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LETTER

# Bark Beetles Increase Biodiversity While Maintaining Drinking Water Quality

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BB collected and analyzed the hydrochemical data, CB and JM collected and analyzed the biodiversity data, JM and BB conceived the idea and wrote the first draft of the manuscript and all authors contributed substantially to writing and revision.

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## Abstract

Increasing natural disturbances in conifer forests worldwide complicate political decisions about appropriate land management. In particular, allowing insects to kill trees without intervention has intensified public debate over the dual roles of strictly protected areas to sustain ecosystem services and to conserve biodiversity. Here we show that after large scale bark beetle *Ips typographus* infestation in spruce *Picea abies* forests in southeastern Germany, maximum nitrate concentrations in runoff used for drinking water increased significantly but only temporarily at the headwater scale. Moreover, this major criterion of water quality remained consistently far below the limit recommended by the World Health Organization. At the same time, biodiversity, including numbers of Red-listed species, increased for most taxa across a broad range of lineages. Our study provides strong support for a policy to allow natural disturbance-recovery processes to operate unimpeded in conifer-dominated mountain forests, especially within protected areas.

## Introduction

Conifer-dominated mountain forests provide, along with fiber and fuel, high quality drinking water as an important ecosystem service (Schröter *et al.* 2005). Furthermore, these forests are refuges for a large proportion of natural biodiversity (Müller *et al.* 2010). Preserving biodiversity and ecosystem services is a major challenge for national parks worldwide, but increasing natural disturbances in coniferous forests of the Northern Hemisphere (Seidl *et al.* 2014) have evoked controversy over the appropriate land management response to these disturbances (Nikiforuk 2011). In Europe most coniferous forests are intensively managed to suppress outbreaks of bark beetles (subfamily Scolytinae). In a social environment of small scale private forest ownership

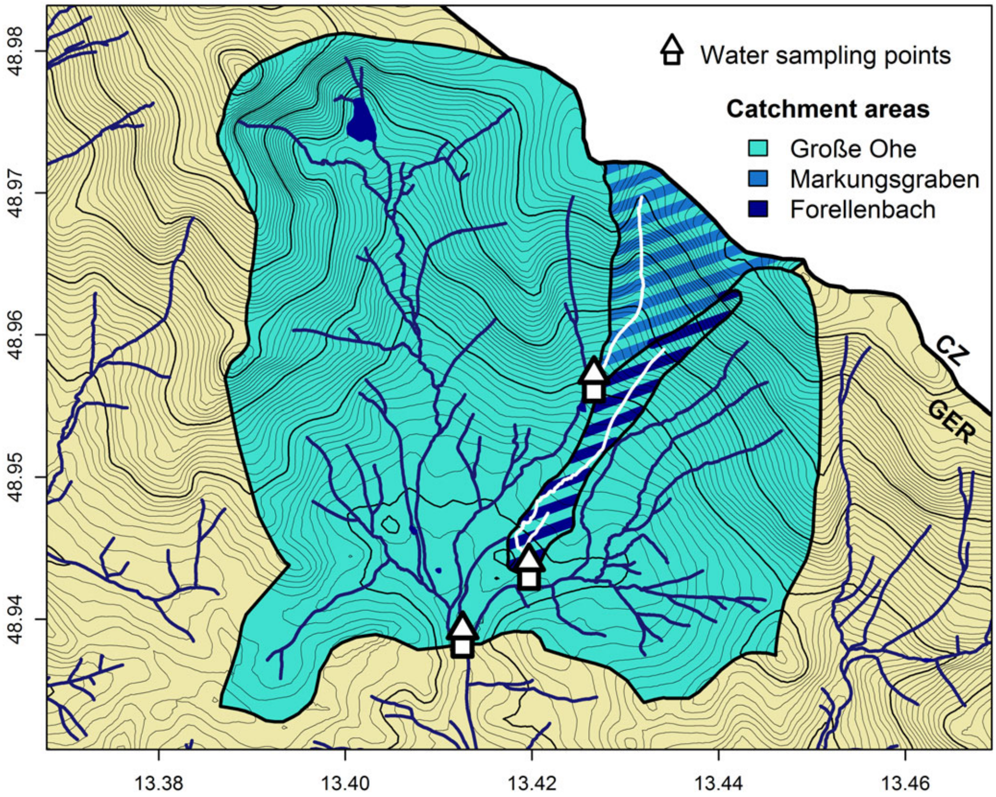

**Figure 1** Topographic map of studied catchments. Large catchment (Große Ohe), medium subcatchment (Markungsgraben) and small subcatchment (Forellenbach) are indicated by different blue colors. Contour lines represent the elevation above sea level (m asl.), while white lines highlight the streams of the studied subcatchments. For catchment characteristics see Table 1. White house symbols indicate sampling locations of the respective catchment.

and intensive forest management, not surprisingly a "benign neglect" approach in strictly protected areas, which allows beetles to kill trees without any human intervention, has intensified public debate over the role of strict protected areas in national biodiversity strategies (Lindenmayer *et al.* 2004; Nikiforuk 2011).

