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Title: How many broad-leaved trees are enough in conifer plantations? The economy of land sharing, land sparing, and quantitative targets

Running title: Economy of land sharing and sparing

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Summary

1. For biodiversity conservation to be an effective and significant social investment, non-marketed values of biodiversity conservation and its associated opportunity costs should be evaluated in monetary terms.
2. In this study, we measured the willingness to pay (WTP) for bird abundance using a choice experiment (CE) based on the random utility model. We performed a cost–benefit analysis to identify the optimal proportion of broad-leaved trees in conifer plantations on a volume basis to maximize the social benefits of bird conservation and wood production.
3. The results suggested that respondents to the CE were not satisfied with their current situation and preferred an increase in bird abundance. However, the estimated WTP indicated diminishing returns of bird conservation. More specifically, WTP first greatly increased before gradually experiencing decreasing marginal values, reaching its peak, and finally decreasing slightly with increasing bird abundance.
4. Optimization analyses indicated that when the relationship between bird abundance and broad-leaved tree proportion was convex, semi-natural plantations with non-zero broad-leaved tree proportion (0.02–0.22) were always optimal options. When the relationship was linear, optimal broad-leaved tree proportion ranged from 0 to 0.78 and was greatly affected by wood values. When the relationship was concave, there were only two optimal broad-leaved tree proportions: a very high proportion (approximately 0.90) and the lowest possible proportion (0). When the convex and concave relationships approached the linear form, comparable benefits could be attained across broad ranges of

broad-leaved tree proportion both within and across the relationships. In such cases, it would be useful to increase the likelihood of a feasible land-use strategy of either land sparing or land sharing in order to be successful.

5. *Synthesis and applications*. It can be difficult to set quantitative targets in biodiversity conservation solely on an ecological basis, and social benefits of biodiversity conservation can create diminishing returns in many situations. The framework we propose shows how to reconcile resource production and biodiversity conservation in the real world.

Key-words: bird, choice experiment, cost–benefit analysis, economics, land use intensity, land use specialization, multiple use, optimization, semi-natural plantation, willingness to pay

Introduction

Biodiversity cannot be conserved for free. In general, conflicts emerge between resource production and conservation (Risser 1999), which is a predominant reason why biodiversity has been lost and its scarcity as well as values have been acknowledged. Effective biodiversity conservation as a social investment requires the evaluation of non-marked values of biodiversity in monetary terms and the accommodation of trade-offs between biodiversity conservation and resource production (Arrow *et al.* 1996; Balmford *et al.* 2002; Bateman *et al.* 2015). Confronting the importance of the economic perspective in biodiversity conservation, Hunter (1990) suggested that money is the bottom line and permeates our culture.

The integration of economics and ecology allows biodiversity conservation to embrace reality and can change the strategy of biodiversity conservation. For example, although primary forests have the highest ecological value (Gibson *et al.* 2011; Edwards *et al.* 2014a), the management of logged forests, which have a lower ecological value, can have priority over the protection of primary forests given certain budgets (Wilson *et al.* 2010; Edwards *et al.* 2014b). This is because it is too expensive to conserve biodiversity in primary forests, and logged forests can be cost-effective habitats for biodiversity conservation compared with forest conversion into agricultural fields (Fisher *et al.* 2011; Wilcove *et al.* 2013).

Setting quantitative targets is a prerequisite process in biodiversity conservation (Tear *et al.* 2005). If there are obvious thresholds across which an indicator of biodiversity

precipitously declines, we could set these thresholds as conservation targets, e.g. minimum habitat structures or areas (Guénette & Villard 2005; Betts, Forbes & Diamond 2007). However, it can be difficult to empirically find clear thresholds (Lindenmayer, Fischer & Cunningham 2005; Swift & Hannon 2010), and the theoretical underpinnings of particular thresholds may not always exist. In such cases, how can quantitative targets be set? Crome (1997) suggested the difficulty of this problem in fragmented landscapes because alternative forest parcel can harbour unique biota. Therefore, solely on an ecological basis, we may end up concluding that every parcel is useful and important (Crome 1997).

Economics, and more specifically cost–benefit analyses, can enable us to set quantitative targets to reduce the costs and maximize the benefits of biodiversity conservation (Lippke & Bishop 1999; Buongiorno & Gilless 2003). A cost–benefit analysis seeks optimal combinations of two products (typically, biodiversity and crops) to maximize the obtained benefits based on the relative values of these products. The solution can greatly depend on the functional forms of trade-offs between biodiversity conservation and resource production (i.e. production possibility frontiers). In addition, functional forms without clear thresholds are usually treated (Perfecto *et al.* 2005; Zhang & Pearse 2011). Therefore, the cost–benefit analysis is promising for setting quantitative targets in many situations, as well as for offering insight into an important land use problem, namely whether resource production and biodiversity conservation should be separated or integrated—the so-called land sparing vs. land sharing debate (Perfecto *et al.* 2005; Yamaura *et al.* 2012; Butsic & Kuemmerle 2015).

Few studies have attempted a cost–benefit analysis of biodiversity conservation and

assumed that economic values per unit of conserved biodiversity are constant with increasing biodiversity conservation (Naidoo & Ricketts 2006; Edwards *et al.* 2014b; Teuscher *et al.* 2015). However, economic returns of products, which can be measured by willingness to pay (WTP), usually diminish (Field 2008; Zhang & Pearse 2011). Fisher *et al.* (2008) suggested that this diminishing return (marginality) should be incorporated in the cost–benefit analysis because political decisions frequently face the problem of what to do with the next unit. However, few studies have employed a formal economic analysis to consider diminishing returns (Naidoo & Adamowicz 2005) and its ecological substitute (i.e., species-area relationships: Wilson *et al.* 2007).

