Habitat enhancements for reptiles in a beech forest may increase fungal species richness

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Received: date / Accepted: date

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Abstract The success of habitat enhancements is typically assessed by subsequent monitoring of the focal taxonomic group. However, enhancement actions are likely to affect other, non-targeted species. On a south-facing slope in the Swiss Jura mountains, a mixed-forest stand was thinned out by irregular removal cuttings to improve the habitat conditions for reptiles. We used this enhancement action as a case study to monitor changes in the macrofungal community that came along with it. During three years before and after forest thinning, the site was visited between six and twelve times per year. Thereby, all apparent fungal species were recorded along a ringlike transect, split into 32 transect sections. We used site-occupancy models to estimate fungal species richness and abundance. These models allow to separately estimate occurrence probability and detection probability of species, and to account for differences in detection probability, depending on habitat and season. After the forest thinning, the occurrence probabilities of ectomycorrhizal and saprobic fungi were significantly higher than before. As a result, we estimated a mean increase in overall species richness by 4.4 % (median 4.3 %, CI 2.1–6.8 %) and an increase in abundance by 20.0 % (median 19.9 %, CI 14.8–25.7 %). The two major habitat changes associated with forest thinning, the decrease in living wood and the increase in dead wood on most transect sections, could not explain the whole extent of the estimated increase in species richness and abundance. We believe that forest thinning may have fostered fungal species richness by creating a larger density and diversity of suitable microhabitats. With some caution, we conclude that the small-scale habitat enhancement for reptiles at the Bolberg, creating islands of open forest, did not negatively affect species richness and abundance of macrofungi, a non-targeted species group.

Keywords biodiversity · forest management · reptile conservation area · forest thinning · site-occupancy · hierarchical Bayes

1 Introduction

The species richness of European temperate forests today is the result of centuries of various human activities, which were carried out at a local scale depending on site conditions, ownership, cultural, economic and social conditions (Küster, 1995). While large-scale natural deciduous forests are almost lacking in Central Europe and our knowledge on their biodiversity remains scanty (Parviainen et al., 2000), more is known about species richness of open woodlands, whose abundance has diminished considerably (well documented for Switzerland in Stuber and Bürgi, 2011). In the last 150 years, these often pastured woodlands have been transformed into even-aged spruce plantations or into closed beech forests (Mather et al., 1999; Brunet et al., 2012), where microsites for light demanding and thermophile species became rare (Korneck et al., 1998). A consequence of this change in land use is that many open woodland species, such as snakes and lizards, became threatened and need specific conservation measures (Kraus and Krumm, 2013).

Habitat enhancements usually aim at fostering specific, often vulnerable taxonomic groups such as plants (e.g., Känzig-Schoch, 1996), birds (e.g., Brichetti and Di Capi, 1987; Buner et al., 2005; Eglington et al., 2009; Fischer et al., 2009), reptiles (e.g., Shoemaker and Gibbs, 2010; Pike et al., 2011; Earl et al., 2017), butterflies (e.g., Heer et al., 2013; Dolek et al., 2018) or fungi (Dove and Keeton, 2015). The success of habitat enhancements is typically assessed by monitoring the targeted taxonomic group. However, enhancement actions are likely to affect other, non-targeted species living in the area. For instance, removal of the tree canopy or its partial removal to create canopy gaps leads to various changes in the conditions at the forest floor level by altering light conditions, temperature regime and micro-climate extremes (Coince et al., 2013). These changes eventually affect the soil water and nutrient dynamics (Železnik et al., 2016).

A decline in species richness of macrofungi in canopy gaps (due to logging or windthrow), at least until the canopy is closed again, was reported in various studies (e.g., Bader et al., 1995; Grebenc et al., 2009; Heine et al., 2019), and subsequent shifts in fungal communities in the soil were observed by Kyaschenko et al. (2017). However, the event of tree cutting and the annual cutting of shrubs and young trees produces a considerable amount of dead wood. If this dead wood remains on the site, wood-inhabiting fungi may profit from such measures in the long run (Heilmann-Clausen and Christensen, 2004; Ódor et al., 2006; Heilmann-Clausen et al., 2014). Moreover, the lack of sporocarps of ectomycorrhizal fungi does not necessarily mean the absence of ectomycorrhiza in the soil, which may still be symbiotically associated with the remaining trees on the site and are important to recruit new trees (e.g., Egli et al., 2002; Grebenc et al., 2009; van der Linde et al., 2012). In fact, in a review on the regeneration of ectomycorrhizal fungal communities after clearcut logging, Jones et al. (2003) concluded that there is no empirical evidence for a reduction in inoculum potential with the age of a clearcut. Ectomycorrhizal fungi may therefore occasionally also produce sporocarps in regeneration plots.