The rapid dieback of mature forests across Europe has sparked public fear of negative impacts of bark beetle outbreaks on drinking water quality because the leaching of nitrate from soils is a common consequence of decoupled nutrient cycles after disturbance (Vitousek *et al.* 1979; Mikkelson *et al.* 2013). Concern also has been expressed about reduced species diversity. In contrast, ecologists increasingly observe rapid recovery of biodiversity and ecosystem function after natural disturbance in formerly intensively managed forests; from a conservation standpoint, naturally disturbed forests are an acceptable alternative to the aging process toward old-growth forest (Lindenmayer *et al.* 2004; Müller *et al.* 2010). As large scale disturbances are difficult both to predict and to investigate experimentally long term or before/after data on their ecological effects are scarce.

We exploited a unique 28-year data set from hydrochemical monitoring in a large catchment Große Ohe (Figure 1), which is embedded in the most heavily bark beetle-affected forest in Europe (Bavarian Forest National Park, Latitude 13.23°E, Longitude 48.53°N). Forests within this national park experienced two bark beetle (*Ips typographus* L.) waves during the last 20 years, affecting more than 50% of the area and 75% of mature Norway spruce (*Picea abies* L.). For the national park area we further quantified the effect of bark beetle outbreaks on biodiversity for 19 taxonomic groups (2,297 species). Our results provide the first demonstration that after bark beetle infestation, nitrate concentrations in runoff used for drinking water remain well within the range considered safe for human consumption, while at the same time biodiversity increases for most taxa across multiple lineages.

## Material and methods

Nitrate concentration in stream water was monitored within a large catchment and within two subcatchments,

**Table 1** Physiographic and hydrometeorological catchment characteristics. Mean air temperature covers 1980–2004, mean precipitation and runoff cover 1992–2010. Tree species composition (status 1990) was dominated by Norway spruce, while European beech is the dominant broadleaf species. The combined contribution of other species is less than 5%. (Minimum and maximum values are in brackets)

| | Large Catchment | Medium Subcatchment | Small Subcatchment |
|---|---|---|---|
| Stream | Große Ohe | Markungsgraben | Forellenbach |
| Area (km$^2$) | 19.1 | 1.1 | 0.7 |
| Elevation (m a.s.l.) | 982 (770 – 1447) | 1128 (890 – 1355) | 894 (787 – 1293) |
| Slope (°) | 11.1 | 16.1 | 8.4 |
| Bedrock | Biotite granite, cordierite-sillimanite gneiss | Biotite granite, cordierite-sillimanite gneiss | Biotite granite |
| Soils (%) | | | |
| –Lithosols, rankers | 16 | 38 | 12 |
| –Cambisols, podsols | 60 | 50 | 58 |
| –Histosols, gleysols | 23 | 12 | 30 |
| Tree species (%) | Norway spruce (70), broadleaves | Norway spruce (84), broadleaves | Norway spruce (69), broadleaves |
| Air temperature (°C) | 5.5 | 5.3 | 6.2 |
| Precipitation (cm) | 162 (129–227) | 176 (141–230) | 160 (127–221) |
| Runoff (cm) | 106 (72–157) | 135 (90–172) | 105 (76–145) |

to account for variability in physiography (Figure 1; Table 1). All areas were dominated by spruce. Water samples were taken bi-weekly in Große Ohe (large catchment, 19.1 km$^2$) and Markungsgraben (medium subcatchment, 1.1 km$^2$) and weekly in Forellenbach (small subcatchment 0.7 km$^2$) streams, whereas for seepage water (ceramic suction cup lysimeter) and groundwater sampling (pumping) the interval was bi-weekly and monthly, respectively. Sampling, storing and preparation of samples strictly followed international manual instructions (ICP-Forests 2010; ICP-Integrated-Monitoring 2010). Analysis of chemical components was performed monthly by certified laboratories (Bavarian Environment Agency, Bavarian State Institute of Forestry, Federal Environment Agency) using ion chromatography for nitrate (EN ISO 10304–1; ICP-Forests 2010; ICP-Integrated-Monitoring 2010).

