Impacts of climate change on the supply of biodiversity in temperate forest landscapes

(With 5 Figures and 2 Tables)

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1. INTRODUCTION

Biodiversity is a cornerstone of multipurpose forest management and an important driver of ecosystem dynamics and multi-functionality (TILMAN et al., 2014). As such, it is critical that biodiversity conservation goals are integrated in the planning and management of forest resources. Yet, biodiversity levels have been decreasing at alarming rates (BUTCHART et al., 2010) and the implementation of conservation actions is urgent, in order to avoid that forest ecosystems develop to undesirable states.

Arguably, the main obstacle to implement biodiversity-oriented management in forest landscapes relates to trade-offs with production objectives (e.g. FELTON et al., 2017). Forest management needs to balance multiple goals (e.g. wood production, carbon sequestration, biodiversity supply), taking into account society's preferences and values towards various ecosystem goods and services. This demands a coupled ecological-economic approach, aiming to define optimal management solutions that increase societal welfare. Disregarding these economic aspects of biodiversity-oriented management may lead to a failure in the implementation of conservation programs and inefficient management solutions. For example, private owners may need to receive adequate compensation for supplying biodiversity in their land and public forests need to be efficiently managed in order to reduce the dependence on external capital for the implementation of biodiversity conservation programs (GUSTAFSSON et al., 2019). Additionally, managers may be interested in the optimal balance among different ecosystem services and the management actions required to achieve such balance. A main difficulty in finding optimal management solutions, however, is the fact that biodiversity is mostly considered to be a public good. As such, there are few regular markets or Payment for Ecosystem Services schemes established for biodiversity and estimates of its social value are largely missing.

In the face of these trade-offs between conservation and production objectives, it is desirable to produce a set of alternative solutions that efficiently harmonize biodiversity conservation and wood production across forest landscapes. CAVENDER-BARES et al. (2015) and POLASKY et al. (2008) propose a framework to cope with this issue, based on the computation of efficient frontiers between biodiversity and profitability, e.g. by constructing optimization models that maximize both objectives simultaneously. Thereby, we can establish a set of optimal management solutions and stakeholders may then choose the preferred option according to their preferences for bundles of ecosystem services, based on their marginal costs and benefits.

In this context, the marginal costs of biodiversity supply may be assessed through the computation of opportunity costs, taking the efficient frontier between biodiversity and profitability as a starting point. Opportunity costs refer to foregone revenues by applying biodiversity-oriented management rather than the baseline management. For example, one may compare the forest profitability under the business-as-usual (BAU) management, in terms of the net present value (NPV), and the profitability of biodiversity-oriented management. The ratio between the NPV reduction caused by biodiversity conservation actions and biodiversity increase yields the opportunity costs of biodiversity supply. The assessment of biodiversity benefits usually requires the application of stated preference methods, such as choice experiments and other indirect assessment approaches (e.g. MEYERHOFF et al., 2012). Once both biodiversity benefits and costs are established, we may decide upon the optimal management solutions with the help of decision support tools.

When computing the opportunity costs of biodiversity-oriented management, it is key to account for the impacts of environmental changes in forest dynamics, since they will cascade to forest profitability (e.g. HANEWINKEL et al., 2013), and consequently to the opportunity costs of increasing the biodiversity supply. Climate change is expected to modify a variety of forest processes and interactions, e.g. forest growth rates, species composition and disturbance activity (LINDNER et al., 2014), affecting forest profitability. These novel environmental conditions will also require new management solutions to anticipate climate impacts and adapt the current forest management portfolio.

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Our study relates to a large body of literature addressing the costs of biodiversity-oriented management and climate impacts on forest ecosystems (e.g. YOUSEFPOUR and HANEWINKEL 2009; HILY et al., 2015; REYER et al., 2014). The approaches usually applied, however, largely neglect biodiversity benefits. In addition, the uncertainty introduced by climate and valuation uncertainty on the optimal balance between conservation and production objectives is seldom addressed. Here we tackle these issues, investigating the supply of biodiversity in publicly owned forests in a temperate forest landscape under climate change. We consider the following research questions:

• What are the impacts of climate change and valuation uncertainty on the supply of forest biodiversity?

• What are the optimal management solutions to balance wood production and biodiversity provision in a temperate forest landscape?

To answer the research questions, we applied a simulation-optimization framework aiming to find an optimal balance between conservation and production objectives in a temperate forest landscape in Southwestern Germany. In our analysis, biodiversity was expressed using the indicator applied in the German Biodiversity Strategy, which is based on the abundance of forest bird indicator species. We simulated forest responses to management and climate change using a process-based growth model and evaluated biodiversity responses applying forest birds as indicators, using an N-mixture Bayesian hierarchical model. We defined the opportunity costs of biodiversity-oriented management through an optimization model, assessing the reduction in Net Present Value (NPV) of biodiversity-oriented management, compared to the baseline management (NPV maximization). Moreover, we evaluated biodiversity benefits based on the estimates from the choice experiment conducted by WELLER and ELSASSER (2018). Finally, we used these pieces of information to find optimal management solutions that take into account both costs and benefits related to forest biodiversity.

2. MATERIAL AND METHODS

Here we adopted a simulation-optimization framework to balance biodiversity supply and forest profitability, coupling ecological and economic models (*Figure 1*). To simulate forest responses, we used forest inventory data to initialize forest stands and applied the climate sensitive forest growth model 4C to evaluate management outputs and structural elements relevant for forest biodiversity under climate change. Based on this information, we quantified the economic output of forest management, in terms of the Net Present Value (NPV), and the efficient frontier between profitability and biodiversity, using an optimization approach. Our model aimed to maximize forest NPV, while increasing the levels of bird abundance across the landscape, enabling the computation of opportunity costs of biodiversity-oriented management. To assess biodiversity benefits (in terms of the willingness-to-pay), we used the results of a choice experiment to parametrize an utility function taking as inputs biodiversity and wood production. Subsequently, we used the marginal costs and the marginal benefits of an increased biodiversity provision to define the optimal management solution to balance production and conservation objectives. Finally, we performed a sensitivity analysis to assess how changes in the input parameters modified the optimal solution. In the optimization cycle, we omitted the implementation of a preferred management solution. Future inventories may be used to reevaluate the results obtained through the optimal solution and revise it accordingly, restarting the simulation-optimization cycle.