In this case study, we monitored species richness and abundance of macrofungi as non-target taxonomic group of an enhancement action in a reptile conservation area. The habitat enhancement for reptiles mainly involved forest thinning to increase soil surface warming. We hypothesized a decrease in species richness and abundance of macrofungi after the enhancement action.

2 Methods

2.1 Study site and set-up

The study site was located in the valley of Laufen near Basel (Switzerland) on the south-facing slope of a hill named Bolberg (375–550 m asl), on calcareous bedrock covered with mixed woodland (Online Resource 1, Fig. 4). Until the end of the 19^{th} century, the forest was over-exploited as coppice and wood pasture. As a consequence of the first Federal Law on Forest, implemented in 1876 to stop the degradation of forests in Switzerland, it gradually developed into a dense forest. Today, the forest is dominated by European beech (*Fagus sylvatica*), mixed with European hornbeam (*Carpinus betulus*), Large-leaved lime (*Tilia platyphyllos*), Scots pine (*Pinus sylvestris*), Common whitebeam (*Sorbus aria*), Norway spruce (*Picea abies*), Sessile oak (*Quercus petraea*) and Italian maple (*Acer opalus*). By the end of the 20^{th} century the moderate forestry use was ceased due to low rentability. Within the scope of a reptile conservation project the woodland was thinned, by removal cuttings between March 22 and April 20 in 2004, creating gaps in an irregular manner across the site (hereafter referred to as "thinning"). The objective of this intervention was to increase the amount of incident infrared radiation on the ground. A ringlike transect of almost 1 km length was established within the study site in 2001 in order to monitor fungal species before and after the intervention. The width of the transect was ca. 400 m in W–E and 150 m in N–S direction. It was situated between 470 and 530 m asl (Online Resource 1, Fig. 5). The transect was divided into 32 equally sized sections of ca. 32 m length.

2.2 Data collection

During three years before (2001–2003) and after (2004–2006) the thinning, two fungal specialists (P.B. and B.E.) regularly visited the site to record all apparent fungal species along each transect section, based on sporocarps. Twelve and eleven visits were conducted in 2001 and 2002, respectively, and six visits in each other year (47 visits in total, first yearly visit no later than April 25, last visit on November 2 at the earliest). All fungal species detected within a band of 8 m width (4 m on each side of the marked transect) were recorded. Before (3^{rd} June 2002) and after thinning (5^{th} November 2005), all trees within a 6 m band and with a minimum diameter at breast height (DBH; 1.3 m) of 5 cm were recorded in each transect section (living wood). Trees were identified to the species level and their DBH was classified in 5 cm classes. Moreover, the amount of dead wood on the ground was determined on 21^{st} March 2004 and 15^{th} April 2007. We paced along the transect line and recorded the diameters (in classes of 2 cm) of all pieces of dead wood we crossed with a minimum diameter of 1 cm. To monitor the weather conditions during the six years of our study we calculated average air temperature and total precipitation per month from the nearest weather station of the Swiss national weather service, Delémont (ca. 10 km from the Bolberg site).

2.3 Data preparation

A total of 77 species of ectomycorrhizal fungi (further referred to as EMF) and 315 species of saprobic fungi (further referred to as SF) were observed over the study period (n=392 in total, species list in Online Resource 3). The amounts of dead and living wood were summarized per transect section. Dead wood was quantified as the sum of the diameters (in cm) of all recorded pieces of dead wood. Living wood was quantified as volume (in m^3). The volume of each tree was estimated by a stand specific tariff function, which only requires DBH as input parameter (a method used for the Swiss National Forest Inventory Kaufmann, 2001), and tree volumes were summed per transect section.

2.4 Site-occupancy models

We used multi-species site-occupancy models (MacKenzie et al., 2002) to estimate fungal species richness and abundance. Site-occupancy models separately model and estimate the probability that a species is present, and the probability to detect a species if it is present. This allows the estimation of species richness and abundance, adjusted for imperfect detection probabilities of species (typically < 1). Moreover, detection probability can be modelled as dependent on species, habitat, and season. If such dependencies exist, ignoring variation in detection probability leads to systematically biased correlations of species richness and abundance with habitat variables. A requirement of site-occupancy models is, however, the availability of multiple assessments during the period of interest (year in our case). It is then assumed that species occurrence is constant within this period, i.e, a species is either present or absent.

