Received: 29 July 2022 | Revised: 6 April 2023 | Accepted: 7 April 2023

DOI: 10.1111/ele.14227

ECOLOGY LETTERS cnrs WILEY

LETTER

Ambient and substrate energy influence decomposer diversity differentially across trophic levels

Peter Kriegel[1] | Sebastian Vogel[1,2] | Romain Angeleri[3,4,5] | Petr Baldrian[6] | Werner Borken[7] | Christophe Bouget[8] | Antoine Brin[9] | Heinz Bussler[10] | Cristiana Cocciufa[11] | Benedikt Feldmann[12] | Martin M. Gossner[5,13] | Elena Haeler[3,5,13,14] | Jonas Hagge[15,16] | Sönke Hardersen[17] | Henrik Hartmann[18,19] | Joakim Hjältén[20] | Martyna M. Kotowska[21] | Thibault Lachat[3,5] | Laurent Larrieu[22,23] | Alexandro B. Leverkus[24] | Anna L. M. Macagno[25,26] | Oliver Mitesser[1] | Jörg Müller[1,27] | Elisabeth Obermaier[28] | Francesco Parisi[29,30] | Stefan Pelz[31] | Bernhard Schuldt[32,33] | Sebastian Seibold[34,35,36] | Elisa Stengel[1] | Anne Sverdrup-Thygeson[37] | Wolfgang Weisser[38] | Simon Thorn[1,39,40]

[1]Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius Maximilians University Würzburg, Rauhenebrach, Germany

[2]Bavarian Environment Agency, Biodiversitätszentrum Rhön, Bischofsheim in der Rhön, Germany

[3]School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences BFH, Zollikofen, Switzerland

[4]Institute of Ecology and Evolution IEE – Conservation Biology, University of Bern, Bern, Switzerland

[5]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[6]Laboratory of Environmental Microbiology, Institute of Microbiology of the Czech Academy of Sciences, Praha 4, Czech Republic

[7]Department for Soil Ecology, University of Bayreuth, Bayreuth, Germany

[8]French National Research Institute for Agriculture, Food and Environment INRAE, 'Forest Ecosystems' Research Unit, Nogent-sur-Vernisson, France

[9]University of Toulouse, Engineering School of Purpan, UMR 1201 INRAE-INPT DYNAFOR, Toulouse, France

[10]Am Greifenkeller 1b, Feuchtwangen, Germany

[11]Arma dei Carabinieri CUFA, Projects, Conventions, Environmental Education Office, Rome, Italy

[12]Juistweg 1, Münster, Germany

[13]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland

[14]Department of Forest Growth, Silviculture and Genetics, Federal Research and Training Centre for Forests Natural Hazards and Landscape BFW, Vienna, Austria

[15]Forest Nature Conservation, Northwest German Forest Research Institute, Hann. Münden, Germany

[16]Department for Forest Nature Conservation, Georg-August-University Göttingen, Göttingen, Germany

[17]Reparto Carabinieri Biodiversità di Verona, Centro Nazionale Carabinieri Biodiversità "Bosco Fontana", Marmirolo, Italy

[18]Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena, Germany

[19]Julius Kühn Institute (JKI), Federal Research Centre for Cultivated Plants, Institute for Forest Protection, Quedlinburg, Germany

[20]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

[21]Department of Plant Ecology and Ecosystems Research, Georg-August University Göttingen, Göttingen, Germany

[22]University of Toulouse, INRAE, UMR 1201 DYNAFOR, Castanet-Tolosan, France

[23]CNPF-CRPF Occitanie, Auzeville-Tolosane, France

[24]Departamento de Ecología, Universidad de Granada, Granada, Spain

[25]Department of Biology, Indiana University, Indiana, Bloomington, USA

[26]Department of Epidemiology and Biostatistics, School of Public Health, Biostatistics Consulting Center, Indiana University, Indiana, Bloomington, USA

[27]Bavarian Forest National Park, Grafenau, Germany

[28]Ecological-Botanical Garden of the University of Bayreuth, Bayreuth, Germany

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Ecology Letters* published by John Wiley & Sons Ltd.

[29]Department of Bioscience and Territory, Università degli Studi del Molise, Pesche, Italy
[30]NBFC, National Biodiversity Future Center, Palermo, Italy
[31]Institute for Applied Science, University of Applied Forest Sciences Rottenburg, Rottenburg, Germany
[32]Chair of Forest Botany, Institute of Forest Botany and Forest Zoology, Technical University of Dresden, Tharandt, Germany
[33]Chair of Ecophysiology and Vegetation Ecology, University of Würzburg, Würzburg, Germany
[34]Ecosystem Dynamics and Forest Management Research Group, Technical University of Munich, Freising, Germany
[35]Berchtesgaden National Park, Berchtesgaden, Germany
[36]Technische Universität Dresden, Forest Zoology, Tharandt, Germany
[37]Faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Sciences NMBU, Ås, Norway
[38]Department for Life Science Systems, TUM School of Life Sciences, Technical University Munich, Freising, Germany
[39]Hessian Agency for Nature Conservation, Environment and Geology, Biodiversity Center, Gießen, Germany
[40]Czech Academy of Sciences, Biology Centre, Institute of Entomology, České Budějovice, Czech Republic

Correspondence
Peter Kriegel, Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius Maximilians University Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany.
Email: peter.kriegel@uni-wuerzburg.de

Funding information
Bauer-und Stemmler Stiftung; Czech Science Foundation, Grant/Award Number: 22-27166S; Deutsche Bundesstiftung Umwelt, Grant/Award Number: 20016/466; Deutsche Forschungsgemeinschaft, Grant/Award Number: TH 2218/5-1

Editor: Akira Mori

Abstract

The species-energy hypothesis predicts increasing biodiversity with increasing energy in ecosystems. Proxies for energy availability are often grouped into ambient energy (i.e., solar radiation) and substrate energy (i.e., non-structural carbohydrates or nutritional content). The relative importance of substrate energy is thought to decrease with increasing trophic level from primary consumers to predators, with reciprocal effects of ambient energy. Yet, empirical tests are lacking. We compiled data on 332,557 deadwood-inhabiting beetles of 901 species reared from wood of 49 tree species across Europe. Using host-phylogeny-controlled models, we show that the relative importance of substrate energy versus ambient energy decreases with increasing trophic levels: the diversity of zoophagous and mycetophagous beetles was determined by ambient energy, while non-structural carbohydrate content in woody tissues determined that of xylophagous beetles. Our study thus overall supports the species-energy hypothesis and specifies that the relative importance of ambient temperature increases with increasing trophic level with opposite effects for substrate energy.

KEYWORDS
biodiversity, coleoptera, deadwood, Europe, saproxylic, species-energy hypothesis, trophic guild

INTRODUCTION

Understanding the mechanisms determining biodiversity in space and time remains a fundamental challenge in ecology. Macroecological patterns, such as species-elevation relationships or species-latitude relationships, are well documented, but underlying drivers remain poorly understood (Gaston, 2000). For instance, variation in species richness along latitudinal gradients can result from variation in solar radiation, mean annual temperature, and annual potential evapotranspiration (Currie, 1991). Such variables are often linked to energy availability in an ecosystem, a major determinant of biodiversity patterns (Gaston, 2000).

Two major theories aim at explaining how energy availability drives biodiversity. First, the *ambient-energy hypothesis* (Turner et al., 1987) states that temperature directly affects individual organisms, e.g., by affecting development and fitness. In a warm climate, ectotherms are more efficient in reproduction and feeding, and endotherms need less energy to maintain body temperature and can thus allocate more resources to, e.g., reproduction (Turner, 2004). This allows larger populations, leading to higher numbers of species. Second, the *productivity hypothesis* (Wright, 1983), proposes that energy transmits through the substrate from lower trophic levels like primary producers to higher trophic levels like predators. Hence, overall biodiversity is driven by plant production, which is in turn related to the availability of limiting factors such as sunlight, water, or nutrients. Here, higher substrate energy supplies larger populations and ultimately higher numbers of species. An interplay of both theories may ultimately explain local biodiversity as incoming solar radiation and ambient temperature are highly interrelated (Chang & Root, 1975; Linacre, 1969). As both theories are ultimately driven by population sizes, which are correlated with potential determinants such as energy availability, disentangling these effects becomes difficult. Therefore, it is important to consider species richness (i.e., diversity standardized by abundance) and observed species densities (i.e., diversity standardized to sampling unit, sensu Gotelli & Colwell, 2001) in parallel. More pronounced effects of energy on species densities indicate that energy

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mainly acts through population sizes (Seibold, Bässler, Baldrian, et al., 2016; Vogel et al., 2021).

Necromass is present in all ecosystems in form of, e.g., dead plant matter, dung, or carrion. It has a significant impact on structure and functioning of ecosystems (Benbow et al., 2019). Furthermore, necromass plays an important role for energy flow within ecosystems and is the foundation for many food webs with significant bottom-up effects in energy cycles (Benbow et al., 2019; Gessner et al., 2010). Arthropod communities play key roles in the decomposition process, e.g., through substrate alterations, enzymatic digestion, biotic interactions, or nutrient cycling (Nichols et al., 2008; Ulyshen, 2016; von Hoermann et al., 2018). Therefore, arthropod decomposers provide major ecosystem functions globally by contributing to the decomposition of deadwood (Seibold et al., 2021), litter (David, 2014), dung (Nichols et al., 2008), and carrion (Pechal et al., 2014) and are strongly dependent on their respective resource. Ambient energy, e.g., temperature and solar radiation, is a major driver of abundance and species richness of arthropod decomposers, as shown for dung beetles (Frank et al., 2018), carrion decomposing insects (Farwig et al., 2014; von Hoermann et al., 2018), and deadwood-decomposing arthropods (Müller et al., 2015; Vogel, Gossner, et al., 2020). However, energy availability in ecosystems also depends on the availability of the energy in the substrate, e.g., amount of dead plant and non-plant biomass (Müller et al., 2008; VanLaerhoven et al., 2015; von Hoermann et al., 2021). Substrate energy is defined by physio-chemical and anatomical properties, which vary significantly between wood from different tree species (Chave et al., 2006; Kotowska et al., 2020; Meerts, 2002; Weedon et al., 2009), or between dung from different vertebrates (Frank, Brückner, et al., 2017). These differences in resource quality define which decomposing organisms can utilize the stored energy. Nitrogen and other macro- and micronutrient contents, as well as sugar content, are important factors to build, uphold and maintain body composition and functions, as well as for reproduction success for arthropod decomposer communities (Benbow et al., 2019; Filipiak & Weiner, 2014; Gittings & Giller, 1998; Riley et al., 2014; Vos et al., 2013). Therefore, it is likely that substrate energy is a better determinant for explaining shifts in biodiversity in lower trophic levels of decomposer communities (Yang et al., 2022).