Including data from monitoring of soil water and groundwater in the small catchment (Figure S1), we applied a nested approach to address scale effects. Differences in tree species composition between catchments depend on elevation and slope, which govern local climate and runoff, and on the proportion of wet and shallow lithic soils (Table 1). Small scale management interventions within the studied catchments took place long before beetle outbreaks (i.e., 1994). Our spatial design allows assessment of two different sources of drinking water supply. Runoff water of the large catchment represents streams feeding large regional reservoirs, whereas waters of the small and medium catchments represent water supplies directly used by local municipalities.

Using R 3.0.2 (www.r-project.org) we applied raw generalized least square models (GLS, "nlme" package) to test the effects of the annual and cumulative area affected by bark beetles (see below) on annual maximum nitrate concentrations for the three catchments. We explored the temporal correlation structure of the model residuals by calculating the autocorrelation function (*acf*) and the partial autocorrelation function (*pacf*; 'stats' package). We used the first order autocorrelation as the correlation structure in the GLS models (Pinheiro & Bates 2000).

For multispecies diversity response, we used standardized species surveys in stands affected and not affected by bark beetles from 2006 to 2009 throughout the national park area (for the design see Bässler *et al.* 2008; for methods see Table 2). Species were classified as endangered if they occur on the German or the Bavarian Red list of endangered species (www.lfu.bayern.de).

Bark beetle infested spruce trees for both data sets were identified on annually recorded color-infrared images (Lausch *et al.* 2011). For the biodiversity data we defined plots as affected if at least 20% of the 100 x 100 m surrounding area of a plot was infested (according to Müller *et al.* 2010). Analysis was restricted to plots in former commercial forests to avoid influence of habitat legacies (e.g., downed and standing dead wood) in old-growth stands. We applied generalized linear mixed models (*glmer*, package "lme4"), using the number of species and the number of Red-listed species within species groups as the response variable and the treatment as a fixed factor and a *taxonomic-group:study-plot*-random effect considering the repeated measure at a *study-plot* and potential overdispersion. Post hoc comparison with adjusted *P* values for each taxonomic group was conducted using the function *glht,* package "multcomp." To compare beta diversity between affected and unaffected

**Table 2** Number of species, red listed species, plots, and methods used for the biodiversity survey

| Taxonomic group | | Number of all species/Red-listed species | Method | Number of plots in | |
|---|---|---|---|---|---|
| | | | | Affected stands | Vital stands |
| Aculeata | Bees, Wasps | 108/9 | Malaise-trap | 18 | 18 |
| Lichens | Lichens | 137/52 | Relevees | 39 | 55 |
| Syrphidae | Hoverflies | 133/12 | Malaise-trap | 18 | 18 |
| Cicada | Cicadas | 99/17 | Malaise-trap, window trap, direct search | 33 | 27 |
| Chiroptera | Bats | 15/11 | Bat-recorders | 18 | 18 |
| Symphyta | Sawflies | 85/5 | Malaise-trap | 18 | 18 |
| Bryophyta | Mosses | 103/21 | Relevees | 39 | 53 |
| Spermatophyta | Vascular plants | 178/14 | Relevees | 98 | 257 |
| Arachnaea | Spiders | 142/28 | Pitfall trap | 65 | 86 |
| Neuroptera | Lacewings | 27/3 | Malaise-trap | 18 | 18 |
| Saproxylic beetles | Saproxylic beetles | 264/95 | Flight-traps | 64 | 85 |
| Aves | Birds | 69/10 | Grid mapping | 97 | 163 |
| Heteroptera | True bugs | 137/18 | Malaise-trap, window trap, direct search | 67 | 78 |
| Collembola | Springtails | 44/0 | Pitfall trap | 66 | 86 |
| Lepidoptera | Moths | 371/31 | Light-traps | 18 | 18 |
| Mollusca | Mollusca | 40/12 | Direct search | 40 | 91 |
| Fungi | Fungi | 272/27 | Direct search | 98 | 162 |
| Carabidae | Carabids | 61/6 | Pitfall trap | 64 | 85 |
| Opiliones | Harvestmen | 9/0 | Pitfall trap | 65 | 86 |

plots we used a sample-size-based rarefaction approach for all taxa, which estimates the rate of increase in species richness with increasing number of plots, and then extrapolates the observed accumulation curve using a recently developed analytical rarefaction-extrapolation approach (Colwell *et al.* 2012).