In this study, we examined the amount of broad-leaved trees required in conifer plantations to improve bird abundance from an economic perspective. Conifer plantations are expanding in areas with increasing wood demands, and their replacement of native forests usually devastates the biota; the reconciliation of biodiversity conservation and wood production is actively discussed (Brockerhoff *et al.* 2008; Paquette & Messier 2010). Our previous stand-level study revealed that bird abundance in conifer plantations can linearly increase with the amounts of mixed native broad-leaved trees. We did not find clear thresholds indicating required amounts of broad-leaved trees to maintain bird abundance on an ecological basis (Yoshii *et al.* 2015). Because broad-leaved trees have lower wood values compared with planted coniferous trees and the increase in broad-leaved trees requires the space of coniferous trees, the improvement in bird abundance in conifer plantations by increasing broad-leaved trees decreases the revenue of foresters. This is a typical trade-off

between conservation and resource production. For this study, we conducted a choice experiment (CE) to measure the WTP to improve bird abundance and sought quantitative targets of bird conservation in monetary terms through a cost–benefit analysis. In addition, we performed a sensitivity analysis to examine how quantitative targets can be changed depending on the situation.

Materials and methods

A choice experiment to measure WTP

CEs allow us to measure individual preferences by asking respondents to choose among various multi-attribute scenarios. This methodology was initially developed by Louviere and Hensher (1982) and Louviere and Woodworth (1983) and is classified as a family of stated preference approaches (Louviere, Hensher & Swait 2000). CEs are currently used in various fields, including marketing, transportation, and environmental (Hensher 1994; Louviere 1994; Adamowicz *et al.* 1998). CEs are also an essential method to evaluate non-marketed values of environmental goods and services in monetary terms (Adamowicz *et al.* 1998).

In the CE, we established hypothetical alternative plans of forest management to improve the bird abundance in conifer plantations by increasing broad-leaved trees in Hokkaido prefecture, which comprises 14 districts. We asked respondents to select preferred scenarios from a range of plans. Hypothetical plans were applied to 1000 ha of plantations

146 that were adjacent to human dwellings in each district. In other words, 14 000 ha of
147 plantations were covered in total, which represents approximately 1% of the total plantation
148 area in Hokkaido. Alternative plans differed according to three attributes: (i) the number of
149 bird individuals in conifer plantations per ha, (ii) the number of bird-watching stations in a
150 district, and (iii) the additional amount of tax payments needed to introduce new forest
151 management plans (Table 1).

152 The number of bird individuals in plantations was assumed to increase depending on
153 the amounts of mixed broad-leaved trees. Based on the previous empirical study that surveyed
154 birds in plantations with different amounts of broad-leaved trees (Yoshii *et al.* 2015), the
155 minimum and maximum values were estimated as bird abundance in “pure” plantations (with
156 no broad-leaved trees) and in natural broad-leaved forests (without planted coniferous trees),
157 respectively. Bird abundance (N) was assumed to increase linearly with the proportion of
158 broad-leaved trees in the basal area (p_{bl}) according to $N = 6.21 + 8.04 \times p_{bl}$, following the
159 results of Yoshii *et al.* (2015). However, we did not find predominant support of the linear
160 response over the nonlinear response, possibly due to the small sample size. Furthermore,
161 population densities can inherently take various forms against environmental gradients,
162 depending on the situations (Austin 2002). Therefore, we changed the functional forms of bird
163 abundance to p_{bl} in the sensitivity analysis (see *cost–benefit analysis*). Bird abundance was
164 highly correlated with bird-species richness ($r = 0.98$, $p < 0.001$), although we used
165 abundance as an attribute since there would not be large differences in species richness among
166 the hypothetical plans at the project level (i.e. in 14 000 ha). In the CE, we showed bird

abundance per ha (6.2–14.3 individuals) as well as project-level abundance (87 000–200 000 individuals) of individual alternative plans to respondents via proportional calculation.

We considered local habitat structure as a single determinant of bird abundance in order to simplify the cost–benefit analysis, especially since habitat structure can have larger effects on bird abundance than landscape structure in forested landscapes where the majority of forestry practices occur (Yamaura, Katoh & Takahashi 2008). We also noted that benefits of bird conservation were only measured by *N*, which was the total abundance of bird communities rather than the abundance of specific endangered species or functional groups sensitive to plantation forestry (e.g. cavity nesters, flycatchers). We excluded three species whose abundance increased with plantation intensity (coal tit *Periparus ater*, goldcrest *Regulus regulus* and Sakhalin leaf warbler *Phylloscopus borealoides*) from *N* (Yoshii *et al.* 2015). In this regard, these species are known for feeding in coniferous trees and are therefore positively affected by forestry plantations (Yamaura *et al.* 2009). In the CE, we told the respondents that bird communities are impoverished in conifer plantations compared with natural forests, and the focal birds are 31 common species inhabiting natural forests in Hokkaido. We expected that this crude attribute allowed the respondents to easily comprehend the benefits of bird conservation.

The second attribute (the number of bird-watching stations) was used to separate recreational use values in conifer plantations with increased bird abundance from values of bird abundance itself. Essentially, new forest management plans were intended to increase the passive use values of forests (higher bird abundance), which is sometimes called non-use

188 values; however, some respondents may highly value forests with higher bird abundance since
189 they may enjoy bird watching there. This effect was accounted for in the second attribute. We
190 used the number of bird-watching stations rather than other facilities (e.g. trail lengths) to
191 confine the intended use to bird-watching. The third attribute was additional tax payments
192 required to achieve new forest management. The WTP for bird abundance was estimated on
193 the basis of the trade-off between the first and third attributes.

194 Each respondent evaluated three profiles (alternative management plans) with
195 different levels of the three attributes. This evaluation process was repeated eight times (i.e.
196 eight choice sets with different combinations of the levels were used). Profiles were designed
197 following an orthogonal main effect design to avoid confounding the effects of individual
198 attributes (Louviere, Hensher & Swait 2000). In February 2015, a research company sent
199 invitation e-mails regarding our internet questionnaire to 11 800 registered respondents in
200 Hokkaido Prefecture. Of these respondents, 1194 (10.1%) completed the questionnaire. After
201 removing 238 respondents who disagreed with the introduction of our proposed forest
202 management plans regardless of the various attributes and levels, we used 956 responses
203 (80%) for the analysis.