We used saproxylic, i.e., deadwood-dependent, beetles (Coleoptera) to rank the importance of ambient energy versus substrate energy in determining species richness. The studied taxa allowed us to track energy through an ecosystem, similar to often studied plant-herbivory interactions, through sampling techniques which enabled us to tie sampled individuals to a specific resource object. For this, we compiled data from experimental studies of saproxylic beetles along a latitudinal gradient in Europe covering 2748 individual deadwood objects from 618 sites. We measured wood traits characterizing

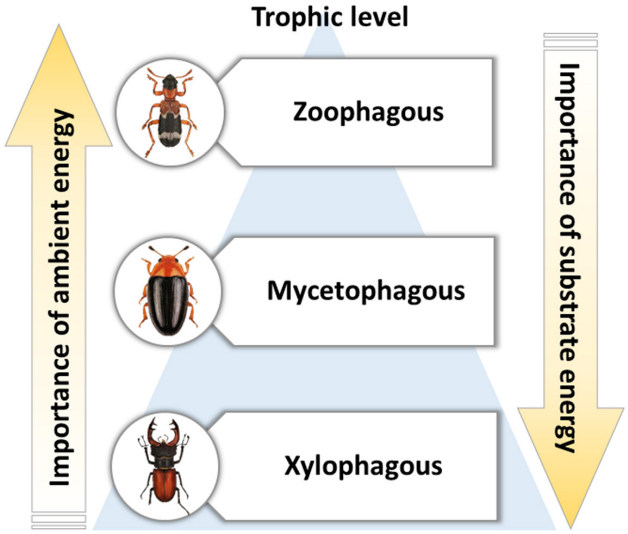

FIGURE 1 Direction of arrows signifies increasing hypothesized importance of substrate energy and ambient energy in defining diversity along trophic levels of decomposer communities. To rank the importance of substrate and ambient energy, we used saproxylic beetle communities separated into three main feeding guilds: zoophagous, mycetophagous and xylophagous.

substrate energy of 75 European woody plants. We hypothesized that: (1) Overall, the effects of ambient energy will be stronger than the effects of substrate energy on saproxylic beetles, when they are not divided into trophic levels; (2) the relative importance of ambient energy will decrease from higher trophic levels like zoophagous beetles to lower trophic levels, while substrate energy will show the opposite effect (Figure 1).

MATERIALS AND METHODS

Species data

We compiled a dataset from experimental studies on saproxylic beetles across Europe, ranging from Mediterranean to boreal forests with mean annual temperatures ranging from −0.1 to 14.9°C, based on published and unpublished experiments available among co-authors (Figure 2; Table S1). We only considered experimental setups that sampled long enough to include the complete adult activity spectrum of all saproxylic beetle species in the respective areas and allowed us to assign emerging species of saproxylic beetles to a specific deadwood object, e.g., stem-emergence traps or rearing of deadwood objects. Comparability of the sampling methods is ensured, as both trap types yield highly correlated measures of biodiversity (Hagge, Leibl, et al., 2019). Furthermore, we only included data without artificial manipulation and experimental treatments of the deadwood objects (e.g., bark-scratching, bark-removal, burning, or exposure in canopy). For classification and definitions of saproxylic beetles and

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

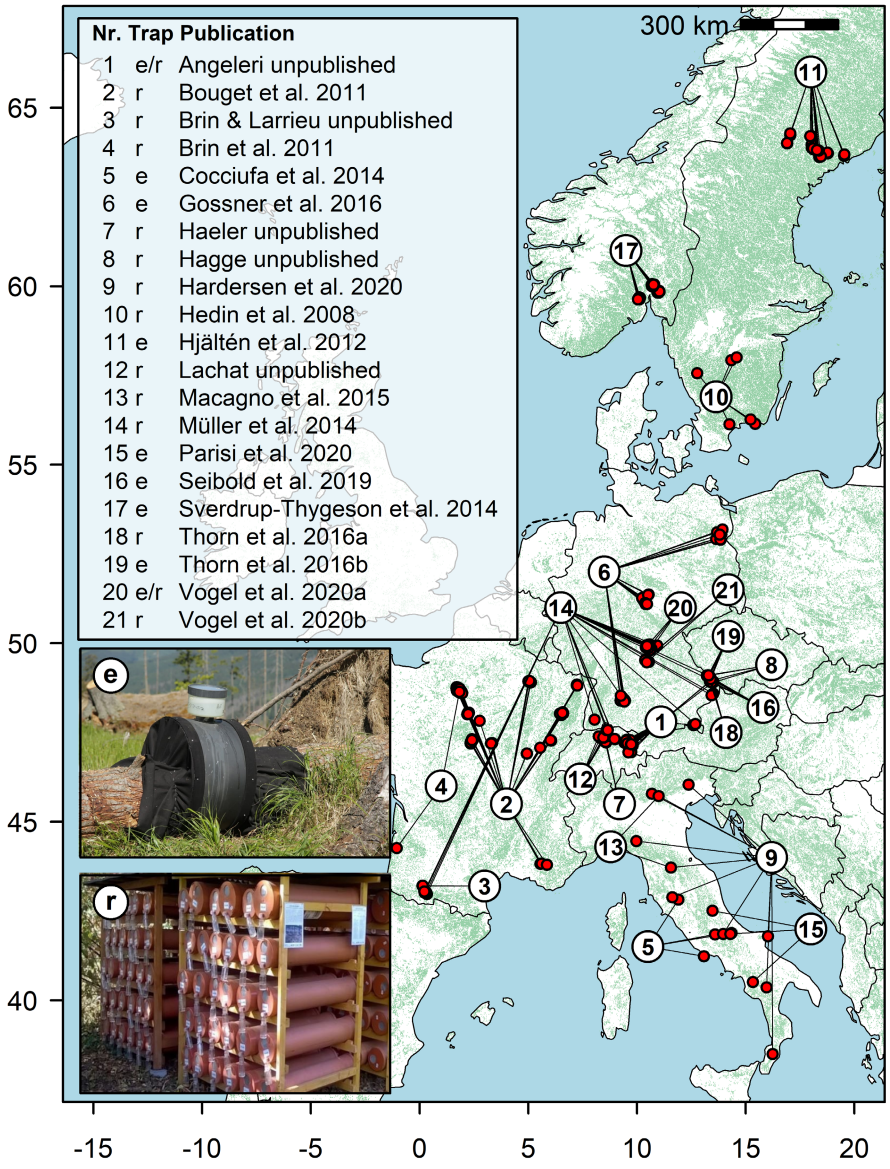

FIGURE 2 Distribution of dataset origins. Sampling methods are marked with 'e' (emergence traps in situ), 'r' (rearing of deadwood objects ex situ) or 'e/r' for both within one dataset. Background shows European forest cover taken from CORINE Land Cover 2018 (EEA, 2018).

their respective feeding guilds see the description in Supplementary information (S1).

Ambient energy

Data on climate was extracted on the object level using R 4.0.4 (R Core Team, 2020). Temperature, temperature seasonality, and solar radiation were extracted from the WorldClim2 database with a spatial resolution of ~1 km^2 aggregated across a target temporal range of 1970–2000 (Fick & Hijmans, 2017) by using the *raster* package (Hijmans et al., 2022). The seasonality of solar radiation and temperature was calculated as the standard deviation of the monthly means. To correct temperature seasonality for influences of temperature, we used the residuals of a linear regression model of both variables. An overview of all variables, including ecological importance, range, and standard deviation is displayed in Table 1 and Table S3.

Substrate energy

We measured 12 anatomical and 24 chemical wood traits from 75 European tree species from branches with 2–4 cm diameter. Branches were collected from natural stands in northern Bavaria, Germany (N 49°50′; E 10°29′) in a temperate climate with mean annual temperatures of 7–8°C and annual precipitation of 750–850 mm (BayFORKLIM, 1996). Forest stands in the region consist mainly of European beech (*Fagus*

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Variables describing ambient energy, substrate energy, and co-variables accounting for differences in environmental conditions, resource amount and evolutionary differences, including their units and ecological importance.