We fitted two site-occupancy models to our data that differ in the sub-model for occurrence probability (model code for both given in Online Resource 2). The *forest thinning model* simply includes the thinning in spring 2004 (before vs. after) as an explanatory factor, without taking into account the actual habitat changes. In contrast, the *habitat model* incorporates (as continuous explanatory variables) the two most obvious habitat changes due to thinning: the increase in dead wood and the decrease in living wood. Whereas the *forest thinning model* was fitted primarily to estimate species richness and abundance before and after the thinning, the *habitat model* was fitted to investigate the relationships with actual habitat changes (potential mechanisms).

The *forest thinning model* can be described as follows: It is a hierarchical model with two sub-models. One sub-model describes the biological process of the occurrence (occupancy, presence vs. absence), z_{aij}, of species a in transect i in year j. The other sub-model describes the observation (observed vs. unobserved), y_{aijv}, of species a in transect i in year j at visit v. A species can only be observed when present, but it may remain unobserved when present. Both processes (occurrence and observation) can be modeled with a Bernoulli-distribution (binary distribution):

$$z_{aij} \sim Bernoulli(\psi_{aij}) \quad (1)$$

$$y_{aijv} \sim Bernoulli(z_{aij} * p_{aijv}) \quad (2)$$

The logit of the occurrence probability ψ_{aij} per species a, transect section i and year j was linearly related to the functional group (fg, saprobic vs. ectomycorrhizal), the phase (ph, before vs. after thinning) and the species. The functional group, the phase and their interaction were modeled as fixed predictors. Species was modeled as normal random factor:

$$logit(\psi_{aij}) = \alpha_{fg(a),ph(j)} + \varepsilon_a \tag{3}$$

$$\varepsilon_a \sim Normal(0, \sigma_a) \tag{4}$$

The hierarchical logistic model thus included a separate intercept, $\alpha_{fg(a),ph(j)}$, for each combination of fg and ph, and a random intercept for each species, ε_a. The random intercepts are normally distributed around a mean of zero with standard deviation σ_a.

The logit of the detection probability p_{aijv} per species a, transect section i, year j, and visit v was linearly related to the day (day 1 to 365 or 366 of the year, for scaling see below), and the square of the day (day^2), the amount of dead wood (dw, sum of branch diameters, for scaling see below), the amount of living wood (lw, tree volume, for scaling see below) and the functional group (saprobic vs. ectomycorrhizal). Thereby, the coefficients of the day (linear and squared) were allowed to differ between species by adding normally distributed, species-specific random slopes to both parameters. Moreover, the interactions of functional group with both habitat parameters (dead wood and living wood) were included:

$$\begin{aligned} logit(p_{aijv}) =& \beta_{0(a)} + \beta_{1(a)} * day_{j,v} + \beta_{2(a)} * day^2_{j,v} + \\ & \beta_3 * dw_{i,j} + \beta_4 * lw_{i,j} + \beta_5 * sap_a * dw_{i,j} + \beta_6 * sap_a * lw_{i,j} \end{aligned} \tag{5}$$

By including species-specific slopes of day, β_1 (linear) and β_2 (quadratic), as predictors in the sub-model for detection probability we took into account that the visible sporocarps appear only during species-specific periods of the year. The parameters β_3 and β_4 represent the associations of dead and living wood (dw and *lw*) with the detection probability of EMF species (one slope each), β_5 and β_6 represent the differences in these associations (slopes) between SF and EMF species. This means that a separate coefficient of dead and living wood was modeled for EMF and SF species, with associations of dead and living wood with the detection probability of SF species being $\beta_3+\beta_5$ and $\beta_4+\beta_6$, respectively. To improve the convergence of the model fitting algorithm, the variable day was centered and scaled to one month (30 days) units. Likewise, the amount of dead wood was centered and scaled to 10 cm units. The amount of living wood was centered only.

Coefficient estimates from the model are reported as odds ratio (OR) estimates on the backtransformed (inverse logit) scale. Note that an OR > 1 indicates an increase whereas an OR < 1 indicates a decrease. In addition, we estimated the following derived parameters from the model: (1) the number of species per transect section and year (species richness of transect sections), (2) the number of transect sections with the species present per species and year (species abundance), (3) the occurrence of each species in each year (to assess the steadiness of species presence over the study period) and (4) the total number of species at the Bolberg per year (species richness of the entire study site).