## Results

Maximum nitrate concentrations in runoff increased significantly with increasing cumulative area of dead spruce from 5 to 9 mg $L^{-1}$ in the large catchment (Figure 2A; Table S1) and to 10 mg $L^{-1}$ in the small catchment (Figure 2C; Table S1) after dead spruce stands exceeded 20% of catchment area. In both catchments concentrations were not exceeded during the second bark beetle wave (60% area), but instead remained constant or decreased slowly. In response to the rapid and almost complete infestation of spruce stands in the medium, high elevation catchment, annual maximum nitrate concentrations increased significantly (Figure 2B, Table S1) with increasing annual area of dead spruce from 8 mg $L^{-1}$ to 24 mg $L^{-1}$, with highest concentrations in the years of greatest disturbance. The exploration of the temporal autocorrelation revealed significant time lags of 2 years for the medium catchment and for the yearly affected area in the small catchment (Figure S2). Nevertheless, 10 years after the dieback nitrate concentrations decreased below the initial level.

Testing for differences in species richness revealed an overall positive effect of bark beetle outbreaks ($P < 0.001$). Seven of 19 groups responded positively in terms of overall species richness ($P < 0.05$; Figure 3), whereas one group (wood-inhabiting fungi) responded negatively. A similar pattern was revealed for Red-listed species. Of the 17 groups with Red list data, Red-listed saw-flies occurred only in bark beetle areas and therefore could not be tested formally. Of the remaining 16 groups, eight showed a significant positive response and fungi again a significant negative response (Figure 3B). Although overall species richness of carabids did not respond positively to bark beetle infestations, Red-listed carabids showed a strong positive response. The rarefaction-extrapolation curves showed higher beta diversity with non-overlapping confidence bands in bark beetle affected areas for 8 out of 19 taxonomic groups and significantly lower beta diversity only for mollusks (Figure 4).

## Discussion

Restoration ecologists and conservation biologists increasingly recommend allowing natural disturbance regimes to operate for restoration of ecosystems homogenized by previous management (Lindenmayer *et al.* 2004), but data to support this recommendation remain