Type	PCA	Trait	Unit	Source	Ecological importance
Ambient energy	—	Temperature	°C	Worldclim2	Straight-forward measurements describing influx of ambient energy within an ecosystem. Often described as drivers for biodiversity through different effects (Archibald et al., 2010; Gaston, 2000; Whittaker et al., 2003)
	—	Temperature seasonality	—	Worldclim2	
	—	Solar radiation	$kJ\,m^{-2}day^{-1}$	Worldclim2	
	—	Solar radiation seasonality	—	Calculated	
Substrate energy	Nutrients	Aluminium (Al)	mg/g dry mass	Measured	Important to build up and maintain body composition, essential for growth and crucial for bodily functional processes (Filipiak & Weiner, 2014)
		Calcium (Ca)			
		Copper (Cu)			
		Iron (Fe)			
		Potassium (K)			
		Magnesium (Mg)			
		Manganese (Mn)			
		Sodium (Na)			
		Phosphorus (P)			
		Sulfur (S)			
		Zinc (Zn)			
	—	Carbon content	%/g dry mass	Measured	In analyses only included as C:N ratio
	—	Nitrogen content	%/g dry mass	Measured	
	—	C:N ratio	—	Measured	Stoichiometric proportion of Carbon (energy source) to nitrogen (essential for growth and survival of consumers) (Filipiak & Weiner, 2014)
	—	Gross calorific value	J/g dry mass	Measured	Direct measurement of energy available in substrate, essential for energy relationships in ecosystems (Singh & Kostecky, 1986)
	NSC xylem	Glucose xylem	mg/g dry mass	Measured	Direct source of energy, usually less rich in xylem layer, led to different life strategies of wood-borers and phloem feeders (Ulyshen, 2018)
		Sucrose xylem			
		Fructose xylem			
		Starch xylem			
	NSC phloem	Glucose phloem	mg/g dry mass	Measured	Direct source of energy, easily accessible, usually richer than in xylem layer, some phloem feeders stay in phloem, others later bore into wood (Ulyshen, 2018)
		Sucrose phloem			
		Fructose phloem			
		Starch phloem			

(Continues)

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 (Continued)

Type	PCA	Trait	Unit	Source	Ecological importance
Co-variables	—	Canopy closure		Measured/ estimated	Acts as filter on ambient energy influx. Sun exposure is an important driver of saproxylic diversity (Seibold, Bässler, Baldrian, et al., 2016; Vogel, Gossner, et al., 2020)
	—	Precipitation	mm	Worldclim2	Water availability can be a limiting factor for biodiversity, especially in areas with high ambient energy influx (Hawkins et al., 2003)
	—	Precipitation seasonality	—	Worldclim2	
	—	Wood pH value	—	Measured	Influences fungal and bacterial communities, therefore alters decomposition process (Moll et al., 2018)
	Anatomical properties	Basic wood specific gravity	—	Measured	Physical stem properties can determine the accessibility, shape defence mechanisms, and control the habitat condition within deadwood (Yang et al., 2022). Furthermore, they can be an indicator of tree life history strategy (Muller-Landau, 2004)
		Lumen-to-sapwood area ratio	%	Measured	
		Vessel density	n/mm^2	Measured	
		Average single vessel diameter	µm	Measured	
		Hydraulically weighted vessel diameter	µm	Measured	
		Potential hydraulic conductivity	$kgm^{-1}MPa^{-1}s^{-1}$	Measured	
	Anatomical fractions	Fibre/conduit wall+fibre lumen fraction	%	Measured	Proportions of wood components are functionally distinct, controlling water transport, mechanical strength and storage or transport of nutrients (Kotowska et al., 2020; Ziemińska et al., 2013)
		Conduit fraction (vessel+tracheid lumen)	%	Measured	
		Ray parenchyma fraction	%	Measured	
		Axial parenchyma fraction	%	Measured	
		Fraction of other rarer cell types	%	Measured	
	—	Decay stage (as years of exposure)	Years	Measured/ calculated	Decay stage influences diversity and abundance of saproxylic organisms (Hammond et al., 2004; Saint-Germain et al., 2007)
	—	Tree evolutionary history	Min. age of genus	Calculated	Tree species and beetle species co-evolved, giving phylogenetically older genera more time for beetles to adapt to their physio-chemical structure, to use them as a food source or for the tree to obtain defensive mechanisms
	—	Wood density	g/cm^3	Measured	Determining available amount of substrate energy per volume
	—	Deadwood object volume	cm^3	Calculated	To account for differences in resource quantity in analyses

Note: Column 'PCA' shows which traits were summarized using principal component analysis.

Abbreviation: NSC, non-structural carbohydrates.

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

sylvatica) sessile oak (*Quercus petraea*) and Scots pine (*Pinus sylvestris*). Branches were cut from lower parts of trees between October 2017 and February 2018. An overview of all measured traits is presented in Table 1 and ranges of traits in Table S3. For a detailed description on how wood traits were measured, see description in the Supplementary information (S2). To reduce and summarize trait information, we grouped traits in five categories, i.e., anatomical properties, anatomical fractions, non-structural carbohydrates in xylem, non-structural carbohydrates in phloem, and nutrients (Table 1; Tables S5 and S6). Afterwards, each group was subjected to a Principal Component Analyses (PCA) using the *princomp* function. To cover more than 50% of variance we included as many axes of each PCA as necessary for further analysis (Figure 3; Figure S1). Remaining single anatomical and physio-chemical tree traits (C:N ratio and dry density) were not included in PCAs and directly used as fixed effects in models, due to their direct relationship to substrate energy. Compiled traits for all 75 tree species are listed in Tables S5–S7.

Co-variables

To obtain precise data on the deadwood, we compiled potentially important co-variables. Those included: (i) the geographic coordinates of the plot, (ii) tree species, (iii) object position (ground, elevated (without contact to soil), snag), (iv) volume calculated as a cylinder using the length of the object for deadwood which was completely enclosed by the trap (rearing) and the length of the trap for objects which were not fully enclosed (emergence traps). Diameters of deadwood objects included in this study ranged from 1 to 85 cm with a mean of 25.40 ± 13.6 cm. Distribution of object diameters separated by sampling years is displayed in Figure S2. Furthermore, we included: (v) decay stage, and (vi) the exposure time in years after the experiment was started. We used the exposure time for each deadwood object as a proxy for decay stage. For studies that were not set up experimentally, but included deadwood of different decay stages on sites, we predicted the exposure time by a linear model of decay stage and exposure (Table S3). Exposure times included in our study ranged from 0 years (sampling took place in the same year as exposition) to a maximum of 8 years with a mean of 2.94 ± 2.0 years. We also gathered the environmental co-variable (vii) canopy closure, which was measured between 0 and 100% with either different laser-, photography-, lidar-, or radar techniques or was visually estimated by the data contributors in 5% steps. Furthermore, we mined data for (viii) precipitation, (ix) precipitation seasonality, and (x) elevation from the *elevatr* package based on raster data of Amazon Web Services Terrain Tiles (Hollister et al., 2021). The seasonality of precipitation was calculated as the coefficient of variance of the monthly values. We extracted the (xi) minimum genus age for each tree species based on the phylogenetic tree provided by Durka and Michalski (2012) as a proxy of phylogenetic isolation to account for differences in the evolutionary history of the tree species.

Data analyses

All analyses were carried out using R v.4.0.4. (R Core Team, 2020). Prior to statistical analyses, abundances of beetles were aggregated to the object level within each year. The phylogenetic relationship of species violates the statistical requirement of independent observations regarding tree physiological traits (Felsenstein, 1985). Hence, we corrected tree species traits by their respective phylogenetic relationship among each other. For this, we used the phylogenetic tree of European flora provided by Durka and Michalski (2012). We decomposed each trait into its phylogenetic component (ancestral contribution to the trait, P-component) and the residual deviation (species-specific variance of the trait, S-component) using Lynch's comparative method (Lynch, 1991). As results of this process are subject to random variation, we replicated this step 999 times and used the mean values of the species-specific variance of each trait in our analyses. Tree species for which we were not able to measure traits (12% of our tree species) were complemented by the mean of each trait from all tree species within the same genus. Weak collinearity among predictor variables was ensured by using the variance inflation factor, provided by the *vifstep* function of the *udsm* package (Naimi et al., 2014), with a threshold of 4. To avoid collinearity in our analyses, we excluded the following variables: anatomy fractions, wood pH-value, gross calorific value, elevation, precipitation, and precipitation seasonality. For an overview of correlation of all initial variables see Figure S3 in the Supporting information.

We used the statistical framework based on Hill numbers with the exponents $q=0$ (species richness), $q=1$ (the exponential of Shannon's entropy index, hereafter referred to as Shannon diversity), and $q=2$ (the inverse of Simpson's concentration index, hereafter referred to as Simpson diversity) (Chao et al., 2014). To disentangle the effects of population sizes from energy availability within the ambient energy- and productivity hypothesis we compared species density and species richness as response variables in our models. We follow the definitions of Gotelli and Colwell (2001), where species density is standardized to a specific sampling unit (deadwood area covered by trap) and species richness is standardized to the number of individuals. Possible sampling effects are mediated by using diversity measures such as species richness as a response variable, which are corrected for respective abundances. Calculation of Hill numbers were conducted on object-by-year-level using the *estimateD* function for abundance data to a sample