204

205 *Random utility model: Measuring the benefits of bird conservation*

206 Results of the CE were analysed using a random utility model with Stata 12
207 (StataCorp, College Station, Texas). Utility for a profile i (U_i) is described as a linear
208 combination of deterministic (V_i) and random (ε_i) terms: $U_i = V_i + \varepsilon_i$. The probability that

209 profile i is chosen is equated to the probability that U_i is larger than U_j:

210 $$\Pr(i|C) = \Pr\left[U_i > U_j\right] = \Pr\left[\left(V_i - V_j\right) \geq \left(\varepsilon_j - \varepsilon_i\right)\right], \forall j \neq i, \forall j \in C \quad \text{eqn 1}$$

211 where C is a choice set. Because we assume that the error term follows a Gumbell distribution
212 (McFadden 1974), the above probability, Pr(i | C), can be expressed as a conditional logit
213 model (McFadden 1974):

214 $$\Pr(i|C) = \exp(\mu\beta x_i) \,/\, \sum_{j \in C} \exp(\mu\beta x_j). \quad \text{eqn 2}$$

215 Without losing generality, deterministic terms can be described as a linear
216 combination of parameters. We modelled the observable part as $\mu\beta x_i$, where x_i denotes a
217 vector of attributes and β denotes its coefficient. The scale parameter, μ, is conventionally
218 assumed to be 1. The marginal WTP for an increase in bird abundance (per ha) is obtained by
219 dividing the "bird abundance" parameter by the "additional tax payment" parameter, which
220 indicates the marginal utility of income. Considering the possibility that the marginal WTP for
221 bird abundance takes a non-linear functional form, we fitted linear and quadratic models for
222 bird abundance and compared the models with Akaike Information Criterion (AIC).

223

224 *Cost–benefit analysis: Searching for optimal plantation intensity*

225 We assumed that forests were mature plantations with 300 m^3 ha^{-1} of wood stock
226 (Forestry Agency 2014b) and that its composition was represented by its proportion of
227 broad-leaved trees in the basal area: (p_{bl}): $p_{bl} + p_{cnf} = 1$, where p_{cnf} was the proportion of
228 planted coniferous trees. The lowest value of p_{bl} (0) indicates pure conifer plantations without
229 any broad-leaved trees, whereas the highest value of p_{bl} (1) indicates mature natural forests

without any planted coniferous trees. Wood values were based on stumpage prices of broad-leaved trees (500 yen m^{-3}) and coniferous trees (1000 yen m^{-3}), according to the current prices in Hokkaido (Forestry Agency 2014a). It means that wood values decreased with increasing p_{bl} due to the replacement of coniferous trees by broad-leaved trees.

We also considered other silvicultural (opportunity) costs, which was represented by further decreases in the amounts of planted coniferous trees. Assuming the retention of broad-leaved trees during the harvest as an alternative silvicultural approach, we expected that there would be few additional harvest and weeding costs with the increase in broad-leaved trees. The major additional costs would be shading effects of the retained trees on the planted coniferous trees (Rose & Muir 1997). Yoshida *et al.* (2005) examined the stand structure of a 60-year-old larch *Larix kaempferi* plantation with retained broad-leaved trees (mostly *Quercus crispula*) in central Japan. Retained trees (larger than 40 cm d.b.h.) occupied 18% of the stand space, and the basal area (BA) of the larches within 10 m of the retained trees could be halved. No silvicultural practices had been conducted in this stand after the initial weeding. We considered this result as the worst-case scenario (with the most severe impacts on the planted trees), and modelled the BA of the planted conifers by 300 $m^3 \times p_{cnf}^2$, which can roughly reproduce this shading effect (Fig. 1a). Conversely, we did not consider the benefits of increasing p_{bl} other than bird conservation, such as the conservation of other taxa (Ohsawa 2007) and the maintenance of long-term site productivity (Franklin 1989).

We considered five possible response forms of bird abundance to broad-leaved tree proportion (p_{bl}): convex, shallow convex, linear, shallow concave, and concave (Fig. 1b). As

described above, we increased bird abundance per ha from 6.2 at 0 p_{bl} to 14.3 at 1 p_{bl}. We converted bird abundance into an amount of money per ha paid by a person using an equation obtained from the CE and random utility model (i.e. eqn 3: see below). We then multiplied this value by 80% (the proportion of respondents who agreed with the introduction of management plans) of the total labour force in Hokkaido (2.12 million) and considered this as a monetary value of bird conservation per ha, which we call bird values.

A question with the cost–benefit analysis was whether forgone wood values as an opportunity cost can be compensated by increasing bird values. The analysis identified the specific p_{bl} required to maximize economic forest values represented by the sums of wood and bird values. We searched for the optimal level of p_{bl} with an algorithm of simulated annealing (SANN) using the "optim" R function. Because net forest values could have more than one peak against p_{bl} (local optima), we conducted optimization analyses with 99 different initial values from 0.01 to 0.99 with 0.01 increments and took the proportion with the highest forest value as the globally optimal proportion. Since p_{bl} only took values ranging from 0 to 1, we used an inverse logit transformation of the parameter in the optimization process and treated the transformed optimized values as optimal p_{bl}.

To examine the sensitivity of the optimal p_{bl}, we iterated this search for each combination of the five bird response forms and three levels of WTP (using factors of 1, 2/3, and 1/3), wood values (using factors of 2, 1, and 0.5), broad-leaved tree values (using factors of 1.5, 1, and 0.5), and silvicultural costs (using powers of p_{cnf} to calculate BA of coniferous trees: 2.0, 1.5, and 1.0: Fig. 1a). The variabilities of wood values were motivated by their

historical ranges in Japan (Yamaura *et al.* 2012), and the lower limit of WTP was set at 1/3 since WTP can be overstated up to three times (List & Gallet 2001) and also given the relatively low response rate of the questionnaire (10.1%). The total number of combinations was $5 \times 3^4 = 405$. In the calculation of the wood values, we first summed the values of broad-leaved and coniferous trees before factoring the wood values. Therefore, broad-leaved tree values are the economic costs of increasing p_{bl}, and the factors of wood values are the general economic wood values. Finally, an ANOVA was conducted for optimal p_{bl} with five control variables as main factors to examine their relative effects on the optimal p_{bl}. We conducted all of the optimization analyses using R version 3.0.3 (R Core Team 2014).

