

Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests

SIMON THORN ^{1,7} ANNE CHAO ² MARKUS BERNHARDT-RÖMERMANN ³ YAN-HAN CHEN,²
KOSTADIN B. GEORGIEV ^{1,4} CHRISTOPH HEIBL ⁴ JÖRG MÜLLER ^{1,4} HANNO SCHÄFER ⁵ AND
CLAUS BÄSSLER ^{4,6}

¹Field Station Fabriksschleichach, Biocenter, University of Würzburg, Glashüttenstrasse 5, Rauhenebrach 96181 Germany

²Institute of Statistics, National Tsing Hua University Hsin-Chu, Hsin-Chu City 30043 Taiwan

³Institute of Ecology and Evolution, Friedrich Schiller University Jena, Dornburger Strasse 159, Jena 07743 Germany

⁴Bavarian Forest National Park, Freyunger Strasse 2, Grafenau 94481 Germany

⁵Plant Biodiversity, Department of Ecology and Ecosystem Management, Technische Universität München, Emil-Ramann Strasse 2, Freising 85354 Germany

⁶Goethe University Frankfurt, Faculty of Biological Sciences, Institute for Ecology, Evolution and Diversity, Frankfurt am Main D-60438 Germany

Citation: Thorn, S., A. Chao, M. Bernhardt-Römermann, Y.-H. Chen, K. B. Georgiev, C. Heibl, J. Müller, H. Schäfer, and C. Bässler. 2020. Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. *Ecology* 101(3):e02949. 10.1002/ecy.2949

Abstract. Following natural disturbances, additional anthropogenic disturbance may alter community recovery by affecting the occurrences of species, functional groups, and evolutionary lineages. However, our understanding of whether rare, common, or dominant species, functional groups, or evolutionary lineages are most strongly affected by an additional disturbance, particularly across multiple taxa, is limited. Here, we used a generalized diversity concept based on Hill numbers to quantify the community differences of vascular plants, bryophytes, lichens, wood-inhabiting fungi, saproxylic beetles, and birds in a storm-disturbed, experimentally salvage logged forest. Communities of all investigated species groups showed dissimilarities between logged and unlogged plots. Most species groups showed no significant changes in dissimilarities between logged and unlogged plots over the first seven years of succession, indicating a lack of community recovery. In general, the dissimilarities of communities were mainly driven by rare species. Convergence of dissimilarities occurred more often than divergence during the early stages of succession for rare species, indicating a major role in driving decreasing taxonomic dissimilarities between logged and unlogged plots over time. Trends in species dissimilarities only partially match the trends in dissimilarities of functional groups and evolutionary lineages, with little significant changes in successional trajectories. Nevertheless, common and dominant species contributed to a convergence of dissimilarities over time in the case of the functional dissimilarities of wood-inhabiting fungi. Our study shows that salvage logging following disturbances can alter successional trajectories in early stages of forest succession following natural disturbances. However, community changes over time may differ remarkably in different taxonomic groups and are best detected based on taxonomic, rather than functional or phylogenetic dissimilarities.

Key words: birds; bryophytes; climate change; forest succession; Hill numbers; natural disturbances; salvage logging; saproxylic beetles; vascular plants; wood-inhabiting fungi.

INTRODUCTION

Understanding successional trajectories and their underlying ecological mechanisms is a major goal of ecological research (Meiners et al. 2015, Arroyo-Rodríguez et al. 2017). Successional theories, including the gradual recovery of species communities in a disturbed area (Fig. 1a) to their predisturbance state (Holling 1996), were originally developed for vegetation (Clements 1916)

but have since been applied to the communities of a broad range of taxonomic groups, including beetles (Fountain-Jones et al. 2015), bryophytes (Jean et al. 2017), and lichens (Ferrenberg et al. 2015). However, prolonged or additional natural and/or anthropogenic disturbances may impede the successional recovery (Fig. 1b) of communities (Pulsford et al. 2016) and, in extreme cases, result in community divergence (Fig. 1c), in which the original communities are replaced by different ones (Lindenmayer et al. 2016). A well-studied example is the logging-induced transition of mountain ash forest to acacia forest after repeated burnings (Pulsford et al. 2016). Hence, altered successional trajectories of forest

Manuscript received 11 July 2019; revised 9 September 2019; accepted 4 November 2019. Corresponding Editor: Daniel Metcalfe.