2.1 Data and forest simulation

To evaluate forest development under climate change, we used tree level forest inventory data from 98 one-hectare plots located in the Southwestern Germany, assessing the DBH and identity of all trees, and the height of 7% of the trees (for details see supplementary I). These plots were used to estimate the average forest responses for each forest age class, in terms of the standing stock, number of snags, deadwood volume, harvesting volume and species composition at each time period. Subsequently, we performed the optimized forest planning of 17503 publicly owned forest stands in the southern Black Forest, covering an area of 54227 ha.

We applied the forest growth model 4C to evaluate forest growth under different climate trajectories. 4C is a process-based model that simulates forest dynamics, forest structure, as well as water and carbon balance, taking into account multiple environmental drivers (LASCH et al., 2005). The model is also capable of simulating a variety of management interventions, including thinning, planting and final harvesting (LASCH et al., 2005). The inputs include site-specific parameters, such as location, root depth, nitrification and mineralization rates. For the stand initialization, the biomass of different tree compartments is required or, alternatively, generated using forest inventory data. The climate drivers include: average temperature, air humidity, precipitation, atmospheric pressure, solar radiation, wind speed, maximum temperature and minimum temperature. In this sense, climate change affects forest growth, mortality and the carbon and nitrogen cycle in trees and soil through changes in these parameters. Besides the processes related to photosynthesis and the water cycle, climate change alters growth patterns through carbon fertilization effects. The outputs used in our study included the carbon cycle of the forest stand, providing the biomass of different tree compartments, biomass of dead and harvested tress and the respective carbon stocks. Moreover, typical stand descriptors were used, such as stand density, DBH, height and volume. A detailed description is available in the model webpage (www.pik-potsdam.de/4c/). Additionally, to estimate the initial age of our plots we applied the stand generation routine of the forest growth model Sibyla (FABRIKA, 2007). This information was used to derive average responses for each forest age class.

We evaluated forest growth dynamics (forest growth rates, mortality and harvesting rates, among others), under five different management strategies (*Table 1*),

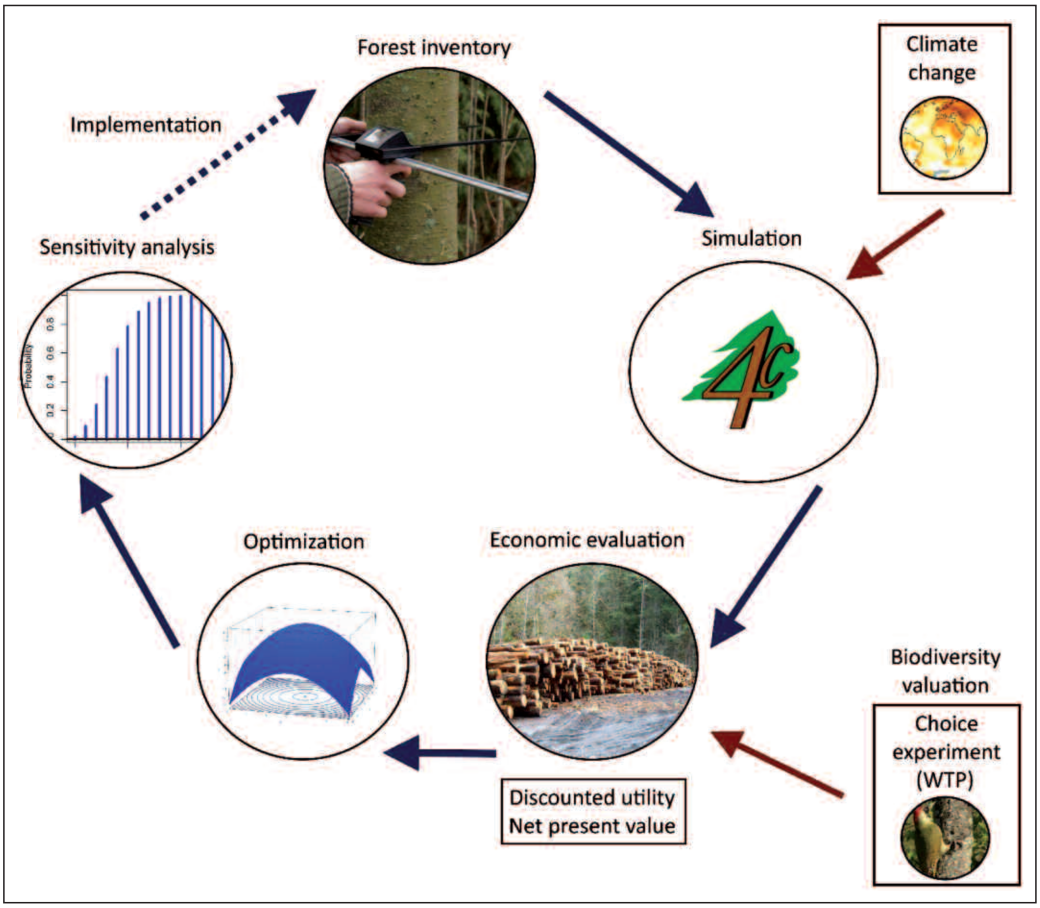

Fig. 1

Flow of the analyses conducted in our study. WTP stands for willingness-to-pay.

Ablauf der in unserer Studie durchgeführten Analysen.
WTP (willingness-to-pay) steht für Zahlungsbereitschaft.

(Sources: https://commons.wikimedia.org/wiki/File:Electronic_caliper.jpg;https://commons.wikimedia.org/wiki/File:Global_Warming_Map-he.jpg;https://www.pik-potsdam.de/4c/4c.htm;https://commons.wikimedia.org/wiki/File:MaximumParaboloid.png;https://commons.wikimedia.org/wiki/File:Forest_products_-_US_Forest_Service_-October_2017_03.jpg;https://commons.wikimedia.org/wiki/File:European_green_woodpecker_(Picus_viridis)_female.jpg)

deriving the outcomes in terms of forest profitability and bird abundance for each management regime. These results were generated under three climate change scenarios, given by a combination of the HadGEM2-ES Global Climate Model and the Representative Concentration Pathways (RCP) 2.6, 6.0 and 8.5, bias-corrected by ISIMIP (Inter-Sectoral Impact Model Intercomparison Project) (https://www.isimip.org/) with a resolution of 0.5° x 0.5°.