Results

Choice experiment for WTP

In the analysis of conditional logit models, all of the estimated parameters except for bird-watching stations were significantly different from zero at the 5% level (Table 2). The parameter of additional tax payments was negative, which indicates that respondents preferred a cheaper alternative. The parameter of alternative-specific constant for status quo profile was also negative, indicating that respondents avoided choosing the current situation, i.e. respondents found values in introducing new forest management plans regardless of their attributes and levels. Comparing AIC of the models suggested that the quadratic model was better supported than the linear model (ΔAIC ~ 36), and both models showed the medium fits

(Table 2). In the linear model, the parameter of bird abundance was positive, but in the quadratic model, the quadratic parameter was negative, suggesting that the WTP for bird abundance had a nonlinear form (Fig. 2a). WTP first greatly increased before gradually experiencing decreasing marginal values, reaching its peak, and finally decreasing slightly with increasing bird abundance (see Appendix S1 in Supporting Information for the estimation uncertainty of this form). Specifically, WTP (yen per ha per person) was modelled as a quadratic function of bird abundance N to take 0 values when $N = 6.21$ as follows:

$$\mathrm{WTP} = -\frac{U_N - U_C}{\partial U / \partial x_{tax}} = -\frac{\beta_1 (N - 6.21) + \beta_2 (N^2 - 6.21^2)}{\beta_{tax}} \quad \text{eqn 3}$$

where U_N is a utility level for a scenario with N and U_C is a utility level for the control scenario ($N = 6.21$). Parameters β_1 (= 0.5823), β_2 (= -2.5493×10^{-2}), and β_{tax} (= -0.0353×10^{-2}) represent linear terms of bird abundance, quadratic terms of bird abundance, and additional tax payments, respectively. The effect of the alternative-specific constant is not included in this formulation of WTP since this effect is not attributable to the WTP for bird abundance. It may rather be attributable to the context for payment (e.g. respondents may always choose the status quo profile because of disapproval of tax increase). Since bird abundance was expressed as the linear combination of p_{bl} (Fig. 1), WTP was accordingly described as a function of p_{bl} (Fig. 2).

Optimization analysis for quantitative targets

Due to the nonlinear form of WTP, bird values as a function of p_{bl} were all unimodal for all five bird response forms, though the p_{bl} with maximized bird values and the deepness

of the curvature varied among the response forms (Fig. 2b). In the standard scenario (Fig. 2b) with the factors of WTP, wood value, broad-leaved tree value, and silvicultural cost equal to 2/3, 1, 1, and 1 respectively, bird values at the highest p_{bl} (i.e. 1) were approximately equal to the wood value. Unimodal forms of bird values created a problem on how to maximize forest values from the identification of optimal p_{bl} to be less than 1. The convex response form had the maximized bird values at low p_{bl} and the corresponding net price (forest value) was the highest among the five forms since its wood value was also high. The concave form had the highest optimal p_{bl} and the lowest forest value at optimal p_{bl}. The linear form had the shallowest curves of bird and forest values. Shallow convex and concave forms also had shallow curves, indicating that they can attain comparable forest values at the broad ranges of p_{bl} within and across these forms although they have different specific optimal p_{bl}.

In the high WTP and low cost scenario (Fig. 2c) with the factors of WTP, wood value, broad-leaved tree value, and silvicultural cost equal to 1, 0.5, 1.5, and 1 respectively, bird values were larger than wood values for many levels of p_{bl}, and the decreased economic disadvantages of increasing p_{bl} made the maximized forest values comparable among the five response forms. Although the optimal p_{bl} of forest values was always smaller than that of bird values, the differences were small in this scenario. In the low WTP and high cost scenario (Fig. 2d) with the factors of WTP, wood value, broad-leaved tree value, and silvicultural cost equal to 1/3, 2, 0.5, and 1 respectively, optimal p_{bl} was more than zero only for the two convex forms. The linear form and the two concave forms had zero optimal p_{bl} since increasing bird values could not compensate for any forgone opportunity costs of wood

values.

Our optimization analyses under varying conditions adequately showed the dependency of optimal p_{bl} on response forms and wood values (Fig. 2–4). The results of the ANOVA suggested that wood values had the greatest effect on optimal p_{bl} (Table 3). When two intermediate (shallow convex and concave) response forms were excluded, bird response forms were the second most important (evaluated by mean SS), followed by WTP. Although silvicultural costs had minor effects, their increases actually decreased the optimal p_{bl} (Fig. 2–3). The mean values of optimal p_{bl} at low, medium, and high silvicultural costs across the 405 combinations were 0.34, 0.30, and 0.28, respectively. The deep convex form was the most robust to the uncertainties in that optimal p_{bl} lay in the relatively narrow range of 0.02 to 0.22 (Fig. 4). Optimal p_{bl} of the linear form ranged from 0 to 0.78 and was greatly affected by the situations. In the deep concave response, there were just two available options: 0 and approximately 0.90. In the scenarios with the lowest wood values, 0.90 p_{bl} was always optimal except for three cases with the lowest WTP and broad-leaved tree values. When wood values increased, however, the optimal p_{bl} suddenly jumped from 0.90 to 0. There were no intermediate options. Optimal p_{bl} of shallow convex and concave forms was higher and lower, respectively, than their respective deep forms.

Discussion

To the best of our knowledge, this is the first study to identify quantitative

conservation targets (optimal plantation intensity) to reconcile biodiversity (bird abundance) conservation and resource production by measuring WTP for biodiversity conservation. Although it has been difficult to set quantitative targets without clear thresholds on an ecological basis (Ficetola & Denoël 2009), we successfully identified optimal targets on an economic basis. Our analysis showed that the optimal plantation intensity depends on a range of factors and found a value of semi-natural plantations (plantations with broad-leaved trees) as social capital in many cases. Semi-natural plantations are optimal forest types that maximize the total benefits of bird conservation and wood production unless bird–broad-leaved tree proportion relationships are concave or unless relationships are linear and wood values greatly exceed the WTP for bird abundance.