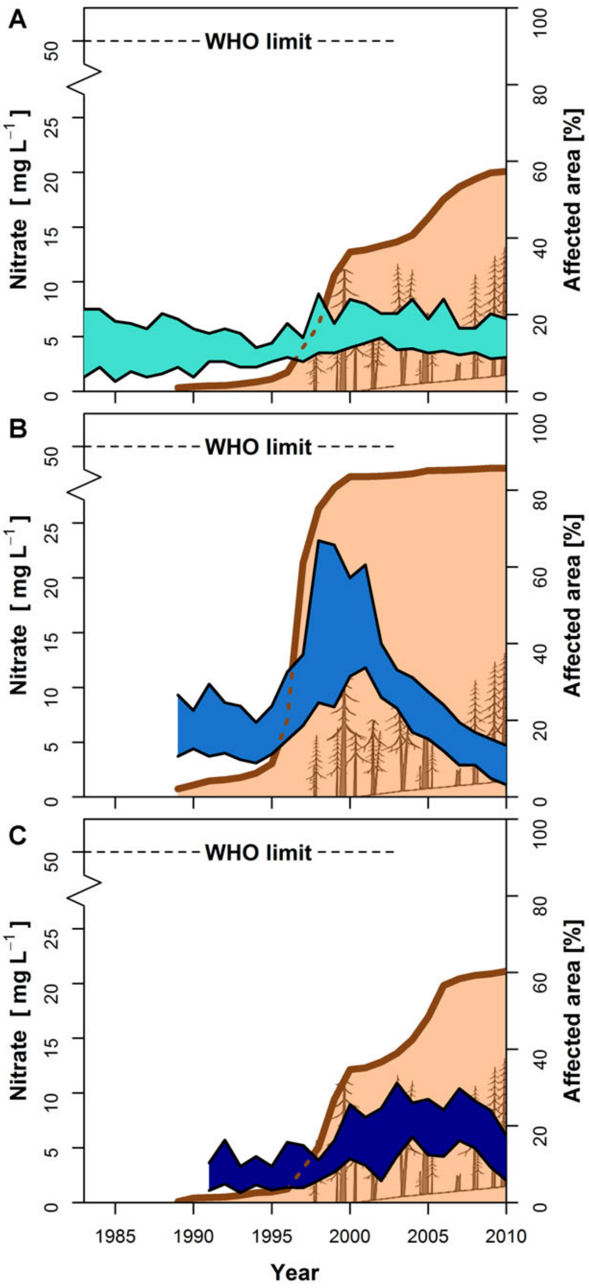

**Figure 2** Times series of bark beetle-affected areas and nitrate concentrations. Brown shaded area represents cumulative percentage of bark beetle-affected areas of each catchment, while blue colored areas indicate the respective annual ranges of nitrate concentrations in runoff water. The World Health Organization (WHO) drinking water guideline limit is 50 mg $L^{-1}$. **A**, Large catchment (Große Ohe), significant increase (GLS) with cumulative beetle area with (t = 2.59∗) and without (t = 2.26∗) temporal autocorrelation. **B,** Medium subcatchment (Markungsgraben), significant increase with cumulative beetle area with (*t* = 2.84∗) and without (*t* = 5.84∗∗∗) temporal autocorrelation. **C**, Small subcatchment (Forellenbach), significant increase with annual affected area without temporal autocorrelation (*t* = 2.22∗). For more details see Table S1.

scarce. In general, spruce forests are a disturbance-prone ecosystem (Svoboda *et al.* 2012), but the current regime has been strongly affected by an anthropogenic increase of mature trees and global temperature (Seidl *et al.* 2014). In this context our findings provide the first evidence for maintenance of high water quality in watersheds disturbed by bark beetles, accompanied by increasing overall biodiversity. These results are complemented by our finding of an increased water supply in our small and medium catchments by about 10–20% of annual precipitation (Beudert *et al.* 2007), due to reductions in transpiration after infestation leading to increased seepage and groundwater contributions to streams (cf. Mikkelson *et al.* 2013; Bearup *et al.* 2014). The persistence of hydrological disturbance effects is still an open question (Adams *et al.* 2012). We expect increasing runoff for perhaps 20–40 years as young spruce grows toward maturity. Our long-term data show that nitrate concentrations in groundwater and stream water increased to about half of the drinking water guideline provided by the World Health Organization (50 mg $L^{-1}$), but only for the maximum concentrations and over only 2 years during the disturbance-recovery period. Thus the general high quality of this water, including dissolved organic carbon, did not suffer from disturbances by bark beetles.

The most affected medium catchment showed maximum nitrate concentrations equivalent to the highest concentrations found in studies of clear-cuts in Europe (Didons-Lescot *et al.* 1993) and North America (Likens *et al.* 1970; McHale *et al.* 2007). Nevertheless, concentrations were three times lower than those recorded in the "herbicide without biomass removal" treatment in the Hubbard Brook Experiment (Likens *et al.* 1978), underscoring the important role of undisturbed residual and regenerating vegetation for nitrate retention (Pardo *et al.* 1995). In contrast, maximum nitrate concentrations of the small and large catchments were considerably lower.

Nitrate concentration in seepage water in an experimental spruce stand within the small catchment helps explaining these results. Following complete dieback during 1 year, nitrate concentrations rapidly increased (Figure S1). Shallow groundwater in an adjacent monitoring well experienced increased nitrate concentration, five times lower than in soil water but equal to runoff water in the medium catchment (Figure 2B). We conclude that a rapid and extensive dieback of spruce, as in the medium catchment (70% area over 4 years), is a prerequisite for a steep increase and high peak level of nitrate concentration, corroborated by the initial nitrate response to 40% affected area in the small catchment, which was as rapid as in the medium catchment. A similar increase in nitrate concentrations from 3 to 22 mg $L^{-1}$ was reported from a tributary to a cirque lake in the