⁷ E-mail: simon@thornonline.de

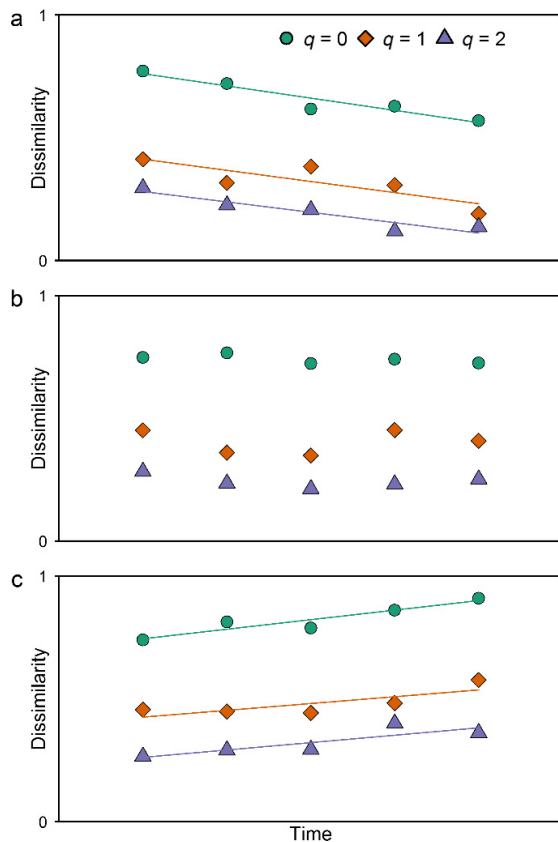


FIG. 1. Hypothetical successional trajectories of artificial biological communities based on incidence data in eight logged and eight unlogged storm-affected forests. (a) Successional trajectories of the communities in the logged plots may gradually follow natural successional trajectories. However, logging may alter communities such that dissimilarities between them (b) persist or (c) increase over time. Different colors illustrate the theoretical importance of rare species ($q = 0$), common species ($q = 1$), and dominant species ($q = 2$) in successional trajectories, based on a framework of Hill numbers (Chao et al. 2014a). If rare species contribute most to the divergence or congruence between successional trajectories over time, then the mean dissimilarity (δ_q) of the diversity order q between unlogged and logged areas should be $\delta_{q=0} > \delta_{q=1} > \delta_{q=2}$ (see *Quantifying dissimilarity* for a description of the two types of dissimilarity indices).

communities exposed to an additional disturbance may indicate the replacement of original communities by different ones (Johnstone et al. 2016).

Although successional changes, including community divergence and convergence, are influenced by many different factors (reviewed in Meiners et al. 2015; and Pulsford et al. 2016), the relative contribution of rare (i.e., infrequently detected species for incidence data), common (i.e., frequently detected species for incidence data), and dominant (i.e., very frequently detected species for incidence data) is thought to be particularly important in determining the changes in communities over time (Halpern 1989, Norden et al. 2009, Dent et al. 2013). While the presence of dominant species may gradually stabilize, rare species are frequently subject to extinction and

immigration (Li et al. 2016). In addition to the response of species communities, other factors that influence community changes over the course of succession include the presence, frequency, and distribution of species' life-history traits within a local community (Halpern 1988, Liebisch et al. 2008, Langlands et al. 2011, Li et al. 2016). Despite evidence that anthropogenic disturbance following natural disturbance leads to higher stochasticity in a functional-phylogenetic space (Thorn et al. 2016a), empirical tests of whether rare, common, or dominant species, functional groups, or evolutionary lineages contribute most to community changes over time are lacking.