Given the most likely scenario (i.e. a linear bird response, present wood values, and 2/3–1 WTP), an approximately 50% coverage of broad-leaved trees was suggested to be optimal (Fig. 3c). However, we only quantified opportunity costs required to maintain semi-natural plantation forests by the presumed decreases in the amounts of planted coniferous trees. If we measure opportunity costs empirically and consider them, the optimal broad-leaved tree proportion may be lower than that of this study. For example, Hunter (1990) and Newton (1994) suggested a retention of 5–10 snags per ha to maintain cavity users, and Gustafsson *et al.* (2012) suggested tree retention levels between 5 and 10% to reduce the ecological impacts of forest harvest. Similar retention levels may be feasible targets under varied opportunity costs.

Optimal broad-leaved tree proportion never reached 1, suggesting that strict nature

reserves excluding any human interventions are always a suboptimal option to maximize forest values. Optimal broad-leaved tree proportion was approximately 90% rather than 100%, even under a deep concave response due to the diminishing returns of conserved bird abundance. It is suggested that the marginal benefits of further bird conservation do not greatly increase given that certain amounts of bird abundance are already conserved. To this extent, the exploitation of lands (and resulting slight loss in bird abundance) would be socially accepted. This idea is already acknowledged and manifested by the existence of multiple types of nature reserves (Cumming *et al.* 2015).

Our analyses also showed situations in which the advantages of semi-natural plantations are limited. These occur when bird abundance responds to broad-leaved tree proportion in a concave way or the value of birds is greatly restricted compared to that of resource production. In such cases, separation of biodiversity conservation and resource production (land sparing or land-use specialization) is superior to their integration on the same land parcels (land sharing or multiple uses). The same observations and conclusions were also made by previous modelling studies (Green *et al.* 2005; Perfecto *et al.* 2005; Butsic & Kuemmerle 2015). Although optimal options can be suddenly shifted even due to small changes in resource prices (Fig. 3), the existence and nature of such thresholds can be predicted *a priori* using the models.

What makes this study distinct from others is that we have formulated economic values of biodiversity conservation as a function of land-use intensity. Without this formulation, we would have to seek land-use strategies that reconcile biodiversity

conservation and resource production by maximizing the resource production while specifying the quantitative target of biodiversity conservation. However, specifying the quantitative target of biodiversity conservation can also be difficult (e.g., Flather *et al.* 2011); we circumvent this problem by evaluating monetary values of two conflicting products. This approach enables us to compare values of biodiversity conservation and resource production, and to manage landscapes to maximize social benefits (see also below).

Conservation implications

We showed that when species response forms approach the linear form, we are able to obtain comparable benefits from forests at the broad ranges of intensity. When linear response forms are competing with other models, to increase the social benefits and the likelihood of an adopted strategy to be successful, it would be useful to adopt a feasible land-use strategy in focal landscapes. Another consideration is the number of products involved. We only dealt with two conflicting products, and it can be difficult to evaluate more than seven products simultaneously with a choice experiment (Miller 1956). However, even if we evaluate additional products in monetary terms (e.g. carbon, water use), our framework can be extended to the landscape-level problem with more than two products (see Appendix S2). Different products are likely to be functions of different land-uses (Raudsepp-Hearne, Peterson & Bennett 2010; Crouzat *et al.* 2015), and their benefits are also likely to show diminishing returns (Field 2008; Zhang & Pearse 2011); we suggest that a flexible hybrid approach may be a sustainable option for real landscapes in varied ecological and social

contexts (Wilson *et al.* 2007; Yamaura *et al.* 2012; Butsic & Kuemmerle 2015).

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Data accessibility

R scripts for the optimization analysis: uploaded as online supporting information.

Data related to the CE: Dryad Digital Repository doi:10.5061/dryad.5145k (Yamaura *et al.* 2016).

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Supporting Information

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

Appendix S1. Estimation uncertainty of willingness to pay.

Appendix S2. R scripts and related files required to conduct optimization analysis.

613 Table 1. Attributes and their levels in choice experiments

Attributes	Levels
Number of bird individuals in conifer plantations*	6.2 (0% broad-leaved trees: a control scenario)
	7.8 (including 20% of broad-leaved trees)
	9.4 (including 40% of broad-leaved trees)
	11.0 (including 60% of broad-leaved trees)
	12.6 (including 80% of broad-leaved trees)
	14.3 (forest of 100% broad-leaved trees)
Number of bird-watching station in a district	1, 2, 3, and 4
Additional amount of tax payments to introduce new forest management plans	1000, 2000, 3000, 5000, and 10 000 JPY

614 * Levels were based on results of a prior empirical study (Yoshii *et al.* 2015).

615

Table 2. Results of conditional logit models

Attribute	Linear model		Quadratic model	
	Coef. (S.E.)	*P*-value	Coef. (S.E.)	*P*-value
Bird abundance in conifer plantations (per ha)				
Linear term	0.0267	0.002	0.5823	0.000
	(0.0084)		(0.0909)	
Quadratic term ($\times 10^{-2}$)			−2.5493	0.000
			(0.4153)	
Number of bird-watching stations in a district	0.0162	0.280	−0.0002	0.990
	(0.0129)		(0.0131)	
Additional amount of tax payments to introduce new	−0.0355	0.000	−0.0353	0.000
forest management plans ($\times 10^{-2}$)	(0.0009)		(0.0009)	
Alternative-specific constant for status-quo profile	−0.9488	0.000	−0.5422	0.000
	(0.0550)		(0.0861)	
Log-likelihood		−7217.3		−7198.3
Adjusted log-likelihood ratio index*		0.1410		0.1433
AIC		14442.6		14406.7

Parameter estimates with positive and negative signs mean that the attributes influence respondents' utility positively and negatively, respectively.