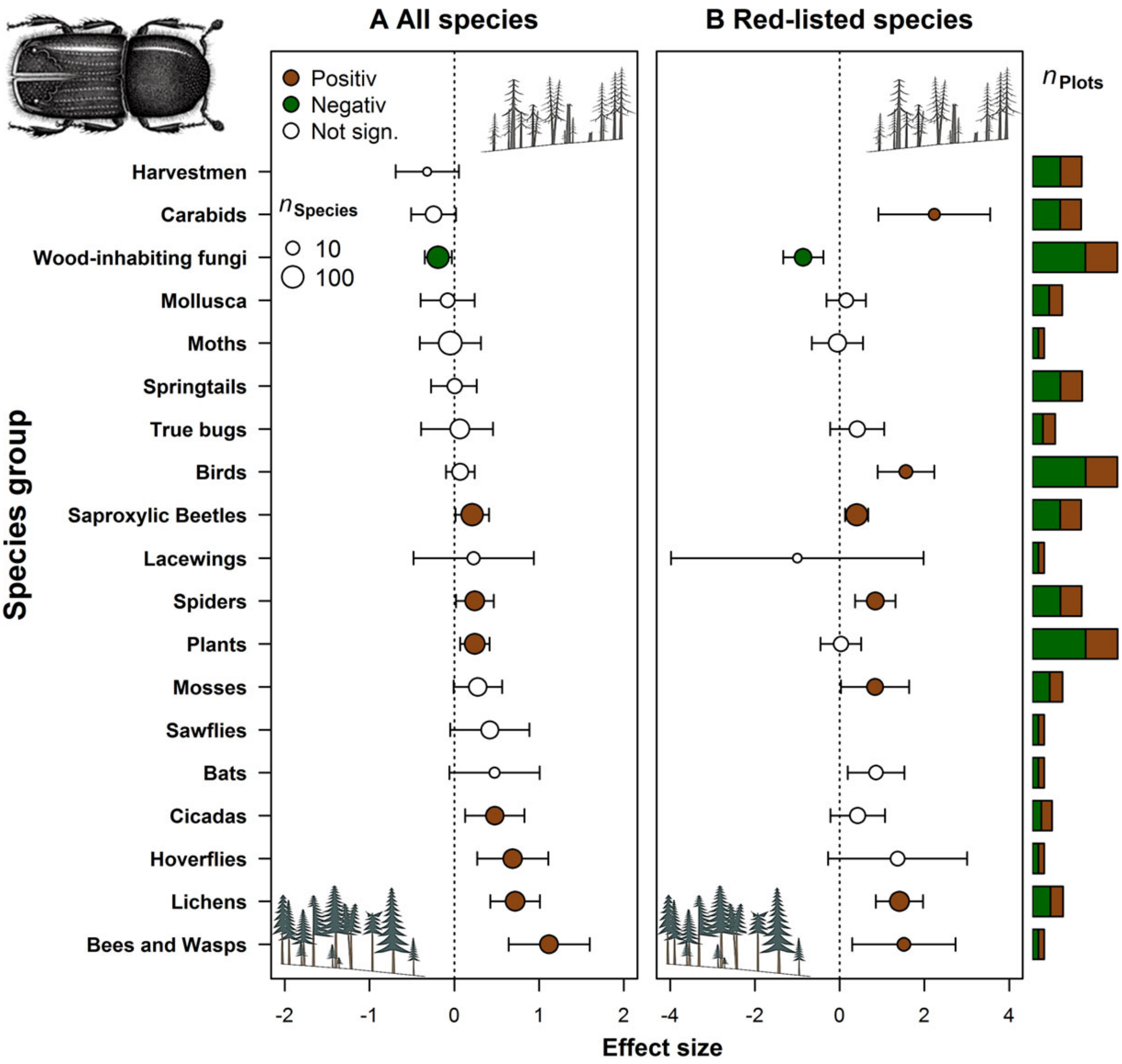

**Figure 3** Changes in (A) species numbers and (B) Red-listed species numbers in bark beetle-affected and non-affected stands. Brown circles show significantly positively and green circles significantly negatively affected taxa, while whiskers crossing the zero-line indicate nonsignificant differences. Note that Red-listed saw-flies occurred only in bark beetle areas and could therefore not be tested formally. Bars show the number of samples with (brown) and without (green) beetle influence in each species group (see Table 1).

Central European Bohemian Forest after bark beetle outbreaks on 93% of the catchment area during a few years (Kopáček *et al.* 2013). These results support model-based predictions for summer-dry subalpine ecosystems of the United States: that the rapidity of tree mortality controls nitrate concentrations in runoff (Rhoades *et al.* 2013).

In contrast to dry summer and cold winter climate regions (Griffin *et al.* 2011; Rhoades *et al.* 2013) where water availability limits microbial activity (Vitousek *et al.* 1979), the prevailing humid climate in our region (Table S1) enables rapid mineralization and nitrification of organic nitrogen during summer, while permeable soils allow rapid transfer of nitrate into aquifers (Figure S2) and streams throughout the year. Nitrate losses via denitrification might be less significant under these conditions (Cameron *et al.* 2013). In contrast to mountain pine beetle outbreaks in North America (Edburg *et al.* 2012; Griffin *et al.* 2012), tree die-off in mature Norway spruce stands is completed within 1 year, disabling the sparse understory vegetation from taking up significant amounts of nitrate. This extent and rapidity of nitrate loss is typical for European spruce