Natural forest disturbances, such as windstorms and bark beetle outbreaks, result in species-rich habitats that undergo significant successional changes (Swanson et al. 2011). Forest disturbances typically produce large amounts of dead wood and increase stand insolation, two major factors that drive community change over time (Thorn et al. 2017). In the present study, we extended incidence-based dissimilarity metrics based on Hill numbers to include dissimilarities in species life-history traits and evolutionary ancestries (Chao et al. 2015, 2019). Our study is based on an extensive data set of eight taxonomic groups, including vascular plants, bryophytes, beetles, and birds, sampled during the early successional stages of a forest affected by windstorm and experimental salvage logging (i.e., the removal of disturbance affected trees; see Thorn et al. 2016a for details). Specifically, we asked whether dissimilarities in successional trajectories of logged and unlogged areas vary with respect to the presence of rare, common, or dominant species. For the analyses, we extended a framework based on Hill numbers to incorporate functional and phylogenetic community dissimilarities.

MATERIAL AND METHODS

Study area and experimental design

The field data were collected in a large experiment on the effects of salvage logging on biodiversity, conducted in the Bavarian Forest National Park in southeastern Germany (49°07' N, 13°31' E). This mountain forest ecosystem has been repeatedly affected by natural disturbances, including windstorms and bark beetles (Thorn et al. 2017). On 16 January 2007, an area of ~1,000 ha of mature Norway spruce forests was felled by the windstorm Kyrill. For our study, from those ~1,000 ha, we selected four larger patches, totaling ~200 ha, to remain unlogged whereas storm-felled trees across the remaining 800 ha were removed by experimental salvage logging until August 2007. Afterward, we established 44 permanent plots, 22 in logged and 22 in unlogged areas. During the experimental salvage logging operations, branches were sawed off the trunks and left on the ground, but the main trunk was removed. This resulted in a reduction of dead-wood resources from ~300 m³/ha to ~50 m³/ha in all 22 logged areas (details in Thorn et al. 2014,

2016b). Beside the removal of dead-wood resources, salvage logging resulted in additional disturbances such as logging trails and soil compaction.

Species surveys

Using a multi-taxon approach, we conducted standardized species surveys on all plots from 2007 to 2014; however, not all taxonomic groups were annually assessed, due to personnel and financial constraints. During the first 6 yr of the study period, we mapped vascular plants on circular plots of 200 m² around the plot center (Thorn et al. 2016a). We mapped bryophytes and lichens on dead-wood objects (i.e., epixylic) and on the ground (i.e., epigeal) separately. Wood-inhabiting fungi, epixylic bryophytes, and epixylic lichens were assessed on the same five randomly selected dead-wood objects around each plot centroid for the first 5 yr (Thorn et al. 2016a). The epigeal bryophytes and epigeal lichens were assessed during the first 5 yr on the same 200-m² plots as the vascular plants. Saproxylous beetles (i.e., beetles involved in or dependent on the fungal decay of wood, or on the products of that decay, and associated with living as well as dead trees; Alexander 2008) were trapped using 44 flight-interception traps placed at the plot centroid from the second to the fifth year of the study period (Thorn et al. 2014). Birds were counted using a fixed-radius point-stop-count method (50 m radius, 5-minute intervals, five visits per year) during years 3, 5, and 7 of the study (Thorn et al. 2016b). Bird surveys were conducted during morning hours in good weather conditions.