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

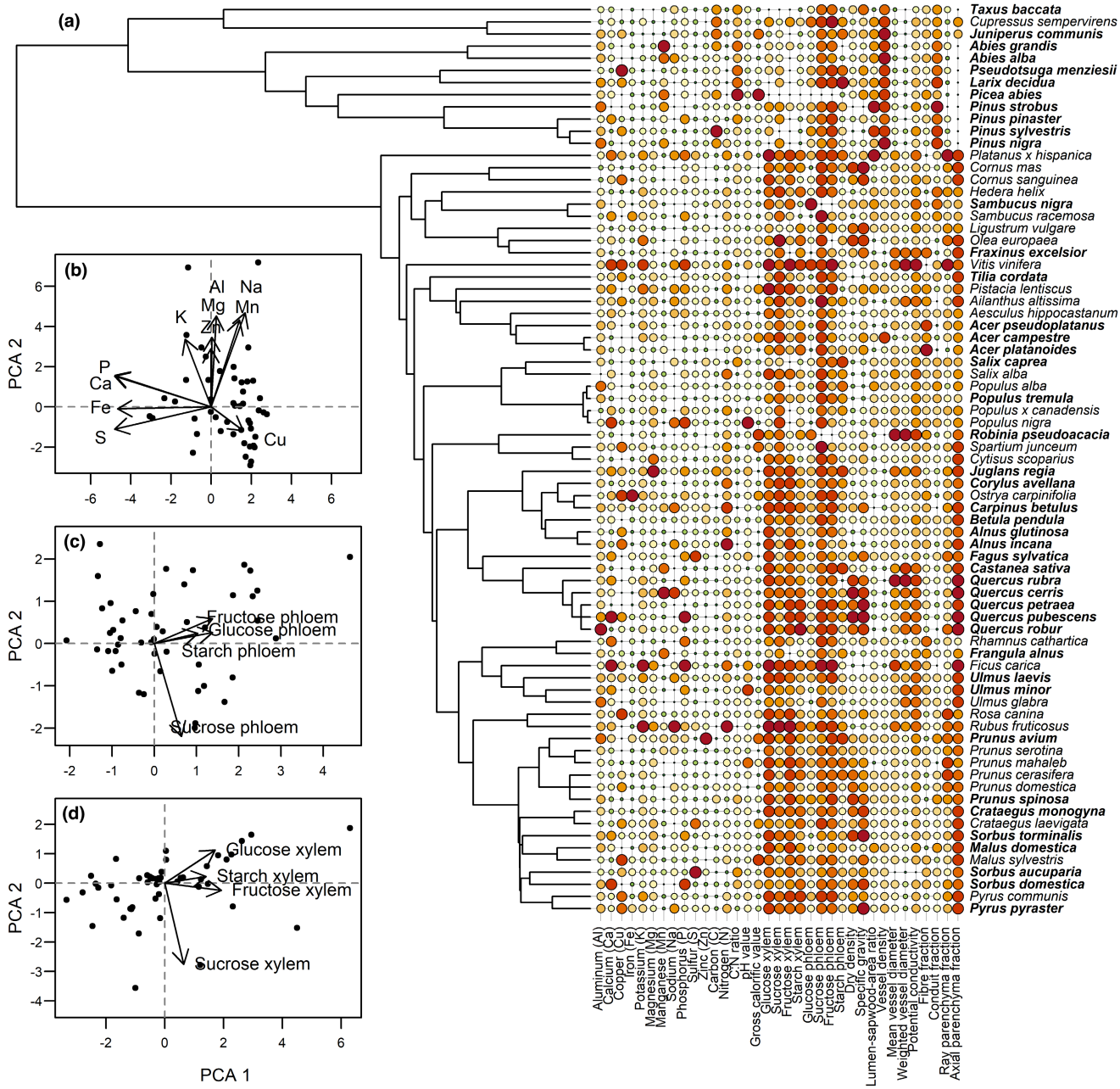

FIGURE 3 (a) Phylogenetic tree of 75 European woody plants provided by Durka and Michalski (2012), with corresponding measured wood traits. Tree species printed in bold were present in our data set. For better visibility of differences, traits were log transformed and scaled to a range of 0.1 to 1.0. Point size as well as colour indicate trait values. Panels (b)–(d) show results from principal component analyses (PCA) for energyrelated grouped traits: (b) nutrients, (c) non-structural carbohydrates in the phloem, and (d) non-structural carbohydrates in the xylem (see Table 1). Results from PCA of the co-variables anatomical traits and anatomical fractions are displayed in Figure S1.

coverage level of 95% from the *iNEXT* package (Hsieh et al., 2016). We used generalized additive mixed models with the *gamm* function of the *mgcv* package (Wood et al., 2016) with a Gaussian error distribution for species diversity measures (q0–q2), and Poisson error distribution for species density as response variables. We used two spline-based smooths (latitude, longitude), which allowed us to account for unmeasured sampling site specific differences to reveal effects of energy controlled by co-variables. We tested for effects of ambient and substrate energy variables as predictors (Table 1). Furthermore, we included important co-variables which either indirectly affect energy measures (e.g., decay stage or physical wood traits) or which control for the resource and energy amount present in each object (e.g., object volume, dry density, decay stage, see Table 1). We used the identity of the respective dataset as a random effect to account for study-specific characteristics. Second, we used the plot identity to account for repeated measurements at the same plot across years. In addition, we

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

added the object position (ground, elevated, snag) and the tree species as random effects.

RESULTS

We compiled 21 datasets from 8 European countries containing 49 tree species (Figures 2 and 3) and 332,557 saproxylic beetles of 901 species. Divided by feeding guild, we accumulated 192,728 (58%) xylophagous, 93,363 (28%) mycetophagous, and 46,383 (14%) zoophagous beetle individuals, excluding detritivorous species. The three most frequent tree species in our data were *Fagus sylvatica* (926 objects; 34%), followed by *Picea abies* (290 objects; 11%), and *Abies alba* (100 objects; 4%). Results of PCA showed high variation of wood traits between broadleaf tree species, but more narrow ranges for coniferous tree species (Figure S5).

Ambient energy was the main driver of overall species diversity of saproxylic beetles (Figure 4; Tables S8–S10). Increasing solar radiation led to higher species richness ($q=0$), Shannon diversity ($q=1$), and Simpson diversity ($q=2$). The opposite effect was observed for seasonality of solar radiation, which lowered all three diversity measures. In contrast, temperature seasonality had a positive effect on species richness. However, when saproxylic beetles were separated by feeding guild, differences of the influence of ambient energy on species richness became apparent (Figure 5; Tables S11–S13). No ambient energy measure significantly affected species richness of xylophagous beetles, but temperature seasonality increased species richness of mycetophagous and zoophagous beetles, and solar radiation and its seasonality increased species richness of mycetophagous beetles.

In contrast, no substrate energy variable had a significant effect on overall saproxylic beetle diversity (Figure 4; Tables S8–S10). However, we observed a shift in effect strength between ambient energy and substrate energy when analysing feeding guilds separately (Figure 5). While significant effects of ambient energy receded when trophic levels were distinguished, non-structural carbohydrates in the xylem fraction of the wood drove species richness of xylophagous beetles. Species richness of mycetophagous and zoophagous beetles were not affected by substrate energy variables. Furthermore, ambient energy measures showed significant impact on species density, also for xylophagous beetles, while substrate

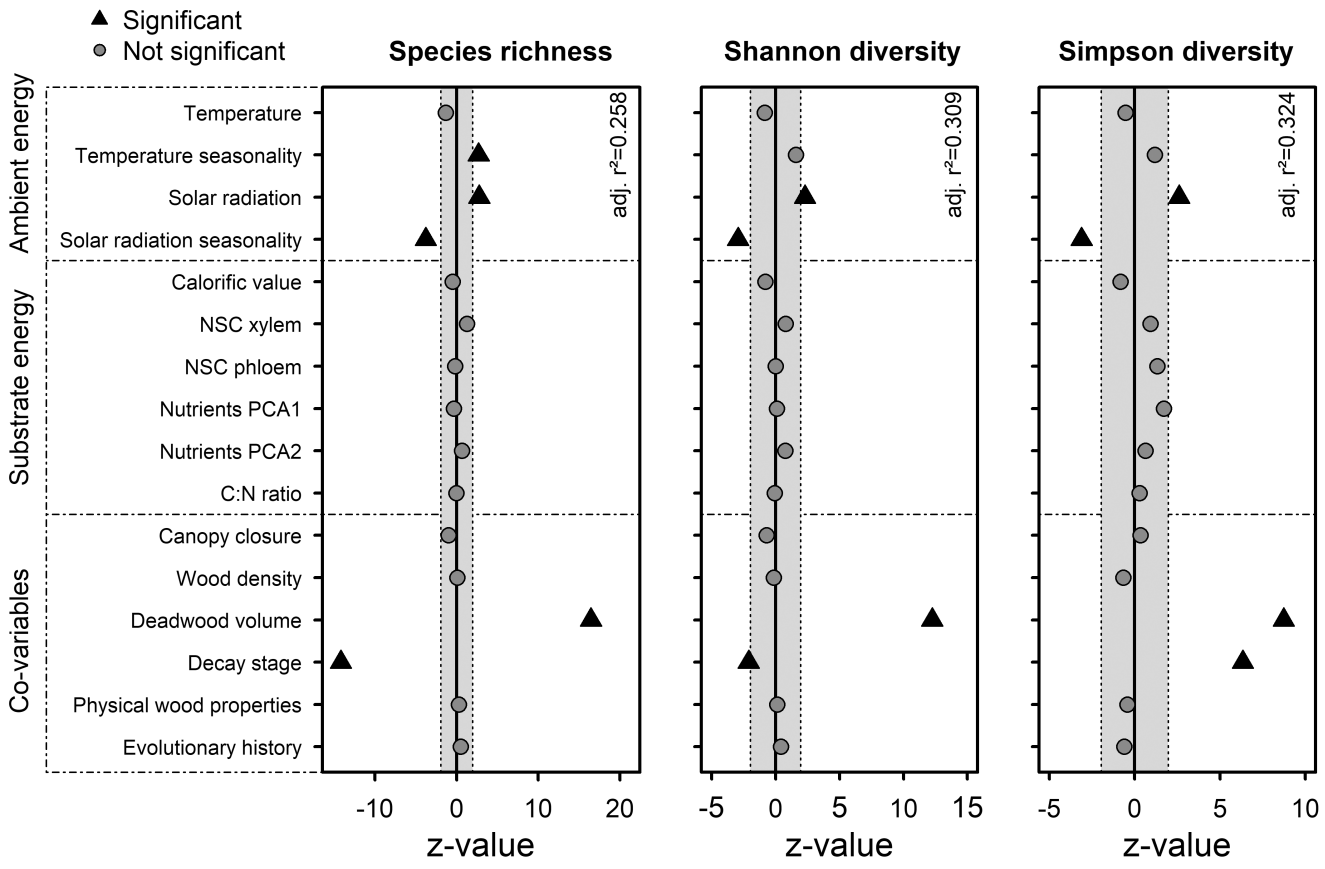

FIGURE 4 Fixed effects of predictor variables on species richness ($q=0$), Shannon diversity ($q=1$) and Simpson diversity ($q=2$) for overall saproxylic beetle communities. Results based on generalized additive mixed models. Black triangles indicate significant effects ($p<0.05$). Adjusted *R*-squared shows goodness-offit for the complete model. Unmeasured geographical co-variables are accounted for by adding two splinebased smooths (latitude, longitude) to the model formula.