The *habitat model* only differs from the *forest thinning model* in the sub-model for the probability of occurrence ψ_{jia}. Instead of attributing each year to either the pre- or post-thinning phase, species occurrence was modeled as dependent on the amount of dead and living wood, measured before and after the thinning (changes in dead and living wood per transect section are shown graphically in Online Resource 1, Fig. 4). As in the model for detection probability, the associations of *dw* and *lw* with occurrence probability were estimated separately for EMF and SF species, i.e., by a separate intercept $\alpha0_{fg(a)}$ and two separate slopes $\alpha1_{fg(a)}$ and

$\alpha 2_{fg(a)}$. The model also includes a random intercept for each species, ε_a.

$$logit(\psi_{jia}) = \alpha 0_{fg(a)} + \alpha 1_{fg(a)} * dw_{i,j} + \alpha 2_{fg(a)} * lw_{i,j} + \varepsilon_a \quad (6)$$

$$\varepsilon_a \sim Normal(0, \sigma_a) \quad (7)$$

2.5 Model fitting and Bayesian analysis

The models were fitted using Markov chain Monte Carlo (MCMC) simulations as implemented in the software package JAGS (Plummer, 2003). Two Markov chains each with 40 000 iterations were simulated. The first 2000 iterations were discarded as burn-in period and the remaining 38 000 iterations were thinned (only every 20^{th} simulation was used). Convergence was assessed by plotting the chains and through the Brooks-Gelman-Rubin statistics (Brooks and Gelman, 1998). This resulted in a total of 3800 random values (1900 per chain) from the posterior distribution of each model parameter and each derived parameter. The means and medians of these simulated posterior distributions represent estimates and the 2.5 % and 97.5 % quantiles represent the lower and upper limits of the 95 % credibility intervals. Species occurrence per year (3800 values from the posterior distribution, estimated by the *forest thinning model*), was then used to estimate the occurrence probability of individual species per year as well as averaged over the three years before and the three years after the thinning. Species with an increase or decrease in occurrence probability of at least 0.2 (20 %) were defined as species with a relevant increase or decrease in occurrence probability (binary), respectively, after the thinning compared to before. Data preparation, data analysis and graphical visualization of the simulated values was performed in the statistical software package R (R Core Team, 2018, Version 3.4.4). The R package R2jags (Su and Yajima, 2015) was used to run JAGS from R.

3 Results

3.1 Species richness and abundance before and after the thinning

The *forest thinning model* estimated higher occurrence probabilities for SF and EMF species after the thinning than before (odds ratios [OR] after vs. before > 1, see Table 1). In other words, most species occurred with higher probability at the Bolberg study site after the thinning than before. The strength of the increase in occurrence probability did not differ between functional groups (no interaction between functional group and phase). Note that estimates for SF are more precise, i.e., have narrower credible intervals (CI), than those for EMF due to the larger number of SF species.

Higher occurrence probabilities after the thinning naturally transformed into higher estimates of species richness per transect section (Fig. 1) and at the whole Bolberg site (Fig. 2, left panels). Fig. 2 shows the estimated increase in species richness at the Bolberg over all species (top left panel) as well as separately for both functional groups (middle and bottom left panels). For the three years before and after the thinning, mean total species richness at the Bolberg was estimated as 334 (median 335, CI 320–348) and 349 (median 350, CI 334–362) species, respectively, indicating a mean increase in species richness by 4.4 % (median 4.3 %, CI 2.1–6.8 %).

Occurrence probabilities of individual species per year and for the three years before and after thinning are given in the species list in Online Resource 3. We found 25 species with an increase in occurrence probability by at least 20 % and 11 species with a decrease in occurrence probability by at least 20 % whereas the occurrence probability of the other 356 species was rather constant (Table 5, Online Resource 1). The species that seemed to benefit from thinning were more likely to be EMF, such as *Lactarius salmonicolor* R.Heim & Leclair or *Suillus collinitus* (Fr.) Kuntze, to be Agaricales (one out of four taxon groups), to have red-list state “vulnerable”, and were slightly more likely to be specialists and to be more common (more widely distributed in Switzerland) than species that seemed to be harmed by the thinning.

In addition to species richness, also the species abundance (measured as the number of transect sections occupied by species) increased slightly after the thinning, mainly for SF (Fig. 2, right panels). For the three years before and after the thinning, the mean number of transects per species (SF and EMF) was estimated as 9.5 (median 9.5 CI 8.3–10.6) and 11.4 (median 11.4, CI 10.1–12.5) transects, respectively, indicating an increase in species abundance by 20.0 % (median 19.9 %, CI 14.8–25.7 %).