* This index is called a McFadden's pseudo R^2, and values of 0.2–0.4 represent an excellent fit

620 (McFadden 1979).

621

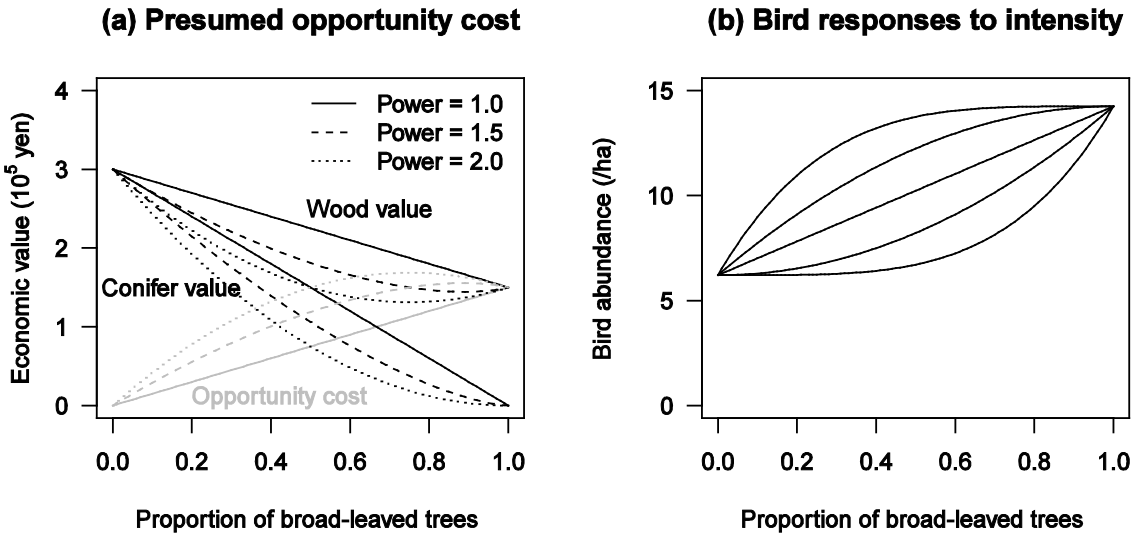
622 Table 3. ANOVA table for optimal broad-leaved tree proportion by five controlling variables as main effects

	Data with five response types*					Data with three response types**				
Variables	d.f.	SS	mean SS	*F*	*P*	d.f.	SS	mean SS	*F*	*P*
Response type	4	3.2	0.80	18.5	0.000	2	2.8	1.39	30.0	0.000
Willingness to pay	2	3.9	1.95	44.8	0.000	2	2.5	1.24	26.6	0.000
Wood value	2	10.7	5.37	123.2	0.000	2	5.9	2.94	63.3	0.000
Broad-leaved tree value	2	2.6	1.28	29.4	0.000	2	1.9	0.93	20.1	0.000
Silvicultural cost	2	0.3	0.13	3.0	0.052	2	0.1	0.04	0.9	0.417
Residuals	392	17.1	0.04	NA	NA	232	10.8	0.05	NA	NA

623 * Overall data (405 combinations of five variables) were used.

624 ** Data for shallow convex and concave responses were excluded (with 243 combinations).

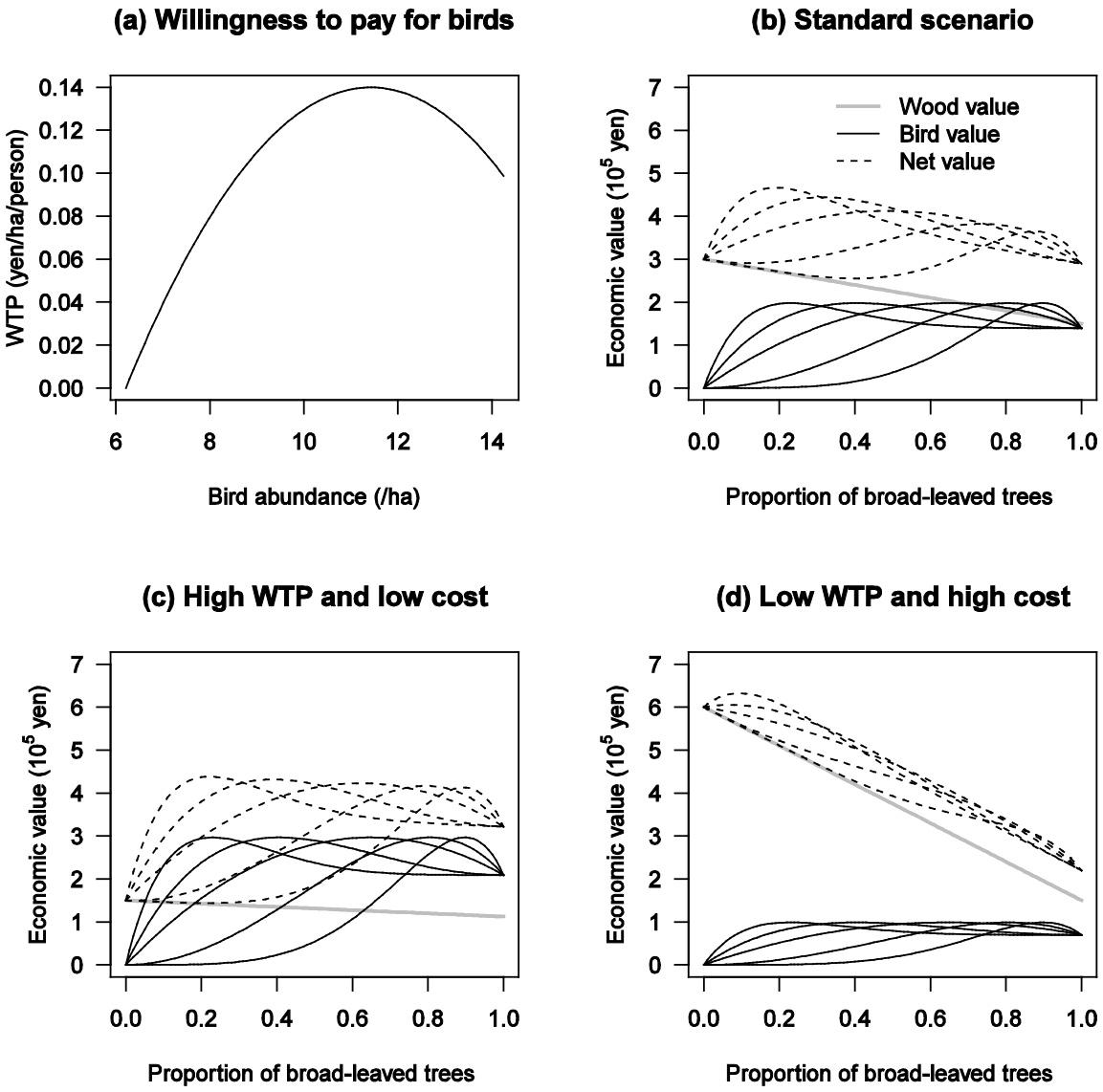
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627 Fig. 1.