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

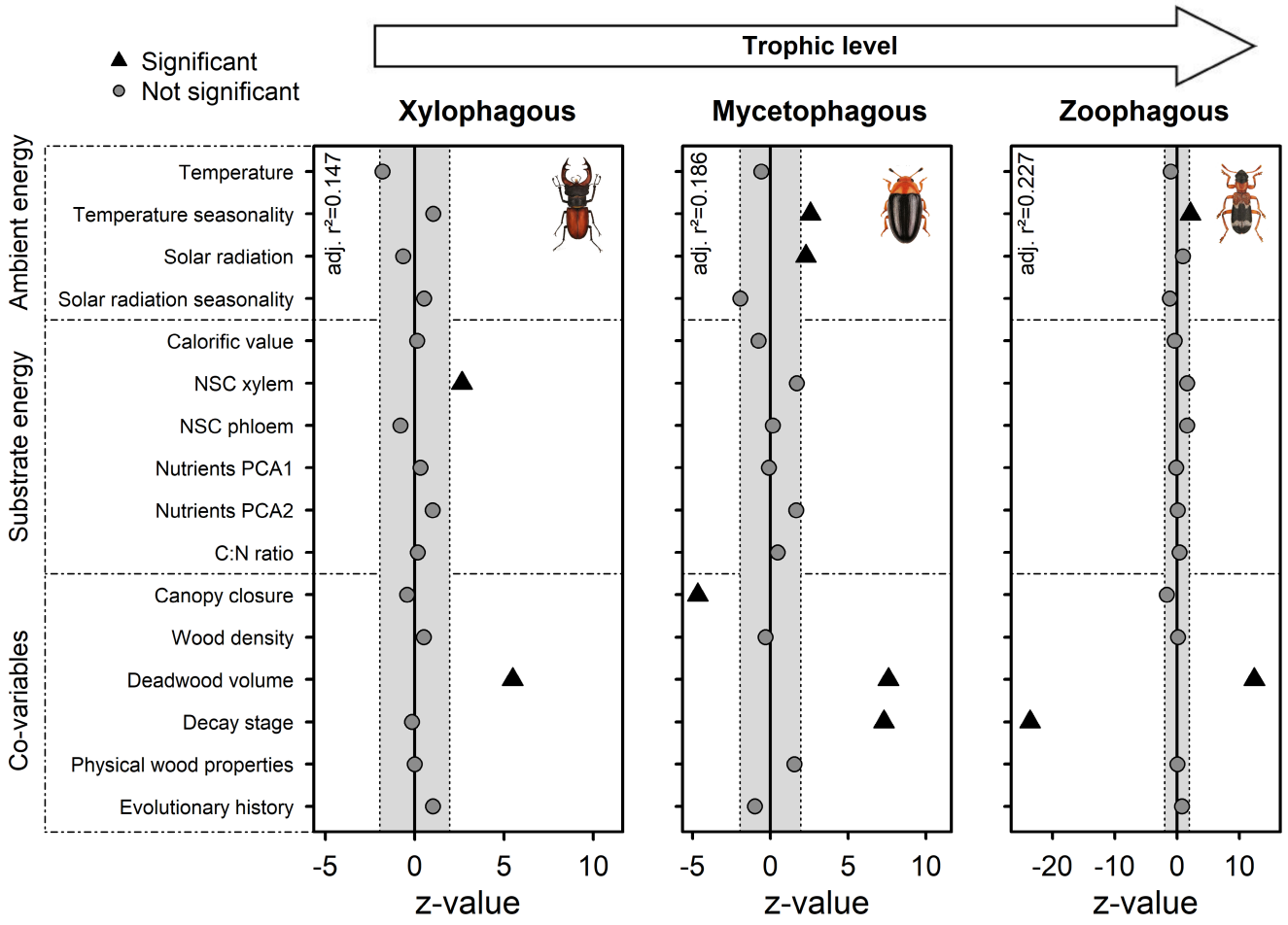

FIGURE 5 Fixed effects of predictor variables on species richness ($q=0$) of different feeding guilds. Results based on generalized additive mixed models. Black triangles indicate significant effects ($p<0.05$). Adjusted R-squared shows goodness-of-fit for the complete model. Unmeasured geographical co-variables are accounted for by adding two spline-based smooths (latitude, longitude) to the model formula.

energy measures had no significant effect on species density of the higher trophic levels mycetophagous and zoophagous beetles (Figure S4; Tables S20–S22). Effects were generally more pronounced for observed species densities (Figure S4) as for species richness, indicating that the effect on diversity is mainly driven by population size.

The co-variables deadwood volume and decay stage had the strongest effects on saproxylic beetle diversity (Figures 3 and 4). Diversity measures increased significantly with increasing deadwood volume for all trophic levels and overall saproxylic beetles (Figures 4 and 5; Figures S6 and S7). Effects of decay stage varied between diversity measures and trophic levels. For overall saproxylic beetles, higher decay stage decreased species richness and Shannon diversity but increased Simpson diversity. Decay stage had a positive effect on species richness for mycetophagous beetles and a negative effect for zoophagous beetles, while no significant effect for xylophagous beetles was observed. In contrast, Shannon diversity and Simpson diversity of xylophagous and mycetophagous beetles were affected positively by increasing wood decay, while Shannon diversity of zoophagous beetles was affected negatively (Figures S6 and S7). Canopy closure had a negative effect on all diversity measures for mycetophagous beetles.

DISCUSSION

Overall saproxylic beetle diversity across Europe was driven by ambient energy measures (Figure 4), but when trophic levels were analysed separately, ambient energy was a major driver of higher trophic levels and substrate energy of lower trophic levels (Figure 5). In addition to energy measures, the amount of available substrate as well as its decay stage had strong effects on saproxylic beetle diversity (Figures 4 and 5). Higher resource amount generally affects decomposer communities positively (Errouissi et al., 2004; Hammond et al., 2004; Lobo et al., 2006; Müller et al., 2015; Turner et al., 2017), while decay stage of substrate influences colonization and species succession (Gittings & Giller, 1998; Jonsson et al., 2005; Saint-Germain et al., 2007). Furthermore,

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

physio-chemical substrate properties impact species diversity in decomposer communities (Benbow et al., 2019; Cox et al., 2001; Gittings & Giller, 1998; Hulme & Shields, 1970). Additionally, diversity is driven by climate variables like ambient temperature or seasonality (Archibald et al., 2010; Benbow et al., 2019; von Hoermann et al., 2020). Even though drivers of decomposer diversity are often investigated, only a few studies disentangle effects between trophic levels, while direct comparisons between influences of ambient and substrate energy are largely lacking.

Global patterns of animal biodiversity are well documented and mostly show a decline of species richness with increasing distance from the equator (Gaston, 2000). However, latitudinal gradients are surrogates for climate-related variables like solar radiation or temperature seasonality, which drive biodiversity of plants, fungi, mammals, birds, amphibians, and invertebrates (Currie, 1991; Currie et al., 2004; Hawkins et al., 2003; Thiele, 1977; Větrovský et al., 2019; Waide et al., 1999). With our results we were able to validate these findings for saproxylic beetles (Figure 4). Autotrophic organisms depend directly on ambient energy to conduct photosynthesis, and ectothermic organisms like many insects rely on ambient energy for thermoregulation to keep their bodies near optimal temperature for physiological or behavioural processes (Norris & Kunz, 2012). However, we also show that species richness of decomposers, which are directly reliant on the substrate, i.e., xylophagous beetles, is driven by substrate energy (Figure 5). Therefore, both forms of energy must be investigated to comprehensively quantify the effects of energy as a driver of biodiversity, while considering trophic levels of target organisms.

Positive correlations of energy availability to the total number of species within an ecosystem are undisputed (Storch et al., 2018) and differences between underlying energy types (i.e., radiation, thermal or chemical) are recognized (Clarke & Gaston, 2006). However, direct comparisons between the impact of ambient energy and different physio-chemical compartments defining substrate energy on species richness are lacking. Furthermore, energy is mainly shared among species in the same trophic level and not generally within ecological communities (Storch et al., 2018). Effects of intraspecific competition which are affecting population sizes and ultimately species richness can therefore vary across trophic levels. This creates the need to analyse trophic levels separately (Storch et al., 2018). Our results show that the relative importance of ambient energy and substrate energy as drivers of biodiversity changes between trophic levels (Figure 5). While ambient energy drives diversity of overall saproxylic beetles (Figure 4), differences become evident between trophic levels. For zoophagous and mycetophagous beetles, which are not directly feeding on deadwood, ambient energy remains the most important energy variable. However, xylophagous beetles that directly consume woody substrate were not affected by ambient energy but by substrate energy. Therefore, we demonstrated that the influence of different forms of energy can vary within a taxonomic group. Specifically, a combination of both the ambient-energy hypothesis and the productivity hypothesis may better explain taxonomic group diversity for taxa encompassing a wide range of trophic guilds such as saproxylic beetles. More significant predictors for species density models further indicated that the effect of energy on diversity is mainly driven by population size (Figure 5; Figure S4). This finding is in line with earlier findings from saproxylic beetles (reviewed in Seibold & Thorn, 2018). Nevertheless, as solar radiation and its seasonality significantly affect species richness, but not species density of mycetophagous beetles, we are able to demonstrate that ambient energy increases species richness beyond simply increasing population sizes (Figure 5; Figure S4). Such effects can be, for instance, caused by habitat heterogeneity (Lettenmaier et al., 2022; Seibold, Bässler, Brandl, et al., 2016).