To assess forest profitability, we computed the forest Net Present Value (NPV) in an 80-year simulation period (the same period used in the forest growth model simulations), applying a 2% interest rate for harvesting revenues (HANEWINKEL et al., 2013), net of harvesting costs, and a 1.5% time preference for biodiversity supply (HM Treasury 2003). The interest rate is related to the market interest rate and expresses the typical return on the capital of forest investments in the region. The time preference used to discount utility represents the rate of preference from increasing the biodiversity supply now rather than some time in the future. Harvesting and planting costs were retrieved from HÄRTL et al. (2013) and for timber revenues we used the average market wood prices in Baden-Württemberg in 2016.

Forest biodiversity was evaluated using the index applied in the German Biodiversity Strategy, which is given by the abundance of 10 forest bird indicator species (DRÖSCHMEISTER and SUKOPP, 2009). To compute the abundance of the bird indicator species, we applied the model proposed in AUGUSTYNCZIK et al. (2019a), for the same research area (see supplementary II for details). The model takes as input the stand structure and site-specific parameters to estimate the abundance of bird species that were subsequently summed to yield the biodiversity indicator value. Due to sensitivity of this model to the share of conifers and the uncertainty relat-

Tab. 1
Management strategies applied in our study.
Angewandte Managementstrategien in dieser Studie.

Strategy j	Thinning	Rotation age	Species composition
1 - Business-as-usual	17% of the standing volume	Current	Current
2 - Biomass production	25% of the standing volume	-20 years	Conversion of Norway spruce to Douglas fir
3 - Biodiversity conservation	10% of the standing volume	+10 years	Conversion of Norway spruce to European beech
4 - Climate adaptation	20% of the standing volume	-10 years	Conversion of Norway spruce to Scots pine
5 - No management	No thinning	No harvesting	Current

ed to this parameter in the model, we reduced one standard deviation from the mean estimate of this parameter to provide more conservative projections of the bird responses, establishing an upper bound on the costs.

2.2 Costs of biodiversity provision and optimal management under climate change

Based on the forest responses obtained in each climate change scenario, in terms of wood production and biodiversity, we quantified the costs of biodiversity provision using an optimization approach. We applied the linear programming model developed in AUGUSTYNCZIK et al. (2019b), to maximize forest profitability (evaluated via the NPV) while respecting biodiversity requirements, in terms of increases in the bird indicator abundance (see supplementary III). Thus, the marginal cost for increasing biodiversity supply to a certain level at the end of the simulation period (referred to as a X%), was defined by the ratio in total NPV loss by applying biodiversity-oriented management and the corresponding gain in bird abundance (Eq. 1).

$$MC_{X\%} = \frac{\Delta NPV_{X\%}}{\Delta Biodiversity_{X\%}} \qquad (1)$$

Where: $MC_{X\%}$: marginal cost of a defined increase (X%) in bird abundance; $\Delta NPV_{X\%}$: change in NPV by increasing bird abundance in the defined amount (X%); $\Delta Biodiversity_{X\%}$: bird abundance gain.

2.3 Biodiversity benefits and definition of the Samuelson condition

Formally, the efficient supply of a public good (such as biodiversity) is defined based on the marginal costs and benefits related to the public good (PINDYCK and RUBINFELD, 2012). This criterion is known as the Samuelson condition (SAMUELSON, 1954), which equates the sum of marginal benefits to individuals who enjoy the good with the marginal costs of provision. In a similar fashion, one may establish optimal biodiversity supply, by equating marginal costs of biodiversity-oriented management, such as deadwood enrichment and increase in the share of broadleaved stands, with their marginal benefits, in terms of biodiversity increase and its corresponding social value.

We followed BAUMGÄRTNER et al. (2017) and applied a constant elasticity of substitution (CES) utility function taking as inputs wood and biodiversity to describe preferences for these two goods. According to the authors, the CES utility is a simple, yet rich-enough functional form that allows the study of substitutability and is compatible with benefit transfer practices. Here we considered only non-use values and computed the marginal benefits to society based on the extensive choice experiment conducted by WELLER and ELSASSER (2018). The authors evaluated the WTP for an increase in the forest biodiversity index used in the German Biodiversity Strategy. We employed the results of their multinomial model, in terms of the WTP for an increased biodiversity supply, to estimate the parameters of the CES utility function, assuming preference homogeneity. Subsequently, we defined the biodiversity benefits based on the marginal rate of substitution (MRS) between both goods and their price ratio. The wood price and consumption estimates were retrieved from the forest and wood cluster statistics (https://www.thuenen.de).

Based on the CES utility function considering wood and biodiversity (Eq. 2), we defined the willingness to pay per unit of the biodiversity indicator (% bird abundance increase) (Eq. 3) (for a description of the parameters' values see supplementary IV). We summed the biodiversity benefits along the planning horizon, discounted at a 1.5% time preference rate (HM Treasury 2003), and subsequently weighted it by the total forest area in the study region. Finally, we generated the marginal benefit curves for biodiversity, based on the sum of the WTP for the whole population and for different supply levels. With the help of this information and the marginal cost curves computed previously, we defined the Samuelson condition for different climate change scenarios.

$$Utility = \left[\alpha w^{\rho} + (1-\alpha) b^{\rho}\right]^{\frac{1}{\rho}} \qquad (2)$$

$$benefit = \frac{-b^{(\rho-1)} w^{(1-\rho)} (\alpha - 1) P}{\alpha} \qquad (3)$$

Where: *Utility*: Utility of biodiversity and wood consumption; *benefit*: WTP per unit (EUR/% bird abundance increase); *b*: Biodiversity supply (% bird abundance increase); *w*: Wood consumption per capita (m^3);

ρ: $\frac{\theta-1}{\theta}$;

θ: Elasticity of substitution between wood and biodiversity; α: Preference parameter for wood over biodiversity; P: Wood price (EUR/m^3).

