppice, stable annual production of charcoal woods in scenario A might be preferable to unstable production at 5-year intervals in scenario C, even though the total income would not differ.

In the simulation, we did not take into account size and arrangement of patches of the coppices. Needless to say, they might relate to the conservation of species diversity at the regional level. Concerning the species diversity of floor plant species, it would be preferable that patches be allocated within the range of seed distribution.

5. Conclusions

The managed coppice had a larger number of plant species on the floor including deciduous shrub, herbaceous and grass species in contrast to abandoned pine and broadleaved forest in which many evergreen understory species were likely to be present. Periodical clear cutting would function as an intermediate disturbance to prevent the dominance of evergreen understory species in the coppice, and also form shifting mosaics, thus contributing to habitat diversity. The management plan of coppices with periodical partial clear cutting would contribute to species abundance while also stably producing wood.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.12.017.

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