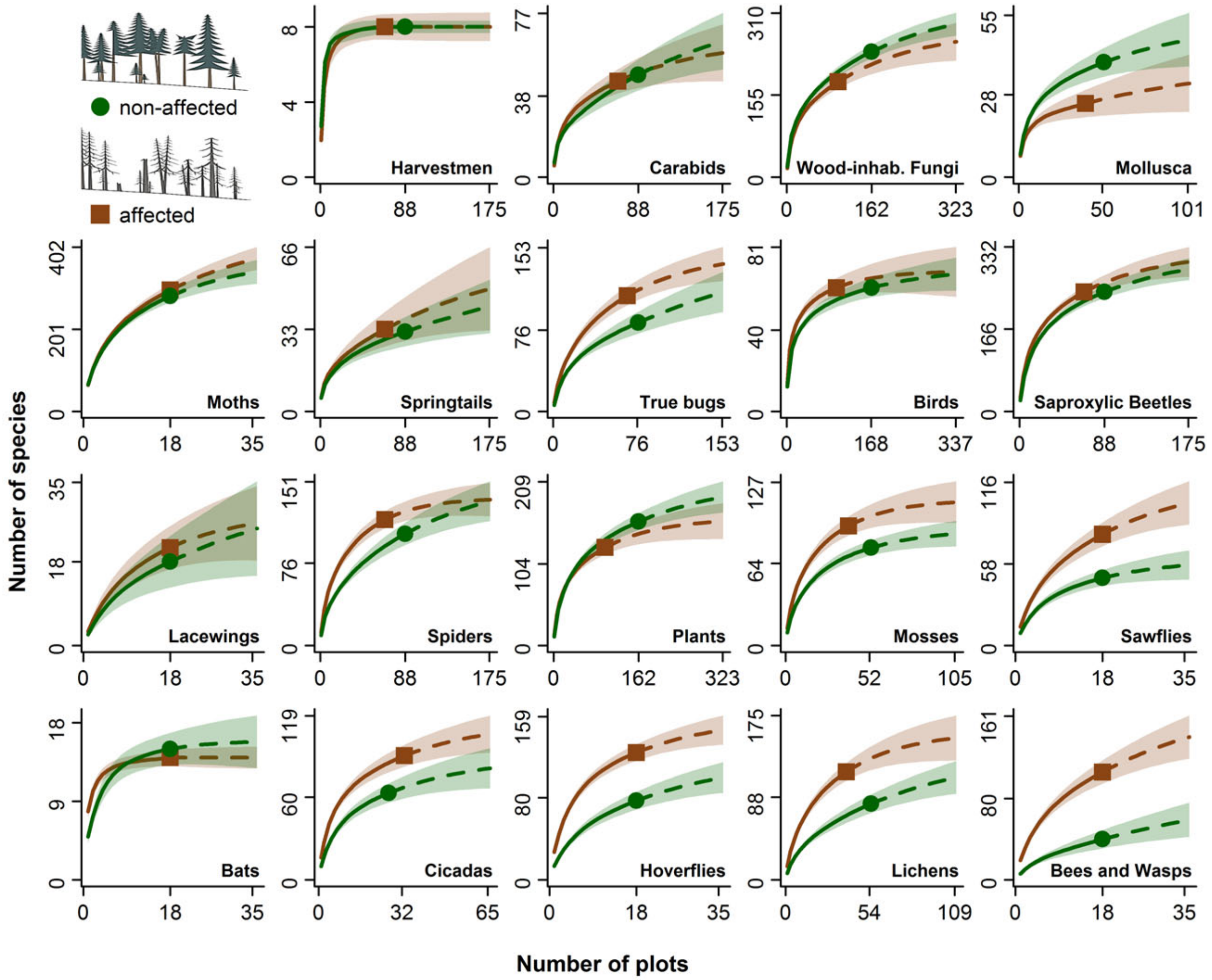

**Figure 4** Sample-size-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the sample size actually taken in the large sample size) of species richness in bark beetle affected (brown) and unaffected (green) sites, along with 95% unconditional confidence intervals (gray shading). Symbols indicate the full sampling extent in this study. All 95% confidence intervals in three panels were obtained by a bootstrap method based on 200 replications.

forests, in which neither nitrate-producing biological processes nor the loss of nitrate is limited by water supply. Under these circumstances available nitrogen stocks in terrestrial soils are subject to "periodic resetting" by harvest or disturbances (Dise *et al.* 2009).

The period of excess nitrate release in our catchments persisted for 6 years on a plot scale (Figure S1), which is further supported by a space-for-time substitution covering completely dead high-elevation spruce plots within the national park (Huber 2005), and for 10 years in shallow groundwater. These findings match the 12 years of increased concentration in runoff of the medium catchment. Due to the 5 years lag-time until the second bark beetle outbreak and the overall smaller extent of affected area (60% vs. 80%), concentrations in runoff of the small catchment remained longer at a moderately elevated level resulting from two superimposed nitrate pulses. This suggests that the period of increased nitrate concentrations is inversely related to the rapidity of tree mortality, given the same areal extent.