3. RESULTS

3.1 Marginal costs of biodiversity provision under climate change and the Samuelson condition

The maximum net present value obtained using the optimization model described in supplementary III ranged between 3292 and 4925 EUR/ha, depending on the climate trajectory considered (*Figure 2*). As expected, there was a trade-off between profitability and increase in the levels of bird abundance. The increase in the biodiversity indicator required an increase in the share of broadleaved species and reduction of more profitable strategies, incurring in conversion costs and the reduction in the average price of the harvested timber. For the upper bound related to the bird abundance increase, the profitability would reduce on average by 72%, ranging from 606 to 1586 EUR/ha.

Based on the efficient production frontier (*Figure 2*), we computed the opportunity costs of biodiversity-oriented management. For intermediary increases in the current bird indicator abundance at the end of the century (2.5 to 12.5%), the marginal costs increased gradually, whereas for abundance increases above this threshold, it was necessary to strongly compromise forest profitability to raise bird abundance levels (*Figure 3*). The marginal cost was highest in the Had8.5 scenario and lowest for the Had2.6 scenario. For example, for a 10% bird abundance increase at the end of the century, the marginal cost amounted to 62.9 and 100.5 EUR/%abundance increase.ha^{-1} for the Had2.6 and Had8.5 scenarios, respectively. This was a result of the higher growth rates under more extreme climate change, which led to increased forest profitability and higher opportunity cost of biodiversity-oriented management.

Similar to the cost behavior, the optimal solution (satisfying the Samuelson condition) was dependent on the climate scenario and on the marginal benefits. The supply level ranged from 8 to 12.3% bird abundance increase and was lowest for the Had8.5 scenario. Due to the higher opportunity cost under this scenario, the supply amounted to a 9% abundance increase and displayed a higher marginal cost (94 EUR/% abundance increase.ha^{-1}) compared to the Had2.6 climate scenario, which required an 11.6% increase in bird abundance and at a cost of 73 EUR/% abundance increase.ha^{-1}. The Had6.0 climate scenario showed intermediary values. *Figure 3* also depicts the confidence interval of the marginal benefits of biodiversity and the supply in the upper bound would range between 10 and 12.3% increase in bird abundance, whereas at the lower bound these figures would range between 8 and 10.7% increase in bird abundance.

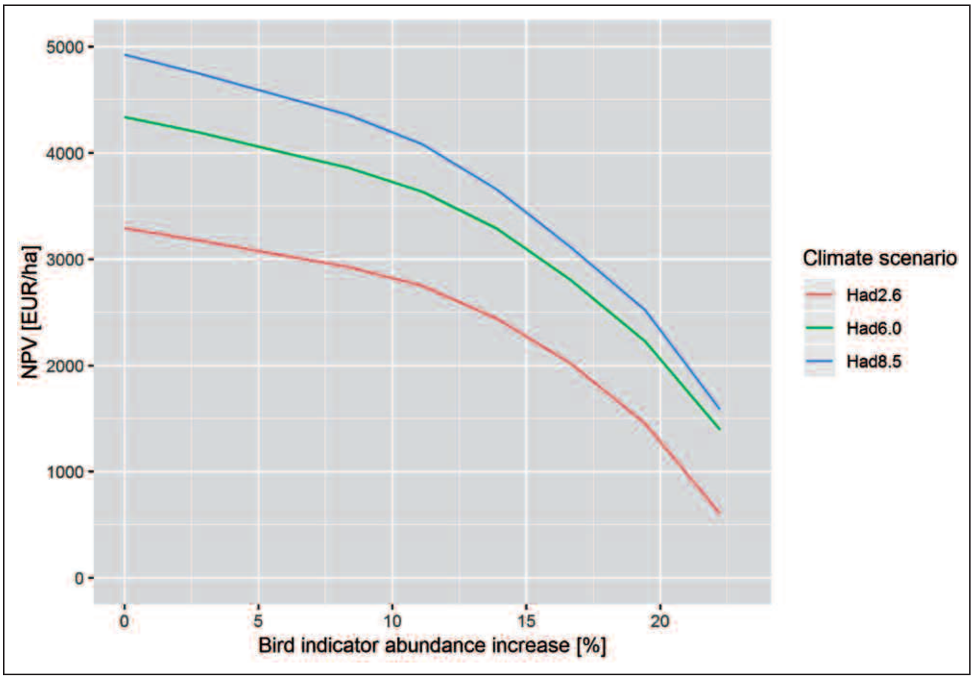

Fig. 2

Efficient production frontier between forest profitability (NPV – net present value) and bird abundance increase at the end of the century for each climate change scenario.

Effiziente Produktionsgrenze zwischen Waldrentabilität (NPV – net present value = Kapitalwert) und prozentualer Zunahme des Artenreichtums von Indikator-Vogelarten für die drei Klimawandel-Szenarien.