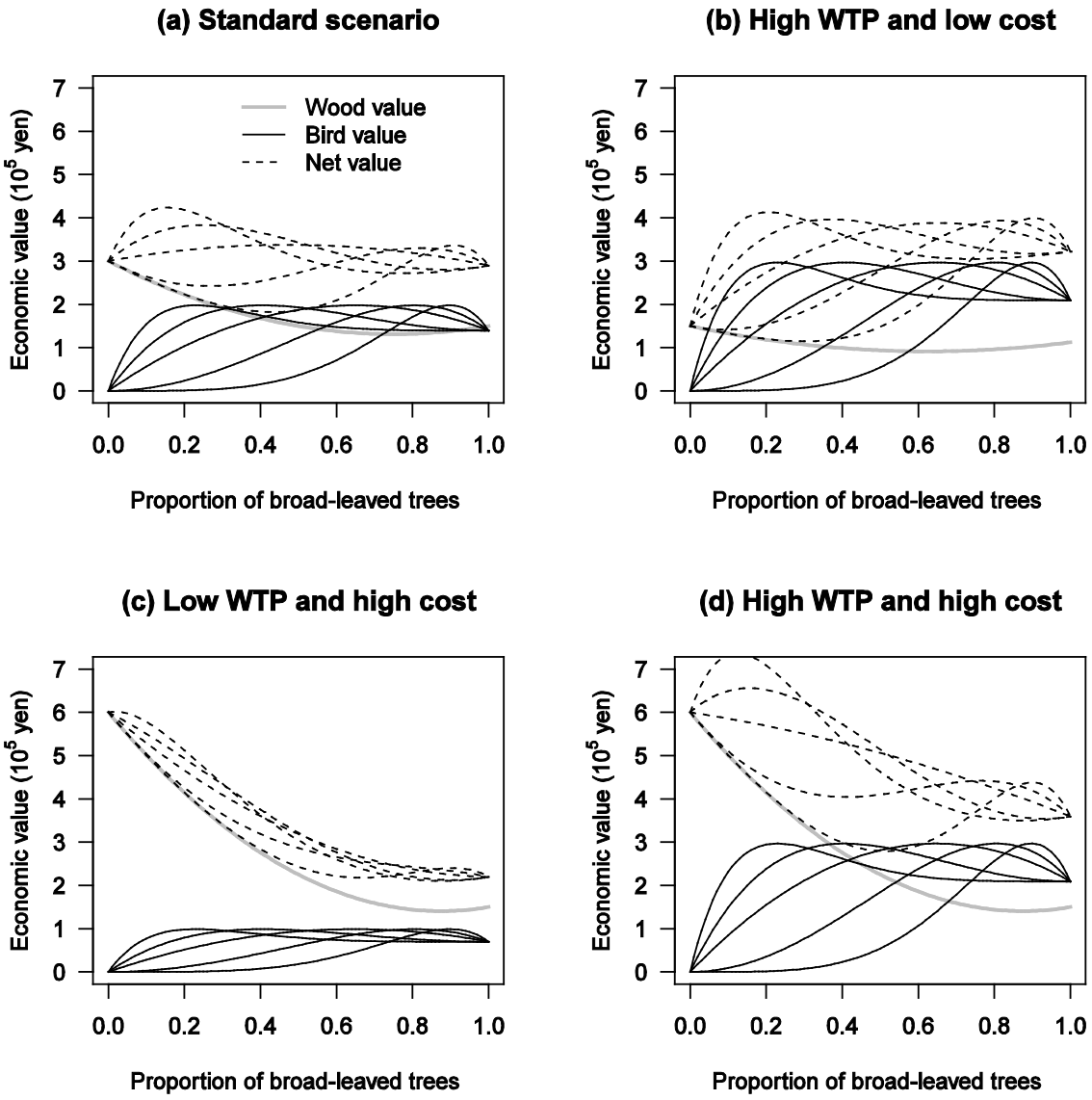
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630 Fig. 2.