Ambient energy drives overall saproxylic diversity

Ambient energy proved to be the main driver of diversity measures when investigating saproxylic beetle communities across trophic levels (Figure 4). We observed a positive effect of increasing solar radiation on all diversity measures for saproxylic beetles. Higher energy influx through increased solar radiation benefits greater primary production, which can lead to larger, more viable populations of niche position specialists (sensu Evans et al., 2005) and a wider range of metabolic specialists (Archibald et al., 2010). This results in increasing species numbers of saproxylic beetles with decreasing latitude in Europe, as already indicated by Nieto and Alexander (2010). For example, these authors provide the following figures for species numbers: Sweden 140; Denmark 89; Germany 209; Austria 215; Italy 255. Furthermore, ectothermic organisms like arthropod decomposers can profit from increased solar radiation through spending less effort in behavioural or physical responses to reach an optimal thermal body temperature. Excess energy can then be spent on additional foraging or mating, reducing risk of extinction (Turner, 2004). These findings are also in line with the Metabolic Theory of Ecology that predicts influences on biodiversity through individual metabolic rates, which depend on ambient temperatures and constrain evolutionary rates through effects on individual turnover and mutation (Gillooly et al., 2007).

Furthermore, we observed negative effects of solar radiation seasonality on overall saproxylic beetle diversity (Figure 4). High solar energy influx combined with low thermal seasonality are the two major climate

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

variables, which separate species rich near-equatorial from higher latitude extratropical ecosystems (Archibald et al., 2010). Increasing seasonality of solar radiation (thermal seasonality) can impede finer niche separation, lowering species density (Klopfer & MacArthur, 1960; MacArthur, 1984). It also limits the active period of insects, resulting in a reduced number of generations per year (Hunt & Amdam, 2005; Seger, 1983; Yamamura & Kiritani, 1998), possibly resulting in lower insect speciation rates, ultimately explaining the negative impact we observed of seasonality of solar radiation on species richness. In contrast, we found positive effects of temperature seasonality on overall species richness as well as for mycetophagous and zoophagous beetles (Figures 3 and 4). Higher seasonality in temperature is characterized by greater temperature differences between summer and winter months. Warmer winter temperatures in northern hemisphere result in harsher conditions for forest floor fauna (Groffman et al., 2012; Harris et al., 2019). For winter active predators, they also allow longer activity periods with extended hunting of diapausing prey (Harris et al., 2019), possibly destabilizing their populations.

However, consistent with our predictions, we noted that effects of ambient energy fade when decomposers were divided into trophic levels (Figure 5). Most notable is the lack of significant effects of ambient energy on species richness of xylophagous beetles in our study. As many decomposer organisms spend a considerable amount of their life inside necromass, (Benbow et al., 2019) either as larvae or imago, the direct physiological effects through higher solar energy influx seem to play an inferior role in driving their diversity. While deadwood provides distinct microclimates within a single log (e.g., upper sun exposed side or lower shaded side) (Lettenmaier et al., 2022), it also mitigates effects of diurnal or seasonal temperature fluctuations within the centre of a log (Halme et al., 2013). In contrast, predatory species often hunt on the surface or under the bark. Similarly, mycetophagous species predominantly forage on sporocarps at the surface of deadwood. Thus, predatory and mycetophagous species are more exposed to ambient temperatures than xylophagous species.

Substrate energy affects trophic levels differently

We found significant effects of substrate energy for lower trophic levels (Figure 5). Different forms of necromass (i.e., carrion, dung, or dead plant matter) vary significantly in their chemical composition and nutritional quality (Benbow et al., 2019) for arthropod decomposer communities. Nutritional value in autotrophically derived necromass is generally much lower than in heterotrophically derived necromass and is often described with the carbon nitrogen (C:N) ratio. Our findings that saproxylic beetle diversity is not driven by nutritional value of the substrate is consistent with findings for other arthropod decomposer communities, e.g., dung beetles (Frank, Brückner, et al., 2017). Nutritional mismatches can likely be overcome through mutualistic relationships with fungi or microbes (Filipiak, 2018; Six & Elser, 2019) or through behavioural adaptations, i.e., opportunistic predation or intraspecific cannibalization (Benbow et al., 2019).

We found higher xylophagous beetle species richness with increasing non-structural carbohydrates in the xylem fraction of the wood (Figure 5). Those results are in line with the assumptions by Hättenschwiler and Jørgensen (2010), who suggest that decomposer communities are not primarily limited by stoichiometric mismatches of nutrients between dietary resource and consumer, but rather by energetic requirements which can be fulfilled by non-structural carbohydrates. Non-structural carbohydrates offer an easily accessible direct energy source for many organisms and determine host preference in herbivorous beetles (Arita et al., 1993) and fungi (Cox et al., 2001; Hulme & Shields, 1970).

Deadwood amount and decay stage drive saproxylic beetle diversity

The strongest effects on saproxylic beetle diversity arose from the co-variables deadwood volume and decay stage. Higher resource amounts drive diversity of decomposer communities, for instance, in dung beetles (Errouissi et al., 2004; Lobo et al., 2006) and saproxylic beetles (Hammond et al., 2004; Müller et al., 2015; Ranius & Fahrig, 2006). These findings are in accordance with our results showing positive effects of deadwood object volume on saproxylic beetles (Figures 4 and 5; Figures S6 and S7). Lower saproxylic beetle diversity in small diameter objects can therefore also be attributed to sparse resource amounts which hinder larval development for some species (Ranius et al., 2019). Furthermore, smaller size of deadwood objects shows less stable microclimatic conditions with higher fluctuations in humidity and temperature, which is avoided by some saproxylic beetle species (Lindman et al., 2022). Additionally, deadwood branches of smaller diameter classes have higher decomposition rates (Hyvönen et al., 2000), which shortens the possible time for colonization or does not leave enough time for larval development for some species.

Higher diversity with increasing size of the sampling unit is also predicted through species-area relationships and sampling effects (Chase & Knight, 2013; Siitonen, 2001). As those effects are largely scale-dependent (Chase & Knight, 2013) and measurements of resource amounts on larger scales (e.g., stand level) were not available, we were not able to quantify these effects directly, but accounted for those differences by including the study and geographical coordinates in our model. Furthermore, resource quantities are not the sole force controlling diversity of decomposer communities. Local

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

habitat characteristics are often superimposed by the regional species pool or other large-scale variables (Hagge, Abrego, et al., 2019), such as historic land-use, land-use intensity, spatial arrangement of the resource as well as effects on landscape level, i.e., adjacent landscape structures affect decomposer diversity (Frank, Hülsmann, et al., 2017; Götmark et al., 2011; Haeler et al., 2021; Sverdrup-Thygeson, Gustafsson, & Kouki, 2014; von Hoermann et al., 2020). These ultimately also control the number and proximity of source populations which enable species to colonize new habitats (Feldhaar & Schauer, 2018; Gibb et al., 2006; Seibold et al., 2017), however saproxylic insects often possess long distance dispersal abilities, especially pioneer species of early decay stages, or are efficient dispersers due to their hitchhiking strategies (Komonen & Müller, 2018).

Differences in the quality of a resource for decomposer communities also vary with its decay stage. Saproxylic decomposer organisms prefer deadwood in early and intermediate stages of decay (Hammond et al., 2004; Jonsson et al., 2005; Lassauce et al., 2012; Saint-Germain et al., 2007). These findings are in line with our results, which show that increasing decay stage of deadwood significantly decreases overall species richness of saproxylic beetles (Figure 4; Figure S6). Positive effects of wood decomposition on Simpson diversity (Figure 4; Figure S6) are due to higher weighting of dominant species, which decline over time, e.g., we found mean abundances per object to gradually decline after the first 2 years of decomposition (Figure S8). However, distinguished by trophic level, decay stage had no significant effect on xylophagous beetles, while mycetophagous beetle diversity increased towards advanced decay stages (Figure 5). Increasing species richness for mycetophagous beetles with decomposition can be linked to increases in fungal diversity (Rajala et al., 2011; Van Der Wal et al., 2015) or increases in fungal biomass.

CONCLUSIONS

Patterns followed the species-energy hypothesis, but as predicted in our hypotheses, separating energy into ambient and substrate energy as well as taxa into trophic levels showed that the relative importance of substrate energy decreased with increasing trophic level, while ambient energy showed the opposite effect. Therefore, analysing trophic levels separately provides deeper insights in species-energy relationships, which is of crucial importance to understand patterns of species richness. Effects of ambient energy may superimpose effects of substrate energy, when investigated taxa are not distinguished by trophic levels. However, as only one substrate energy variable showed significant effects and direct ambient energy measurements like solar radiation were not significant for the highest trophic level studied, we encourage future research to continue disentangling effects of ambient and substrate energy among trophic levels to advance general theory in ecology.

AUTHOR CONTRIBUTIONS

Simon Thorn & Sebastian Vogel conceived the study. Bernhard Schuldt, Elisa Stengel, Henrik Hartmann, Martyna M. Kotowska, Sebastian Vogel & Werner Borken measured physio-chemical traits. Peter Kriegel, Oliver Mitesser & Simon Thorn analysed and interpreted the data. Peter Kriegel led the writing of the manuscript with substantial input from all co-authors.

ACKNOWLEDGEMENTS

Peter Kriegel received funds from the Bauer-und Stemmler Stiftung, as well as the DFG Project TH 2218/5-1. Sebastian Vogel was supported by a personal dissertation fellowship of the German Federal Environmental Foundation (Deutsche Bundesstiftung Umwelt, fellowship number 20016/466). The study was supported by the Czech Science Foundation (22-27166S). Furthermore, we thank the projects *Biodiversity Exploratories* and *BioHolz* for making their data available for this research. ABL acknowledges grant LifeWatch-2019-10-UGR-01 by the Spanish Ministry of Science and Innovation/FEDER. CC thanks the University of RomaTre (Rome) and the Arma dei Carabinieri, National Focal Point of the Italian ICP Forests—CON.ECO.FOR. Network (Rome) for their cooperation. We thank Cherie Lee for proof-reading the article. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

Bauer-und Stemmler Stiftung; Czech Science Foundation, Grant/Award Number: 22-27166S; Deutsche Bundesstiftung Umwelt, Grant/Award Number: 20016/466; Deutsche Forschungsgemeinschaft, Grant/Award Number: TH 2218/5-1

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14227.