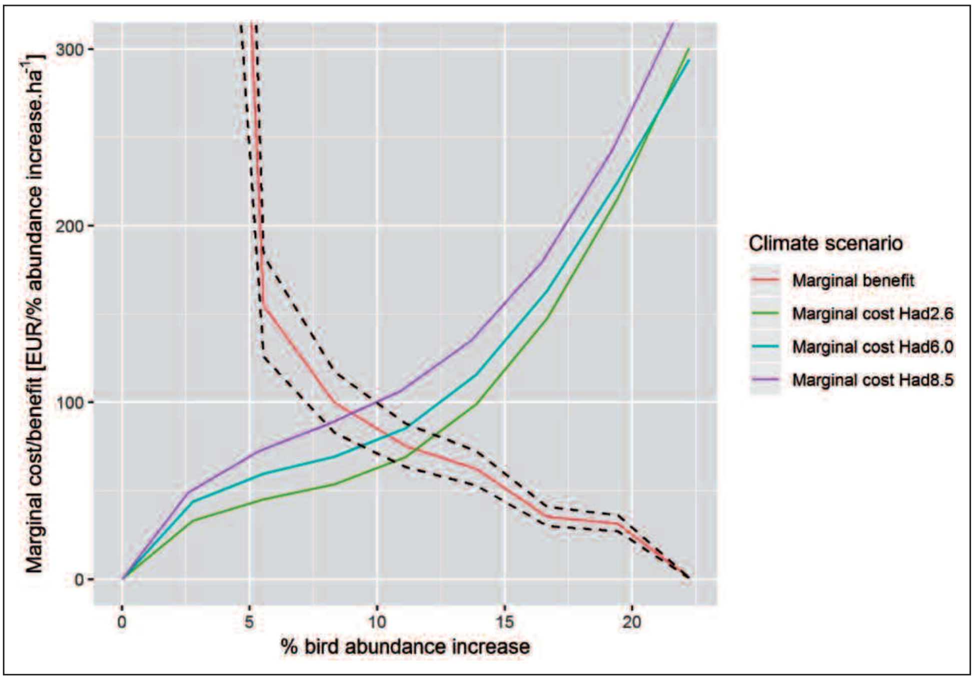

Fig. 3

Marginal costs for increasing bird abundance levels in each climate change scenario and marginal benefits, derived using a constant elasticity of substitution (CES) utility function. The dashed lines show the confidence interval of the marginal benefits.

Grenzkosten (marginal cost) für die Erhöhung des Artenreichtums von Indikator-Vogelarten Vogelarten für die drei Klimawandel-Szenarien und die Grenznutzen (marginal benefit), die sich aus einer konstanten Elastizität der Substitutionsfunktion (CES = constant elasticity of substitution) ergeben. Die gestrichelten Linien zeigen das Konfidenzintervall der Grenznutzen.

3.2 Optimal forest management

The spatial allocation of the optimal management portfolio over the stands in our study region is shown in Figure 4 and the area of each management strategy in the optimal solution is displayed in *Table 2*. *Figure 4a* displays the approximate management schedule for the solution under the climate scenario Had6.0, corresponding to a 10.4% increase in the current bird indicator abundance. We assigned to each stand in the research area an age class and used its average response (i.e. the standing volume, bird abundance levels and harvesting volumes) to derive wood production and biodiversity supply. Thus, all stands corresponding to a same age class had identical forest dynamics (same stand structure and harvesting patterns). In this sense, the landscape management pattern shown in *Figure 4* arose from the age class responses and the area of each stand (which controls its stock), in the face of the production constraints enforced in the optimization model.

We perceived a heterogeneous distribution of management strategies across the landscape, giving rise to a mosaic of management strategies. The optimal solution showed a dominant application of BAU management (22875 ha), followed by the biodiversity strategy (12036 ha) (*Table 2*). The biomass-oriented management (11242 ha) was mainly allocated to stands in youngest age classes (10-30 years old), promoting a more intense utilization of fast growing stands along the planning horizon. The biodiversity management was primarily allocated to stands in intermediary age classes (70-80 years old). This allowed to spread the planting costs for the conversion of Norway spruce stands to European beech stands. *Figure 4b* shows the approximate results for the Had2.6 scenario (11.6% increase in the current bird indicator abundance) and Figure 4c for the Had8.5 scenario (9% increase in the current bird indicator abundance). For the Had2.6 scenario, there was a wider application of the biodiversity management (13796 ha), due to the higher supply required. Conversely, under the most intensive climate change scenario (*Figure 3c*), the management portfolio needed to be diversified, increasing the area of the biomass production strategy (15276 ha), while the biodiversity strategy reduced to 10649 ha, as a result of the higher costs and lower biodiversity supply requirements.

3.3 Sensitivity analysis

The sensitivity of the results in respect to the market interest rate (IR) and the time preference for the utility discounting (TP) is shown in *Figure 5*. As expected, an increase in the IR and the TP resulted in a decrease in the marginal costs and benefits, whereas a decrease in