A separate analysis of estimated species richness among 18 red-listed species (Senn-Irlet et al., 2007, Swiss Red List for macrofungi) also showed a tendency for an increase in species richness by 6.2 % (median 4.9 %, CI -4.4–21.6 %) and an increase in abundance by 15.7 % (median 15 %, CI 6.0–28.8 %) after the thinning (Online Resource 1, Fig. 6). The 14 saprobic and 4 ectomycorrhizal red-listed species observed at the Bolberg had the threatened state vulnerable or endangered according to the Swiss Red List (after criteria of the International Union for Conservation of Nature, IUCN).

3.2 Relationship between habitat and occurrence probability

The thinning led to decreased amounts of living wood and increased amounts of dead wood in the majority of the 32 transect sections (Online Resource 1, Fig. 7). The increase in living wood on a few transect sections may be explained by tree growth between 2002 and 2005, when the amounts of dead and living wood were recorded, and possibly due to imprecision of the recording. The *habitat model* yielded different coefficient estimates for the relationships between the amounts of dead and living wood and the occurrence probabilities of SF and EMF species (significant functional group × dead wood and functional group × living wood interactions, Fig. 3 and Online Resource 1, Table 1). The occurrence probability of EMF in a given transect section decreased with the amount of dead wood (OR < 1) and increased with the amount of living wood (OR > 1). In contrast, the occurrence probability of SF was unaffected by the amount of dead wood, but decreased with the amount of living wood (OR < 1).

Although this was primarily done with the *forest thinning model*, the *habitat model* was also used to estimate numbers of species per transect section and at the Bolberg before and after the thinning. The *habitat model* estimated relatively constant numbers of species per transect section and at the Bolberg (Online Resource 1, Fig. 8 and 9). A slight increase was estimated for the number of SF species at the Bolberg, while a decrease was estimated for EMF species (Online Resource 1, Fig. 9, left panels). These results contrast with those from the *forest thinning model*, which estimated increasing species richness of both functional groups. The opposing trends found with the *habitat model* are due to the different associations of SF and EMF occurrence probabilities with the amount of dead and living wood (Fig. 3).

3.3 Detection probabilities

The *forest thinning model* estimated a decrease in detection probability of EMF species with the amount of dead wood (OR < 1), but an increase with the amount of living wood (OR > 1, Table 2). The relationships between the detection probability of SF with dead wood and living wood, respectively, were different. A less negative relationship with the amount of dead wood was shown than for EMF (interaction OR > 1), and a negative instead of positive relationship with the amount of living wood (interaction OR < 1, see 3$^{\text{rd}}$ and 6$^{\text{th}}$ row in Table 2). Estimates of seasonal dependence of detection probabilities, at mean levels of dead and living wood, peaked in summer for most species (Online Resource 1, Fig. 10). The OR for the relationships between the habitat variables and the detection probabilities estimated by the *forest thinning model* in Table 2 are quite similar to those regarding occurrence probabilities estimated from the *habitat model* (Online Resource 1, Table 1). In contrast, the coefficients for the relationships between dead and living wood and the detection probabilities of species, as estimated with the *forest thinning model* (Table 1), differ from those estimated by the *habitat model* (Online Resource 1, Table 2).

4 Discussion

The aim of this study was to monitor and model changes in macrofungal community as non-targeted species group along a habitat enhancement action for reptiles in a beech forest. Fungal species richness and abundance before and after the thinning was estimated by two site-occupancy models. With one model we estimated species occurrence probabilities before and after the cut (*forest thinning model*), with habitat parameters (amount of dead and living wood) used to model detection probabilities. With the other model we estimated species occurrence probabilities as dependent on habitat changes (*habitat model*) presumably mostly induced by the thinning (decrease in living wood and increase in dead wood). The sub-model for detection probabilities was kept equal to that of the *forest thinning model*.

We estimated an increase in occurrence probabilities for SF and EMF species with the *forest thinning model* (Table 1), resulting in slightly higher species richness and abundance after the thinning at the Bolberg (Fig. 2). When explicitly accounting for the two major habitat changes induced by the thinning, as done with the *habitat model* we at least estimated a relatively constant species richness and abundance (Online Resource 1, Fig. 9), due to opposing changes in the two functional groups (Fig. 3). The finding that the two functional groups responded differently to the habitat changes suggests that apart from inducing changes in species richness and abundance, the thinning intervention had consequences for the species composition of both functional groups.