DATA AVAILABILITY STATEMENT

Data is available at the public repository Dryad with the following DOI: https://doi.org/10.5061/dryad.brv15dvch.

ORCID

Peter Kriegel https://orcid.org/0000-0003-4099-5295
Romain Angeleri https://orcid.org/0000-0001-6652-4921
Petr Baldrian https://orcid.org/0000-0002-8983-2721
Martin M. Gossner https://orcid.org/0000-0003-1516-6364
Oliver Mitesser https://orcid.org/0000-0002-3607-877X
Simon Thorn https://orcid.org/0000-0002-3062-3060

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

REFERENCES

Archibald, S.B., Bossert, W.H., Greenwood, D.R. & Farrell, B.D. (2010) Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology*, 36, 374–398.

Arita, L.H., Furutani, S.C., Fukada, M.T. & Nakayama, T.R. (1993) Feeding response of the Chinese rose beetle (Coleoptera: Scarabaeidae) to nonstructural carbohydrates in plants. *Journal of Economic Entomology*, 86, 1416–1419.

BayFORKLIM. (1996) *Klimaatlas von Bayern*. München: Bayrischer Klimaforschungsbund, c/o Metereologisches Institut der Universität München.

Benbow, M.E., Barton, P.S., Ulyshen, M.D., Beasley, J.C., DeVault, T.L., Strickland, M.S. et al. (2019) Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, 89, 1–29.

Bouget, C., Brin, A. & Brustel, H. (2011) Exploring the "last biotic frontier": are temperate forest canopies special for saproxylic beetles? *Forest Ecology and Management*, 261, 211–220.

Brin, A., Bouget, C., Brustel, H. & Jactel, H. (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *Journal of Insect Conservation*, 15, 653–669.

Chang, J. & Root, B. (1975) On the relationship between mean monthly global radiation and air temperature. *Archiv Für Meteorologie, Geophysik und Bioklimatologie: Series B*, 23, 13–30.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. et al. (2014) Rarefaction and extrapolation with hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67.

Chase, J.M. & Knight, T.M. (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters*, 16, 17–26.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, 16, 2356–2367.

Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2257–2266.

Cocciufa, C., Gerth, W., Luiselli, L., De Zan, L.R., Cerretti, P. & Carpaneto, G.M. (2014) Survey of saproxylic beetle assemblages at different forest plots in Central Italy. *Bulletin of Insectology*, 67, 295–306.

Cox, P., Wilkinson, S.P. & Anderson, J.M. (2001) Effects of fungal inocula on the decomposition of lignin and structural polysaccharides in *Pinus sylvestris* litter. *Biology and Fertility of Soils*, 33, 246–251.

Currie, D. (1991) The University of Chicago Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, 137, 27–49.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A. et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134.

David, J.F. (2014) The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biology and Biochemistry*, 76, 109–118.

Durka, W. & Michalski, S.G. (2012) Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, 93, 2297.

EEA. (2018) *Corine Land Cover. Eur. Union, Copernicus L. Monit. Serv.* Available from: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018 [Accessed 5th April 2020].

Errouissi, F., Haloti, S., Jay-Robert, P., Janati-Idrissi, A. & Lumaret, J.P. (2004) Effects of the attractiveness for dung beetles of dung pat origin and size along a climatic gradient. *Environmental Entomology*, 33, 45–53.

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, 80, 1–25.

Farwig, N., Brandl, R., Siemann, S., Wiener, F. & Müller, J. (2014) Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. *Oecologia*, 175, 1291–1300.

Feldhaar, H. & Schauer, B. (2018) Dispersal of Saproxylic insects. In: Ulyshen, M.D. (Ed.) *Saproxylic insects diversity, ecology and conservation*. Berlin, Heidelberg: Springer, pp. 515–546.

Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, 125, 16–15.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Filipiak, M. (2018) Nutrient dynamics in decomposing dead Wood in the context of Wood eater requirements: the ecological stoichiometry of Saproxylophagous insects. In: Ulyshen, M.D. (Ed.) *Saproxylic insect diversity, ecology and conservation*. Berlin Heidelberg: Springer, pp. 429–469.

Filipiak, M. & Weiner, J. (2014) How to make a beetle out of wood: multi-elemental stoichiometry of wood decay, xylophagy and fungivory. *PLoS ONE*, 9, 1–20.

Frank, K., Brückner, A., Hilpert, A., Heethoff, M. & Blüthgen, N. (2017) Nutrient quality of vertebrate dung as a diet for dung beetles. *Scientific Reports*, 7, 1–12.

Frank, K., Hülsmann, M., Assmann, T., Schmitt, T. & Blüthgen, N. (2017) Land use affects dung beetle communities and their ecosystem service in forests and grasslands. *Agriculture, Ecosystems and Environment*, 243, 114–122.

Frank, K., Krell, F.T., Slade, E.M., Raine, E.H., Chiew, L.Y., Schmitt, T. et al. (2018) Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. *Ecology Letters*, 21, 1229–1236.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. et al. (2010) Diversity meets decomposition. *Trends in Ecology & Evolution*, 25, 372–380.

Gibb, H., Hjältén, J., Ball, J.P., Atlegrim, O., Pettersson, R.B., Hilszczański, J. et al. (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography (Cop.).*, 29, 191–204.

Gillooly, J.F., Allen, A.P. & Allen, P. (2007) Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology*, 88, 1890–1894.

Gittings, T. & Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography (Cop.).*, 21, 581–592.

Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E. et al. (2016) Deadwood enrichment in European forests—which tree species should be used to promote saproxylic beetle diversity? *Biological Conservation*, 201, 92–102.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391.

Götmark, F., Åsegård, E. & Franc, N. (2011) How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. *Forest Ecology and Management*, 262, 2297–2305.

Groffman, P.M., Rustad, L.E., Templer, P.H., Campbell, J.L., Christenson, L.M., Lany, N.K. et al. (2012) Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. *BioScience*, 62, 1056–1066.

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C. et al. (2021) Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. *Landscape Ecology*, 36, 89–104.

Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H. et al. (2019) Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *Journal of Biogeography*, 46, 1054–1065.

Hagge, J., Leibl, F., Müller, J., Plechinger, M., Soutinho, J.G. & Thorn, S. (2019) Reconciling pest control, nature conservation, and recreation in coniferous forests. *Conservation Letters*, 12, e12615.

Halme, P., Vartija, N., Salmela, J., Penttinen, J. & Norros, V. (2013) High within- and between-trunk variation in the nematoceran (Diptera) community and its physical environment in decaying aspen trunks. *Insect Conserv. Divers.*, 6, 502–512.

Hammond, H.E.J., Langor, D.W. & Spence, J.R. (2004) Saproxylic beetles (Coleoptera) using Populus in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Canadian Journal of Forest Research*, 34, 1–19.

Hardersen, S., Macagno, A.L.M., Chiari, S., Audisio, P., Gasparini, P., Lo Giudice, G. et al. (2020) Forest management, canopy cover and geographical distance affect saproxylic beetle communities of small-diameter beech deadwood. *Forest Ecology and Management*, 467, 118152.

Harris, J.E., Rodenhouse, N.L. & Holmes, R.T. (2019) Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biological Conservation*, 240, 108219.

Hättenschwiler, S. & Jørgensen, H.B. (2010) Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology*, 98, 754–763.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M. et al. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.

Hedin, J., Isacsson, G., Jonsell, M. & Komonen, A. (2008) Forest fuel piles as ecological traps for saproxylic beetles in oak. *Scandinavian Journal of Forest Research*, 23, 348–357.

Hijmans, R.J., van Etten, J., Sumner, M., Cheng, J., Baston, D., Bevan, A. et al. (2022) *raster: geographic data analysis and modeling*. R package version 3.5-15. *R Packag.* version 3.5-15, 1–249.

Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K. et al. (2012) Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. *PLoS ONE*, 7, e41100.

Hollister, J., Shah, T., Robitaille, A., Beck, M. & Johnson, M. (2021) *Elevatr: access elevation data from various APIs*. R package version 0.4.2.

Hsieh, T.C., Ma, K.H. & Chao, A. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.

Hulme, M.A. & Shields, J.K. (1970) Biological control of decay fungi in wood by competition for non-structural carbohydrates. *Nature*, 227, 300–301.

Hunt, J.H. & Amdam, G.V. (2005) Bivoltinism as an antecedent to Eusociality in the paper wasp genus *Polistes*. *Science*, 308, 264–267.

Hyvönen, R., Olsson, B.A., Lundkvist, H. & Staaf, H. (2000) Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvestris* L. logging residues. *Forest Ecology and Management*, 126, 97–112.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood—lessons for dead wood management. *Silva Fennica*, 39, 289–309.

Klopfer, P.H. & MacArthur, R.H. (1960) Niche size and faunal diversity. *The American Naturalist*, XCIV, 293–300.

Komonen, A. & Müller, J. (2018) Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, 32, 535–545.

Kotowska, M.M., Wright, I.J. & Westoby, M. (2020) Parenchyma abundance in wood of Evergreen trees varies independently of nutrients. *Frontiers in Plant Science*, 11, 1–15.

Lassauce, A., Lieutier, F. & Bouget, C. (2012) Woodfuel harvesting and biodiversity conservation in temperate forests: effects of logging residue characteristics on saproxylic beetle assemblages. *Biological Conservation*, 147, 204–212.

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J. et al. (2022) Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, 198, 825–834.

Linacre, E.T. (1969) Empirical relationships involving the global radiation intensity and ambient temperature at various latitudes and altitudes. *Archiv Für Meteorologie, Geophysik und Bioklimatologie: Series B*, 17, 1–20.