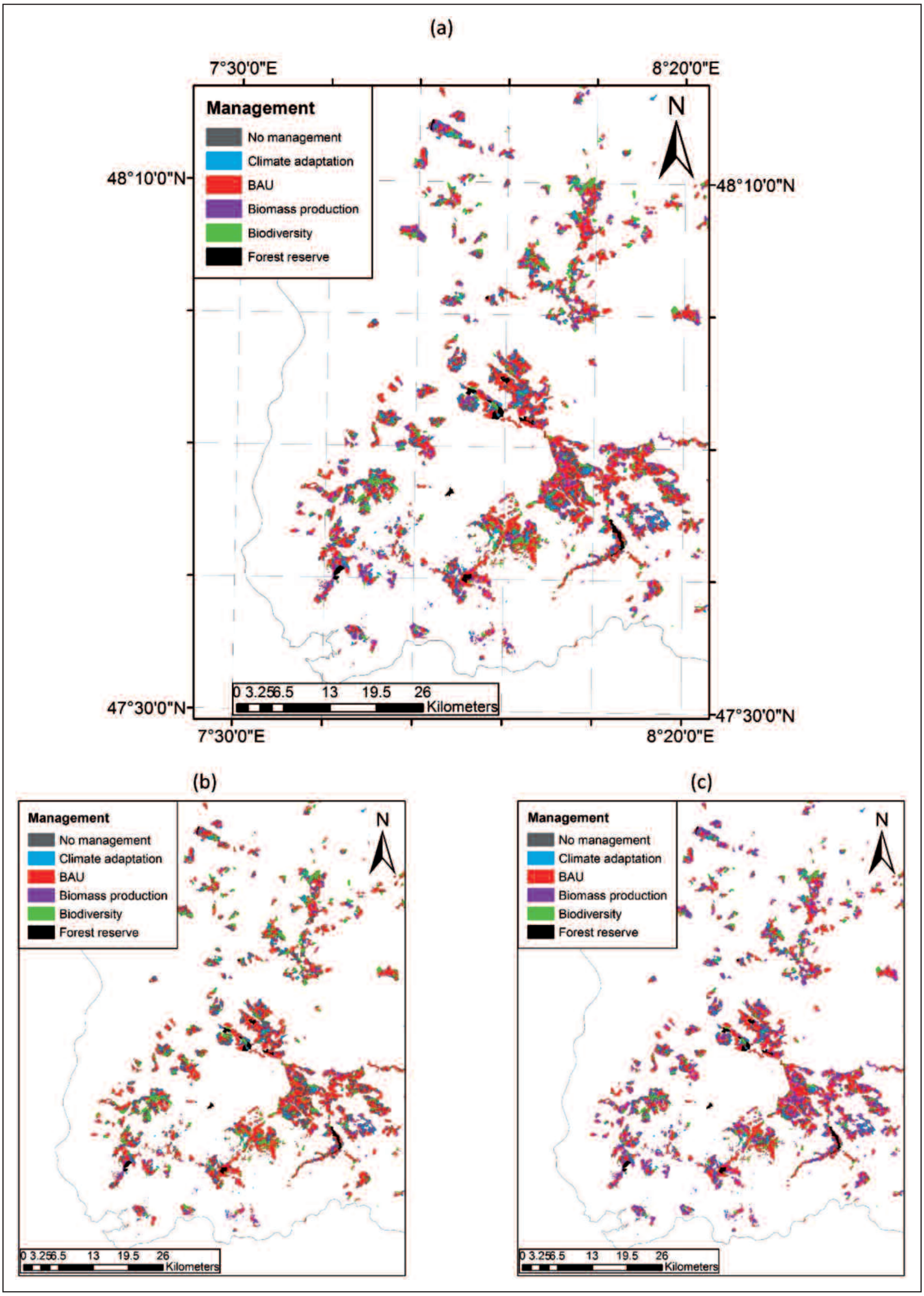

Fig. 4

Spatial allocation of management regimes across the study area for the climate scenarios Had6.0 (a), Had2.6 (b) and Had8.5 (c), at the corresponding optimal solution (Bird abundance increase = 10.4, 11.6 and 9%, respectively). BAU refers to the business-as-usual management.

Räumliche Zuordnung von Managementstrategien über das Untersuchungsgebiet für die Klimaszenarien Had6.0 (a), Had2.6 (b) und Had8.5 (c), bei der entsprechenden optimalen Lösung (Zunahme des Artenreichtums von Vogelindikatorarten= 10.4, 11.6 bzw. 9%). BAU steht für Business-as-usual-Management.

Tab. 2

Area under each management strategy for the climate scenarios Had2.6, Had6.0 and Had8.5. The percentages show the relative change in the area of each management strategy compared to the Had6.0 scenario.

Flächenanteile von jeder Managementstrategie für die Klimaszenarien Had2.6, Had6.0 und Had8.5. Die Prozentsätze zeigen die relative Veränderung der Fläche jeder Managementstrategie im Vergleich zur Fläche des Had6.0-Szenarios.

	Area (ha)		
Management strategy	**Had2.6**	**Had6.0**	**Had8.5**
1 - Business-as-usual	25048 (9.5%)	22875	21149 (-7.5%)
2 - Biomass production	5534 (-50.8%)	11242	15276 (35.9%)
3 - Biodiversity conservation	13796 (14.6%)	12036	10649 (-11.5%)
4 - Climate adaptation	5250 (0%)	5250	5250 (0%)
5 - No management	3376 (110.9%)	1601	680 (-57.5%)

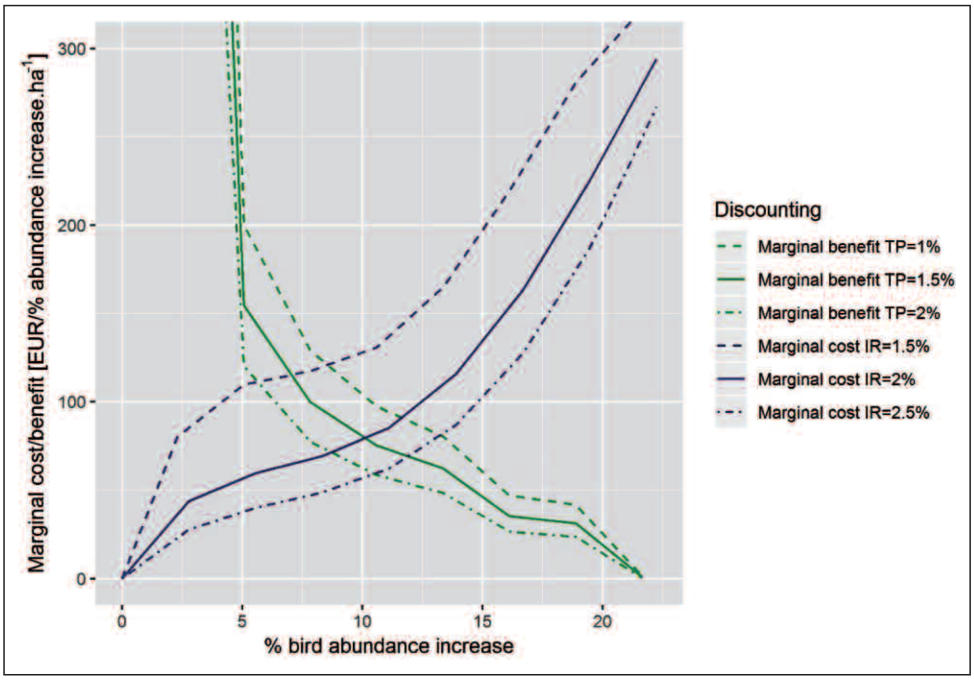

Fig. 5

Impacts of varying interest rate (IR) and the rate of time preference for the utility discounting (TP) for the Had6.0 scenario.

Veränderung der Grenzkosten/Grenznutzen in Abhängigkeit von unterschiedlichen Zinssätzen (IR = interest rates) und Zeitpräferenzsätzen für die Utility-Funktion (TP = time preference) für das Had6.0-Szenario.

these values increased costs and benefits. This means that changes in interest rate and the rate of time preference had opposing impacts on the optimal solution. An increase in market interest rates reduced forest profitability, leading to a cheaper implementation of biodiversity-oriented management and an increase in the supply level. Conversely, an increase in the rate of time preference reduced the aggregated marginal benefit, decreasing the supply level. For the Had6.0 scenario, we observed a provision level of 10.4% increase in bird abundance for a 2% interest rate and a 1.5% time preference. An increase (decrease) in the market interest rate to 2.5% (1.5%) would shift the provision level to 12% (7.1%). On the other hand, an increase (decrease) in the time preference rate to 2% (1%) would shift the provision level to 8.7% (11.7%).