Despite being equally affected, the large catchment showed very small changes in nitrate concentrations, which provides a hint of the likely mechanism behind the scale effect. Across hydrological pathways, mixing of nitrate-rich soil and hypodermic water from disturbed areas with nitrate-poor soil water from undisturbed areas and ground water exerts control over stream nitrate concentration. As slow-flowing ground water (Figure S1) exhibits a mean residence time of 8–15 years (Beudert *et al.* 2007), higher ground water contribution to runoff, as in the large catchment, places an effective ceiling on nitrate concentrations.

As monitoring on different scales allowed deeper insight into the nitrate cycle after disturbance, our multitaxa survey allowed a comprehensive evaluation of the biodiversity-enhancing effect. In line with our results early successional forests have been identified as highly diverse due to natural legacies such as dead wood and bare ground (Swanson *et al.* 2011) as well as sunlight on the forest floor (Lehnert *et al.* 2013). The only significantly contrasting group for species numbers was fungi. Here, despite an increase in the quantity of dead wood caused by bark beetles, tree trunks and other woody debris desiccate under the open canopy, which disfavors many fungi. For beta diversity we found mollusks showing significantly lower beta diversity in affected stands. This finding adds to the knowledge that richness of mollusks in acidic forests is supported by mature stands and long-term stable microclimate (Müller *et al.* 2005).

With respect to the negative findings only for fungi and mollusks it is important to underline that we compared early successional stages after bark beetle infestations with mature spruce stands and not with old growths. The value of old growths for a broad array of organisms is beyond dispute and has been shown also in our study area for the few small relict stands (e.g., Müller *et al.* 2010; Bässler *et al.* 2012). Unfortunately old growth is virtually nonexistent now in Europe, and development of mature stands to old-growth condition will require more than 100 years in most forests. Evidence that unmanaged disturbance areas can provide legacies functionally equivalent to those found in old-growth forests (Swanson *et al.* 2011; Donato *et al.* 2012) opens new opportunities for conservation. Furthermore, it is important to note that we only investigated unmanaged bark beetle areas. Thus our study does not inform a second major discussion, the complex and negative impacts of salvage logging on biodiversity (e.g., Thorn *et al.* 2014). Finally, we used three measures of biodiversity that can be easily compared across taxa, are relevant to conservation, and are easy to communicate in political decision processes, but biodiversity has many faces. For several taxa earlier studies show that species composition also responds to bark beetle infestation (Müller *et al.* 2010; Bässler *et al.* 2012). Further studies are required to develop a deeper ecological understanding of the ecological processes behind this community response.

Mountain forests in Europe and elsewhere provide several major ecosystem services: fiber production, social and cultural services such as landscape aesthetics and recreation, prevention of soil erosion, protection of human infrastructure, habitats for species to ensure biodiversity and ecosystem functioning, and provisioning of drinking water. The first service is excluded in strictly protected forests. The second is well fulfilled in naturally disturbed forests (Müller & Job 2009). Changes in sediment transport or increased flooding risk are not reported and are not likely in unmanaged forests where logging and scarification of soil surfaces do not occur. For the last two services our results demonstrate that unmanaged large disturbances by bark beetles in central European mountain forests also enhance species richness of most taxa, including Red-listed species, while not impairing water quality.

Current policies in most European countries favor intensive management of forests and, where possible, suppression of natural disturbances. A "benign neglect" approach to forest management is seen as naïve and backwards, even within protected areas. Our results support a change in policy, where politicians and decision makers on a national level agree to allow more natural disturbances to operate as a useful conservation tool in the homogenized forests of Europe. Our results also suggest that, when establishing protected areas, decisions of governments to allow or to suppress natural disturbance-recovery processes should not be governed by fears of reduced biodiversity or loss of water quality, because naturally disturbed forest landscapes provide both benefits. Similarly, managers of production forests, where economic impacts of disturbances are a more valid concern, should not base their decisions on fears about the impacts of natural disturbances on drinking water quality or loss of biodiversity.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

**Table S1:** Physiographic and hydrometeorological catchment characteristics. Mean air temperature covers 1980–2004, mean precipitation and runoff cover 1992–2010. Tree species composition (status 1990) was dominated by Norway spruce, while European beech is the dominant broadleaf species. The combined contribution of other species is less than 5%. (Minimum and maximum values are in brackets).

**Table S2:** Number of species, red listed species, plots, and methods used for the biodiversity survey.

**Figure S1:** Nitrate concentrations in seepage water and groundwater.

**Figure S2:** Autocorrelation function plots for annual maximum nitrate concentration versus affected area by bark beetles.

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