Lindman, L., Öckinger, E. & Ranius, T. (2022) Microclimatic conditions mediate the effect of deadwood and forest characteristics on a threatened beetle species, Tragosoma depsarium. *Oecologia*, 199, 737–752.

Lobo, J.M., Hortal, J. & Cabrero-Sañudo, F.J. (2006) Regional and local influence of grazing activity on the diversity of a semiarid dung beetle community. *Diversity and Distributions*, 12, 111–123.

Lynch, M. (1991) Methods for the analysis of comparative data in evolutionary biology. *Evolution (N. Y).*, 45, 1065–1080.

Macagno, A.L.M., Hardersen, S., Nardi, G., Lo Giudice, G. & Mason, F. (2015) Measuring saproxylic beetle diversity in small and medium diameter dead wood: the "grab-and-go" method. *European Journal of Entomology*, 112, 510–519.

MacArthur, R.H. (1984) *Geographical ecology: patterns in the distribution of species*. Princeton: Princeton University Press.

Meerts, P. (2002) Mineral nutrient concentrations in sapwood and heartwood: a literature review. *Annals of Forest Science*, 59, 713–722.

Moll, J., Kellner, H., Leonhardt, S., Stengel, E., Dahl, A., Bässler, C. et al. (2018) Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. *Environmental Microbiology*, 20, 3744–3756.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E. et al. (2015) Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography (Cop.).*, 38, 499–509.

Müller, J., Bußler, H. & Kneib, T. (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in southern Germany. *Journal of Insect Conservation*, 12, 107–124.

Muller-Landau, H.C. (2004) Interspecific and inter-site variation in Wood specific gravity of tropical trees. *Biotropica*, 36, 20–32.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography (Cop.).*, 37, 191–203.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M.E. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141, 1461–1474.

Nieto, A. & Alexander, K.N.A. (2010) *European red list of Saproxylic beetles*. Luxembourg: Publications Office of the European Union.

Norris, A.L. & Kunz, T.H. (2012) *Effects of solar radiation on animal thermoregulation*. In: Babatunde, E.B. (Ed.) *Solar radiation*. Rijeka: InTech, pp. 195–220,

Parisi, F., Frate, L., Lombardi, F., Tognetti, R., Campanaro, A., Biscaccianti, A.B. et al. (2020) Diversity patterns of Coleoptera and saproxylic communities in unmanaged forests of Mediterranean mountains. *Ecological Indicators*, 110, 105873.

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M. & Tomberlin, J.K. (2014) Delayed insect access alters carrion decomposition and necrophagous insect community assembly. *Ecosphere*, 5, 1–21.

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.r-project.org/ [Accessed 16th November 2020].

Rajala, T., Peltoniemi, M., Hantula, J., Mäkipää, R. & Pennanen, T. (2011) RNA reveals a succession of active fungi during the decay of Norway spruce logs. *Fungal Ecology*, 4, 437–448.

Ranius, T. & Fahrig, L. (2006) Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scandinavian Journal of Forest Research*, 21, 201–208.

Ranius, T., Hämäläinen, A., Sjögren, J., Hiron, M., Jonason, D., Kubart, A. et al. (2019) The evolutionary species pool concept does not explain occurrence patterns of dead-wood-dependent organisms: implications for logging residue extraction. *Oecologia*, 191, 241–252.

Riley, R., Salamov, A.A., Brown, D.W., Nagy, L.G., Floudas, D., Held, B.W. et al. (2014) Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 9923–9928.

Saint-Germain, M., Drapeau, P. & Buddle, C.M. (2007) Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography (Cop.)*., 30, 737–748.

Seger, J. (1983) Partial bivoltinism may cause altering sex-ratio biases that favour eusociality. *Nature*, 301, 59–62.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M.D. et al. (2016) Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, 204, 181–188.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S. et al. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53, 934–943.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M. et al. (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology*, 98, 1613–1622.

Seibold, S., Müller, J., Baldrian, P., Cadotte, M.W., Šťursová, M., Biedermann, P.H.W. et al. (2019) Fungi associated with beetles dispersing from dead wood – Let's take the beetle bus! *Fungal Ecology*, 39, 100–108.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J. et al. (2021) The contribution of insects to global forest deadwood decomposition. *Nature*, 597, 77–81.

Seibold, S. & Thorn, S. (2018) The importance of dead-wood amount for Saproxylic insects and how it interacts with dead-wood diversity and other habitat factors. In: Ulyshen, M.D. (Ed.) *Saproxylic insects—diversity, ecology and conservation*. Berlin Heidelberg: Springer, pp. 607–637.

Siitonen, J. (2001) Forest management, coarse Woody debris and Saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.

Singh, T. & Kostecky, M.M. (1986) Calorific value variations in components of 10 Canadian tree species. *Canadian Journal of Forest Research*, 16, 1378–1381.

Six, D.L. & Elser, J.J. (2019) Extreme ecological stoichiometry of a bark beetle–fungus mutualism. *Ecological Entomology*, 44, 543–551.

Storch, D., Bohdalková, E. & Okie, J. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, 21, 920–937.

Sverdrup-Thygeson, A., Bendiksen, E., Birkemoe, T. & Larsson, K.H. (2014) Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. *Forest Ecology and Management*, 330, 8–16.

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014) Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and Conservation*, 23, 513–535.

Thiele, H.-U. (1977) *Carabid beetles in their environments—a study on habitat selection by adaptations in physiology and behaviour*. Berlin Heidelberg: Springer-Verlag.

Thorn, S., Bässler, C., Bußler, H., Lindenmayer, D.B., Schmidt, S., Seibold, S. et al. (2016) Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. *Forest Ecology and Management*, 364, 10–16.

Thorn, S., Bußler, H., Fritze, M.A., Goeder, P., Müller, J., Weiß, I. et al. (2016) Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging. *Forest Ecology and Management*, 381, 188–195.

Turner, J.R.G. (2004) Explaining the global biodiversity gradient: energy, area, history and natural selection. *Basic and Applied Ecology*, 5, 435–448.

Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48, 195–205.

Turner, K.L., Abernethy, E.F., Conner, L.M., Rhodes, O.E. & Beasley, J.C. (2017) Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. *Ecology*, 98, 2413–2424.

Ulyshen, M.D. (2016) Wood decomposition as influenced by invertebrates. *Biological Reviews*, 91, 70–85.

Ulyshen, M.D. (2018) *Saproxylic insects diversity, ecology and conservation*. Zoological monographs. Berlin Heidelberg: Springer.

Van Der Wal, A., Ottosson, E. & De Boer, W. (2015) Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology*, 96, 124–133.

VanLaerhoven, S.L., Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (2015) Modeling species interactions with carrion food webs. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (Eds.) *Carrion ecology, evolution, and their applications*. Boca Raton: CRC, pp. 231–245.

Větrovský, T., Kohout, P., Kopecký, M., Machac, A., Man, M., Bahnmann, B.D. et al. (2019) A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nature Communications*, 10, 5142.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2020) Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. *Insect Conservation and Diversity*, 14, 132–143.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J. & Thorn, S. (2020) Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. *Journal of Applied Ecology*, 57, 2075–2085.

Vogel, S., Prinzing, A., Bußler, H., Müller, J., Schmidt, S. & Thorn, S. (2021) Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood. *Ecology and Evolution*, 11, 6881–6888.

von Hoermann, C., Jauch, D., Kubotsch, C., Reichel-Jung, K., Steiger, S. & Ayasse, M. (2018) Effects of abiotic environmental factors and land use on the diversity of carrion-visiting silphid beetles (Coleoptera: Silphidae): a large scale carrion study. *PLoS ONE*, 13, e0196839.

von Hoermann, C., Lackner, T., Sommer, D., Heurich, M., Benbow, M.E. & Müller, J. (2021) Carcasses at fixed locations host a higher diversity of necrophilous beetles. *Insects*, 12, 1–18.

von Hoermann, C., Weithmann, S., Deißler, M., Ayasse, M. & Steiger, S. (2020) Forest habitat parameters influence abundance and diversity of cadaver-visiting dung beetles in Central Europe. *Royal Society Open Science*, 7, 191722.

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Vos, V.C.A., van Ruijven, J., Berg, M.P., Peeters, E.T.H.M. & Berendse, F. (2013) Leaf litter quality drives litter mixing effects through complementary resource use among detritivores. *Oecologia*, 173, 269–280.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. et al. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, 30, 257–300.

Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C. & Coomes, D.A. (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters*, 12, 45–56.

Whittaker, R.J., Willis, K.J. & Field, F. (2003) Climatic- energetic explanations of diversity: a macroscopic perspective. In: Blackburn, T.M. & Gaston, K.J. (Eds.) *Macroecology: concepts and consequences*. Oxford: Blackwell Science, pp. 107–129.

Wood, S.N., Pya, N. & Säfken, B. (2016) Smoothing parameter and model selection for general smooth models. *Journal of the American Statistical Association*, 111, 1548–1563.

Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, 41, 496–506.

Yamamura, K. & Kiritani, K. (1998) A simple method to estimate the potential increase in the number of generations under global warming in tmeperate zones. *Applied Entomology and Zoology*, 33, 289–298.

Yang, S., Poorter, L., Kuramae, E.E., Sass-Klaassen, U., Leite, M.F.A., Costa, O.Y.A. et al. (2022) Stem traits, compartments and tree species affect fungal communities on decaying wood. *Environmental Microbiology*, 24, 1–15.

Ziemińska, K., Butler, D.W., Gleason, S.M., Wright, I.J. & Westoby, M. (2013) Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB Plants*, 5, 1–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Kriegel, P., Vogel, S., Angeleri, R., Baldrian, P., Borken, W., Bouget, C. et al. (2023) Ambient and substrate energy influence decomposer diversity differentially across trophic levels. *Ecology Letters*, 00, 1–17. Available from: https://doi.org/10.1111/ele.14227

14610248, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14227 by MPI 322 Chemical Ecology, Wiley Online Library on [09/05/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License