4. DISCUSSION

Here we characterized the Samuelson condition for the supply of forest biodiversity under climate change in a temperate forest landscape. This condition requires that biodiversity is provided so that the marginal cost of supply equals the sum of marginal benefits to society. Our results show that future climate has important implications for the supply level of forest biodiversity, with increasing marginal costs under more intensive climate change. Additionally, uncertainty regarding the social value of biodiversity may further increase the range of possible management solutions in temperate landscapes.

4.1 Biodiversity supply under climate change

Climate change had important implications for forest dynamics that cascaded into the opportunity costs of biodiversity supply. In more productive climate scenarios, wood production became comparatively more advantageous than biodiversity provision, shifting the marginal cost curve (biodiversity supply) and reducing the supply level. Several studies show similar patterns and report that climate change may have important implications for forest management and its economic output, as well as to the costs of conservation practices (AUGUSTYNCZIK and YOUSEFPOUR, 2019; HANEWINKEL et al., 2013; TIAN et al., 2016). It is thus crucial to take into account climate impacts on conservation policies and inform decision-makers of the possible ranges of the desired outputs and to identify robust solutions towards climate and other sources of uncertainty (YOUSEFPOUR et al., 2017).

The optimal solutions obtained in our study suggest that a substantial increase in forest biodiversity is demanded in the study region. Biodiversity-oriented management can be applied to reduce the gap between current and efficient biodiversity supply, fostering a sustainable and efficient use of forest resources (CUBBAGE et al., 2007). Promoting such diverse ecosystems will be essential to increase resilience and resistance under climate change (DUVENECK and SCHELLER, 2016; ISBELL et al., 2015). In this context, the creation of compensation schemes and market-like mechanisms need to be further promoted, in order to correct biodiversity supply and avoid irreversible losses in ecosystem functioning under climate change. Options to implement these schemes may include biodiversity auctions, voluntary contribution mechanisms and tradable permits (e.g. ROESCH-MCNALLY et al., 2016; TÓTH et al., 2010), which can be tailored to regional conditions, in terms of habitat quality and preferences for forest biodiversity.

The definition of the Samuelson condition required the quantification of marginal costs and benefits from biodiversity. The evaluation of biodiversity benefits is time and resource-intensive, and particular to the study cases. As a result, comprehensive biodiversity benefits evaluations are largely missing in the literature. Since different taxa may have diverging habitat requirements, these evaluations are urgently needed, in order to handle trade-offs in the provision of habitat for different species and to improve management efficiency according to societal demands. In this sense, the assessment of the responses of multiple taxa to forest management and their respective social value is necessary and deserves a closer investigation.

We assessed biodiversity applying the indicator of the German Biodiversity Strategy, based on the abundance of forest bird indicator species. Although the use of bird indicator species can be appropriate for forest biodiversity (MIKUSINSKI et al., 2001), it may also display shortcomings. Particularly, forest birds have different requirements, in terms of habitat, compared to other taxa. For example, species dependent on old growth habitats and deadwood may respond better to deadwood enrichment and increased area of set asides, rather than increasing the share of broadleaved trees at the landscape scale. In this sense, future studies may investigate the responses of different indicator species and additional management options for biodiversity enrichment.

Apart from climate change impacts, other input parameters may affect the biodiversity provision levels. Particularly, the discounting schemes had a significant influence in the decision-making process. An increase in the market interest rate would reduce forest profitability, shifting the supply curve downwards and increasing the supply level. Conversely, an increase in the rate of time preference in the utility discounting would reduce future biodiversity benefits, shifting the demand and decreasing the supply level. Other points of uncertainty not included in our analysis also deserve further investigation, e.g. the uncertainty in wood prices and wood demand, as well as the development of preferences for biodiversity in the future and the uncertainty introduced by forest disturbances on forest dynamics.

4.2 Optimal forest management

Our study suggests that a diversified portfolio of management strategies was required to achieve a balance between conservation and production objectives, taking into account the local potential for the supply of different goods and services. Apart from the diversification of forest management, integrative approaches need to be further encouraged to harmonize conservation at landscape and local scales, for example through an optimal allocation of habitat trees and deadwood enrichment efforts (AUGUSTYNCZIK et al., 2018; DOERFLER et al., 2018). Thereby, we may maintain ecosystem complexity at multiples scales and promote alpha, beta and gamma diversity to create resilient forest landscapes.

Our results indicate that current management is often not well suited to account for the adequate social value of forest biodiversity and policy mechanisms are required to internalize the value of forest biodiversity into forest management. The uncertainty on the societal values, however, allied to climate change results in a range of the biodiversity provision level (8 to 12.3% increase in the biodiversity index). In this sense, approaches to cope with these uncertainties are required. Mechanism design is a natural approach to tackle these issues when deciding upon the supply of forest biodiversity (e.g. ESPINOLA-ARREDONDO, 2008) and a closer investigation of this framework regarding the implementation of biodiversity conservation policies is encouraged.

In our analysis, we considered the benefits generated by wood production and biodiversity supply. Nevertheless, optimized management solutions ideally need to include the full range of ecosystem goods and services enjoyed by society. Hence, future studies may focus on resolving trade-offs among a multitude of ecosystem goods and services, including for example water quality, carbon sequestration and soil protection. We highlight, however, that our framework may be easily adapted to such scenarios, by an extension of the outputs considered in the economic analysis and the inclusion of extra objectives in the objective function of the optimization model. This may then be solved by the application of multi-objective optimization methods, such as compromise programming and goal programming (e.g. YOUSEFPOUR et al., 2018).

5. CONCLUSIONS

Forests are embedded in strongly coupled ecological-economic systems that involve numerous stakeholders and their respective demand for different goods and services. Economic aspects are among the main drivers of decision-making in forestry and therefore need to be taken into account when managing forest resources and planning conservation actions. Due to the complex nature of forest ecosystems and its dependence on the underlying socio-economic conditions that drive its management, a multidisciplinary approach is required to tackle the supply of biodiversity and other ecosystem goods and services in forest landscapes. Coupling ecological and economic models in a simulation-optimization framework is a promising way to improve the description of forest ecosystem processes and better inform decision-making. This is key to promote biodiversity-oriented forest management and increase the resistance and resilience of these ecosystems under environmental pressures, securing the flow of goods and services that constitute human well-being.