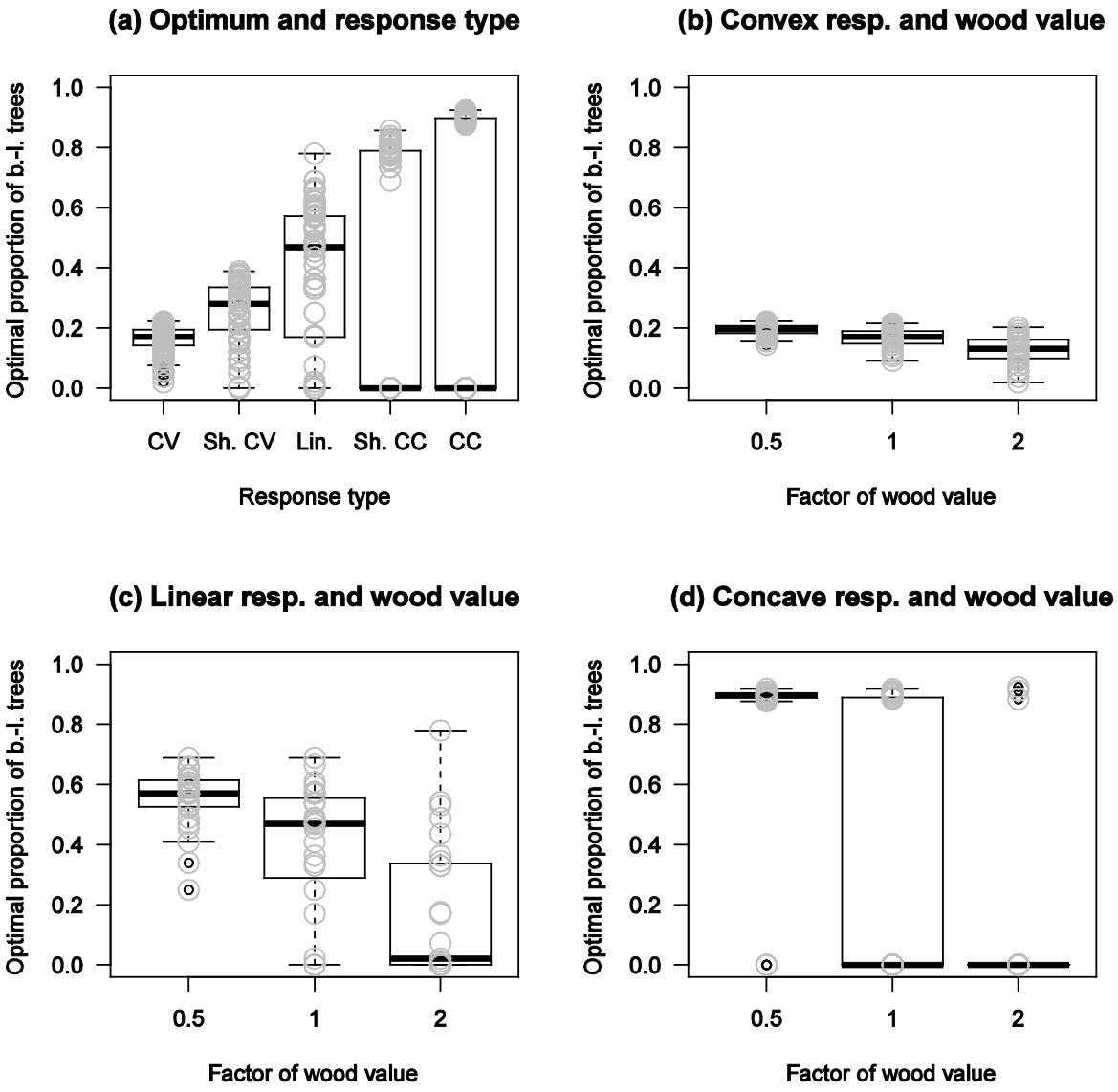
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633 Fig. 3.

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635

636 Fig. 4.

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638 Figure captions

639

640 Fig. 1. Modelled response forms of opportunity cost and bird abundance to increasing
641 broad-leaved tree proportion. (a) Opportunity cost (shown in grey) was expressed as the
642 differences between the wood value of pure plantation (p_{bl} = 0) and that of plantations with
643 broad-leaved trees (p_{bl} >0). Wood value was summed values of coniferous trees and
644 broad-leaved trees, and the single model was used to express the value of broad-leaved trees
645 (masked by the model for opportunity cost with power = 1.0). The values of coniferous trees
646 (and thus wood value) were modelled in different ways using three different levels of powers
647 in BA calculation to account for the additional silvicultural costs: 1.0, 1.5, and 2.0 (i.e. 300 m^3
648 × $p_{cnf}^{1.0}$, 300 m^3 × $p_{cnf}^{1.5}$, 300 m^3 × $p_{cnf}^{2.0}$, respectively). (b) With regard to bird abundance in
649 relation to broad-leaved tree proportion, deep convex, linear, and deep concave forms are
650 represented by $6.21 + 8.04 \times (1 - ((1 - p_{bl})^2)^2)$, $6.21 + 8.04 \times p_{bl}$, and $6.21 + 8.04 \times (1 - (1 -$
651 $((1 - (1 - p_{bl}^2))^2)))$, respectively. Shallow convex and concave forms are represented by
652 intermediate formulations.

653

654 Fig. 2. Willingness to pay (WTP) for birds and dependency of forest values on WTP, wood
655 values, and bird response forms. (a) We calculated bird prices (per ha) by multiplying the
656 WTP (per ha per person) by the total labor force in Hokkaido. (b–d) Five bird response forms
657 led to varied forms of bird and forest values as a function of p_{bl}. Wood values decreased with
658 increasing p_{bl} due to low prices of broad-leaved trees. Net values (forest values) were

obtained by summing bird and wood values. The deep convex form (the top line in Fig. 1) corresponds to the leftmost lines of bird and net values, while the deep concave form (the bottom line in Fig. 1) corresponds to the rightmost lines. Silvicultural costs were held constant at the most optimistic scenario (power = 1.0).

Fig. 3. Dependency of forest values on willingness to pay (WTP), wood values, and bird response forms under the severe silvicultural costs. The most severe silvicultural costs were presumed (power = 2.0). (a–c) The same scenarios from Fig. 2 were used. The optimal proportions with the highest net forest values were decreased from Fig. 2. (d) The highest WTP and wood value as well as lowest broad-leaved tree value were used.

Fig. 4. Boxplots of optimal broad-leaved tree proportion to maximize total benefits from the forests in relation to bird response forms and wood values. (a) Optimal broad-leaved tree proportion was separated by five response forms. (b–c) Results of deep convex, linear, and deep concave responses were also individually shown in relation to factors of wood values. Individual optimal values for the combination of four factors with three levels were depicted by grey circles.