As we hypothesized the opposite, the increase in species richness and abundance at the Bolberg is a surprising result. A mature forest stand with a closed canopy is often viewed as optimal for a rich fruiting of macrofungi. For example, a positive relationship between stand age and species richness of the ectomycorrhizal genus *Cortinarius* was shown in a survey on 134 plots in Switzerland (Senn-Irlet et al., 2003). This may be due to the micro-climate, which shows lower temperature fluctuations under a dense canopy (von Arx et al., 2013; Heine et al., 2019).

A higher mean age of the trees and more debris left on the ground are known to favor many fungi, especially wood-decaying fungi (Siitonen, 2001). Further, decay stage and wood volume were identified as key variables influencing species richness as well as the occurrence of red-listed species (Heilmann-Clausen and Christensen, 2005). Moreover, a meta-analysis on the diversity of forest-dwelling species in managed vs. unmanaged forests in Europe found that fungi were among those species groups that were negatively affected by forest management (Paillet et al., 2010). However, contrary to the expectations of many field mycologists, there is also evidence for forestry interventions such as thinning, especially on a smaller scale, to even promote terrestrial fungal species richness and abundance (Egli et al., 2010; Küffer and Senn-Irlet, 2005; Brazee et al., 2014). Egli et al. (2010) observed an increase in the number of fungal species and sporocarps after thinning which was most pronounced for EMF and was paralleled by an increase in tree ring width of formerly suppressed beech trees. Results from randomly selected plots in Swiss forests showed that forests with a recent management intervention varied from very species rich to rather species poor in wood-inhabiting fungi (Küffer and Senn-Irlet, 2005). On cleared stands and in forest gaps, e.g., after wind-throws, fungal communities are very different from those of closed-canopy forests established in the open areas, mainly due to the change in micro-habitat factors (Schlechte, 2002; Heine et al., 2019), enriching the overall species richness. Moreover, Brazee et al. (2014) found that species richness of wood-inhabiting fungi was not reduced in plots with canopy gaps compared to unharvested control plots in a North-American hardwood forest, but that species richness was even increased in plots where gap creation was combined with the addition of coarse woody debris.

The different response of SF and EMF to thinning, reducing the amount of living wood while increasing the amount of dead wood, is not surprising, due to the particular dependence on dead wood and living wood. The *habitat model* which focused on these two most obvious habitat changes, revealed a strong positive relationship between the amount of living wood (i.e., larger volume, indicating more trees and/or larger trees) and the occurrence probability of EMF species. This is in line with other results on ectomycorrhizal fungal succession (Twieg et al., 2007; Wallander et al., 2010). In contrast, the same model indicated a negative relationship between the amount of dead wood on the ground and the occurrence probability of EMF species. Apart from being paralleled by lower densities of host trees, high amounts of dead wood might have exerted adverse physico-chemical effects on the underlying mycelium of EMF. However, more dead wood should promote the species richness of SF due to a greater diversity and density of suitable microhabitats (Dove and Keeton, 2015; Ódor et al., 2006). While we could not show this positive relationship explicitly with the *habitat model* (Online Resource 1, Table 1), we could show a negative relationship with the amount of living wood (which may be interrelated). The lack of a positive relationship between the amount of dead wood and the occurrence probability of saprobes may also be due to our way of quantifying dead wood on the transect line, while macrofungi were recorded on a band of 8 m width. Overall, this led to slightly higher estimates of SF species richness and abundance after the thinning, along with slightly lower values for EMF. Our results from the *forest thinning model* clearly show higher fungal species richness and abundance after the thinning, for both SF and EMF. In contrast, the *habitat model* suggests that species richness and abundance increase for SF but decrease for EMF when the forest is thinned, due to the increase in dead wood and the decrease in living wood. However, thinning may produce other changes in the habitat that also promote EMF. The *forest thinning model* accounted for all changes induced by the thinning, but without characterizing them. In contrast, the *habitat model* explicitly accounted for two affected habitat parameters, amounts of dead and living wood, but for no other changes. Hence, the difference in the estimates indicates that the decrease in the amount of living wood and the increase in the amount of dead wood together only partly accounted for the habitat changes induced by the enhancement intervention. There must have been additional factors associated with the thinning that positively affected fungal species richness, for example increased growth of formerly suppressed trees generating a carbohydrate surplus, as suggested by Egli et al. (2010). Overall, thinning may have resulted in a more diverse habitat with a higher diversity of micro-climates, plant communities and hence biological, chemical and physical properties. These factors are all known to influence the fungal community, especially of soil-inhabiting fungi (Jones et al., 2003).