6. ZUSAMMENFASSUNG

Titel des Beitrages: *Auswirkungen des Klimawandels auf die Biodiversitätsversorgung in gemäßigten Waldlandschaften.*

Biodiversität ist die Basis für das Funktionieren von Waldökosystemen und für die Bereitstellung einer Vielzahl von Ökosystemgütern und -dienstleistungen, und kann damit einen großen Beitrag zum Wohlbefinden des Menschen beitragen. Dieser sozio-ökonomische Wert der Biodiversität wird jedoch bei der Waldbewirtschaftung selten berücksichtigt. Da Biodiversität den Charakter eines öffentlichen Guts hat, ist die Miteinbeziehung ihres sozio-ökonomischen Wertes in den Entscheidungsprozess der Waldwirtschaft besonders schwierig. Neue Strategien sind erforderlich, die die Biodiversitätsversorgung gewährleisten und sozio-ökonomische Funktionen fördern, während gleichzeitig Waldressourcen weiterhin nachhaltig genutzt werden können. Hier schlagen wir einen gekoppelten, modellbasierten Lösungsansatz vor, in dessen Rahmen wir das effiziente Versorgungsniveau der Biodiversität unter Klimawandel berechnen und Waldavifauna als Biodiversitäts-Indikatoren verwenden. Präferenzen für Holznutzung oder Biodiversität wurden mit einer konstanten Substitutions-Elastizitäts Funktion festgelegt und die Samuelson-Bedingung für die Biodiversitätsversorgung unter Klimawandel berechnet Anschließend wurde die Walddynamik unter Klimawandel mit dem prozessbasierten Waldwachstumsmodell 4C bewertet. Unser Untersuchungsgebiet war der Südwesten Deutschlands angewandt. Unsere Ergebnisse zeigen, dass die effiziente Biodiversitätsversorgung, ausgedrückt in einer Zunahme des Artenreichtums von Vogelindikatorarten, zwischen 8 und 12.3% liegt, abhängig von den Klimaszenarien und der mit der Biodiversitätsbewertung verbundenen Unsicherheit. Stärkere Klimawandelszenarien erhöhen die Opportunitätskosten der Biodiversitätsversorgung und senken das effiziente Versorgungsniveau. Darüber hinaus zeigen wir, wie eine optimale Verteilung der Managementstrategien auf der Landschaftsebene diese effiziente Versorgung realisieren kann. Gekoppelte ökologisch-ökonomische Modelle sind vielversprechende Instrumente, um den sozio-ökonomischen Wert der Biodiversität in die Waldbewirtschaftung zu integrieren und damit entscheidende Information für Planungsprozesse bereitzustellen.

7. ABSTRACT

Forest biodiversity underpins ecosystem functioning and the provision of multiple ecosystem goods and services that are essential to human well-being. Still, the social value of biodiversity is rarely taken into account in the management of forest resources. Forest biodiversity is a public good and, as such, it complicates the process of internalizing its social value in the decision-making process. New forest conservation strategies are needed to correct biodiversity supply and promote an efficient use of forest resources. Here we propose a simulation-optimization framework to tackle this issue and compute the supply level of forest biodiversity under climate change, using forest birds as indicators. We describe preferences for wood and biodiversity using a constant elasticity of substitution utility function, and evaluate forest dynamics under climate change using the process-based growth model 4C. We applied our framework to a temperate forest landscape in Southwestern Germany and computed the Samuelson condition for biodiversity supply in the region under climate change. Our results show that the biodiversity supply, expressed as an increase in the abundance of bird indicator species, ranged between 8 to 12.3%, depending on the climate trajectory and the uncertainty related to biodiversity valuations. More intensive climate change scenarios increased the marginal costs of biodiversity provision and reduced the supply level. Moreover, we show how an optimal allocation of management strategies across the study area could realize the required supply. We conclude that coupled ecological-economic models are a promising tool to internalize the social value of biodi-

versity into forest management plans and to better inform decision-makers.

8. RESUMÉ

Titre de l'article: *Impacts du changement climatique sur l'offre de biodiversité dans les paysages forestiers tempérés.*

La biodiversité forestière est à la base du fonctionnement de l'écosystème et de l'offre de multiples biens et services écosystémiques essentiels au bien-être humain. Néanmoins, la valeur sociale de la biodiversité est rarement prise en compte dans la gestion des ressources forestières. La biodiversité forestière est un bien public et, en tant que tel, elle complique le processus d'internalisation de sa valeur sociale dans le processus de prise de décision. De nouvelles stratégies de conservation des forêts sont nécessaires pour corriger l'offre de biodiversité et promouvoir une utilisation efficace des ressources forestières. Nous proposons ici une approche combinée de simulation-optimisation afin de traiter ce problème et de calculer le niveau d'offre de biodiversité forestière sous changement climatique, en utilisant les oiseaux forestiers comme indicateurs. Nous décrivons les préférences pour le bois et la biodiversité en utilisant une fonction d'utilité à élasticité de substitution constante et évaluons la dynamique de la forêt sous l'effet du changement climatique à travers le modèle de croissance 4C. Nous avons appliqué notre méthologie à l'échelle du paysage en forêts tempérées d'Allemagne du Sud-Ouest et calculé les conditions de Samuelson pour l'offre de biodiversité de cette région sous changement climatique. Nos résultats montrent que l'offre de biodiversité, correspondant à une augmentation de l'abondance des espèces indicatrices d'oiseaux, varie entre 8 et 12.3%, en fonction de la trajectoire climatique et de l'incertitude liée à l'évaluation de la biodiversité. Des scénarios de changement climatique plus intensifs ont augmenté les coûts marginaux de l'offre de biodiversité et réduit le niveau de l'offre. De plus, nous montrons de quelle manière une allocation optimale des stratégies de gestion dans la zone d'étude pourrait réaliser ce niveau d'offre requis. Nous concluons que les modèlesécologiques et économiques couplés sont un outil prometteur pour intégrer la valeur sociale de la biodiversité dans les plans de gestion des forêts et pour mieux informer les décideurs.

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