Our analysis of individual species for which we estimated an increase or decrease in occurrence probability (Table 5, Online Resource 1 and Online Resource 3) revealed that more species seem to have benefited from the thinning than were harmed (25 vs. 11 species), which reflects the estimated increase in species richness. Species with an increase in occurrence probability do not seem to be fundamentally different from those with a decrease, i.e., both groups contain SF and EMF, different taxon groups, red list species, specialists, and rare species. However, because the number of species with a relevant increase or decrease in occurrence probability is relatively small, we avoid further interpretation of their characteristics.

The use of site-occupancy models to estimate species richness and abundance allowed us to account not only for imperfect detection probabilities (< 1) of species, but also for variation in detection probabilities due to the habitat and season. While ignoring imperfect detection simply leads to an underestimation of species numbers, ignoring the dependence of detection probabilities on habitat or season may have more substantial consequences. For instance, positive effects of habitat changes on species occurrence may be easily overlooked or even misinterpreted as being negative, whenever they are paralleled by negative effects on species detection (MacKenzie et al., 2002; Kéry and Schmidt, 2008). In the present study the detection probabilities of both functional groups, as estimated by the *forest thinning model* were negatively associated with the amount of dead wood (Table 2). The detection probability of EMF species was also negatively associated with decreasing amounts of living wood (or positively with increasing amounts), whereas the detection probability of SF species was positively associated with decreasing amounts of living wood (negatively with increasing amounts). These dependencies of the detection probabilities might have concealed the increase in the abundance of SF and EMF species estimated by the *forest thinning model* (Fig. 2), had they not been accounted for. However, while Adams et al. (2010) explored the use of occupancy models to analyze the occurrence of *Batrachochytrium dendrobatidisis*, a fungal pathogen that is threatening amphibians around the world, we are not aware of any study that used occupancy models to estimate species richness of macrofungi.

Being conducted on a single, south-facing, mixed forest slope on calcareous bedrock in north-western Switzerland, our study represents a small-scale case study, and the results can not be easily generalized. Moreover, because the different sections of our transect were affected by the habitat enhancement action to varying degrees (see Online Resource 1, Fig. 7) rather than strictly being treated or control, our data are of an observational rather than experimental nature, implying that the causal effect of forest thinning can not be estimated. In particular, although we observed no distinct differences in the weather conditions before and after the thinning (Online Resource 1, Fig. 11), we can not exclude that the specific weather conditions during the study influenced our results.

Opposite to our hypothesis, we found that fungal species richness and abundance increased after a forest thinning at the Bolberg, and that this increase cannot be explained solely by the change in dead and living wood. We believe that the forest thinning fostered species richness through a larger density and diversity of suitable microhabitats. With some caution, we conclude that the small-scale habitat enhancement for reptiles, creating islands of open forest, did not negatively affect species richness and abundance of macrofungi, a non-targeted species group.

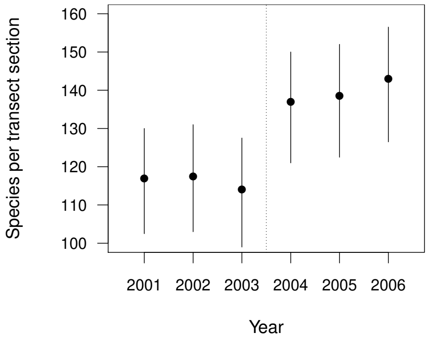

Fig. 1 Species richness per transect section and year for all fungal species at the Bolberg, Switzerland, as estimated from the *forest thinning model*. Closed circles are medians of the posterior distribution, lines define 95 % credible intervals. The dashed line indicates the thinning.

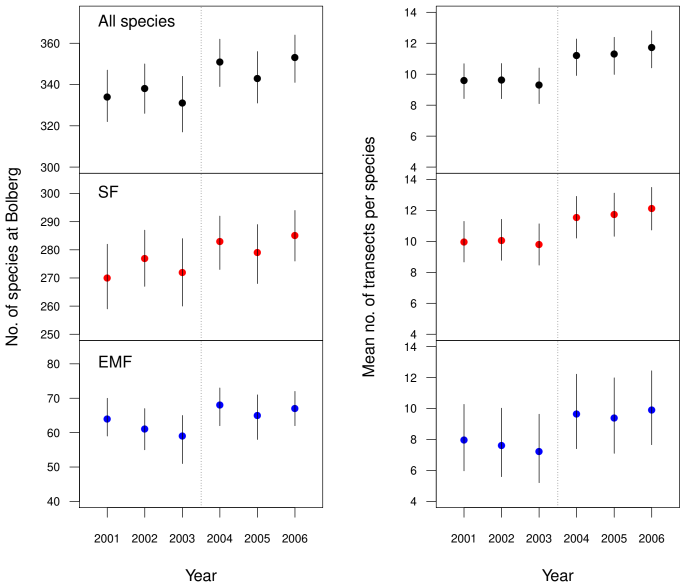

Fig. 2 Fungal species richness (left panels) and abundance (right panels, mean number of transects occupied by species) at the Bolberg, Switzerland, per year. Species richness and abundance are shown for all fungal species (top), SF (middle), and EMF (bottom) as estimated from the *forest thinning model*. Closed circles are medians of the posterior distribution, lines define 95 % credible intervals. The dashed line indicates the thinning.

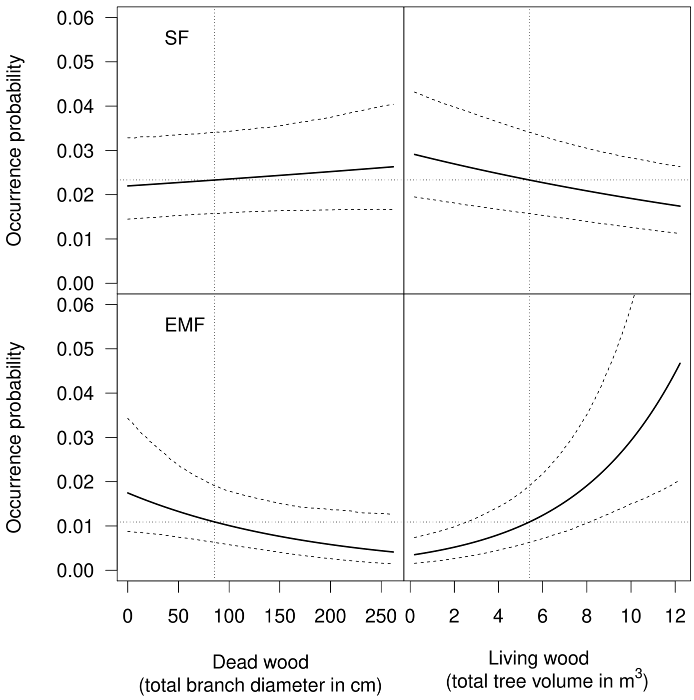

Fig. 3 Occurrence probabilities of SF (top panels) and EMF species (bottom panels) per transect section at the Bolberg, Switzerland, depending on the amount of dead wood (left panels) and living wood (right panels) as estimated from the *habitat model*. Solid lines show means, dashed lines show 95 % credible intervals. Vertical dotted lines show the average observed amount of dead or living wood per transect section, horizontal dotted lines show the estimated occurrence probability for this amount, respectively. See Online Resource 1 (Table 1) for odds ratio estimates.

Table 1 Odds ratio (OR) estimates for the effects of thinning on the occurrence probabilities of fungal species at the Bolberg, Switzerland, as estimated from the *forest thinning model*. The functional group $\times$ phase interaction (bottom row) could also be described as: SF (after – before) – EMF (after – before). Note that OR estimates derived as mean and median of the posterior distribution, are equivalent when rounded to two digits.

	OR (mean)	OR (median)	95 % credible interval
SF after - before	1.56	1.56	[1.39, 1.75]
EMF after - before	1.70	1.70	[1.23, 2.34]
Functional group x phase	0.92	0.92	[0.66, 1.30]

Table 2 Odds ratio (OR) estimates for the effects of dead wood (DW) and living wood (LW) on the detection probabilities of fungal species at the Bolberg, Switzerland, as estimated from the *forest thinning model*. OR estimates for SF were derived by adding the estimates b5 or b6 (functional group $\times$ habitat interaction terms) to b3 and b4 (on the logit scale). Note that OR estimates derived as mean and median of the posterior distribution, are equivalent when rounded to two digits.

	OR (mean)	OR (median)	95 % credible interval
DW in EMF (exp[b3])	0.95	0.95	[0.92, 0.97]
DW in SF (exp[b3+b5])	0.99	0.99	[0.98, 1.00]
DW in SF - DW in EMF (exp[b5])	1.05	1.05	[1.01, 1.08]
LW in EMF (exp[b4])	1.07	1.07	[1.02, 1.11]
LW in SF (exp[b4+b6])	0.97	0.97	[0.95, 0.98]
LW in SF - LW in EMF (exp[b6])	0.91	0.91	[0.87, 0.95]

Acknowledgements We are grateful to Marc Kéry for comments on an earlier version of this manuscript. Funding of this work was provided by the Canton of Basel-Landschaft and by oikostat GmbH.

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