Trait characterization and phylogenetic trees

Species ecological trait data were compiled for each taxonomic group. The weak colinearity of the selected traits was ensured by applying a stepwise trait selection based on variance inflation factors, using the function `vifstep` in the R package `usdm` (Dormann et al. 2013; see Appendix S1: Table S1 for the traits finally selected according to the `vifstep` output). Phylogenetic trees for each species group were compiled from the literature (see Appendix S1: Table S1 for literature references of phylogenetic trees). If phylogenetic trees did not include all studied species, we used `addTips` in the R package `megaptera` to add the missing species based upon their current taxonomic affiliation (details in Thorn et al. 2016a; R package *available online*).⁸

Quantifying dissimilarity

Dissimilarities between communities of logged and unlogged plots were quantified by treating each plot within each year as a sampling unit and then extracting the species incidence (presence/absence) to obtain an occurrence count (incidence-based frequency) for each

species. This procedure yielded a species-incidence-based frequency vector for each taxonomic group in grouped logged and unlogged plots during each sampling year. Analyses based on multiple incidence data are less sensitive than abundance data to possible clustering or aggregation of individuals. For example, because epixylic bryophytes typically cluster together on dead-wood objects, they do not represent statistically independent individuals, violating the basic sampling assumption for the model based on abundance data (Colwell et al. 2012). Yet, in estimations of diversity, incidence-based approaches are as powerful as the corresponding abundance-based approaches (Chao and Colwell 2017).

Based on a multi-author *Ecology* forum (Ellison 2010), a consensus has emerged regarding the use of Hill numbers (i.e., the effective number of species) to quantify and decompose taxonomic diversity measures (Hill 1973). Chao et al. (2014b) formulated the corresponding incidence data version of Hill numbers based on species' relative incidence/occurrence probabilities. Similar as abundance-based Hill numbers, incidence-based Hill numbers differ among themselves by a parameter q that reflects their respective sensitivity to species relative occurrence probabilities. A major advantage of using Hill numbers (abundance or incidence) is that they obey the replication principle (Chao et al. 2014b) and can thus be decomposed into independent components of alpha and beta diversity.

In general, the multiplicative beta (ratio of gamma and alpha) diversity measure quantifies the effective number of study plots; it has a minimum value of one (when all plots are identical in species occurrence probability) and a maximum value of the number of plots (when there are no shared species among plots). Thus, the range of beta diversity depends on the number of plots. The resulting beta diversity can then be monotonically transformed to obtain two general classes of the Jaccard- and Sørensen-type dissimilarity measures in the range of [0, 1] (Chao et al. 2014a).

These two classes of taxonomic measures include most of the commonly used dissimilarity indices. For example, setting $q = 0$ in the class of Sørensen-type measures yields the classic richness-based Sørensen index, which weighs all species equally, while $q = 1$ yields the Shannon-entropy-based Horn index, which weights all occurrences equally, i.e., each species is weighted according to its incidence-based frequency. Setting $q = 2$ yields the frequency-based Morisita-Horn index, which is very sensitive to dominant species but assigns little weight to rare species. The Jaccard-type dissimilarity measures include the classic richness-based Jaccard index ($q = 0$), Horn index ($q = 1$), and regional non-overlap measure as special cases; see Chao et al. (2014a). Another major advantage of using Hill numbers is that the framework provides a unified approach to include species differences with respect to species' evolutionary ancestries (i.e., phylogenetic trees; Chao et al. 2014a) or species traits (Chao et al. 2019). This unified framework led to

⁸ <https://github.com/heibl/megaptera>

Jaccard- and Sørensen-type phylogenetic and functional dissimilarity indices.

We applied a tree-based approach to quantify the phylogenetic dissimilarity between logged and unlogged plots (Chiu et al. 2014). Within each taxonomic group, the time reference point was selected as the age of the root of the phylogenetic tree spanned by all observed species of that group. This approach uses all species inter-relations; that is, it incorporates species relations not only for species pairs, but also for every possible combination of three species, four species, or any subset of a species. For functional dissimilarity, we followed a recent approach, based on species pairwise-distances computed from species traits (Chao et al. 2019); we simultaneously considered all plausible threshold levels of functional distinctiveness between any two species.

Annual species-incidence frequencies on the logged and unlogged plots were compared using dissimilarity measures based on the unified Sørensen- and Jaccard-type taxonomic, phylogenetic, and functional dissimilarity indices for three orders $q = 0, 1, \text{ and } 2$. The Sørensen-type dissimilarity measures quantify the effective average proportion of non-shared species (taxonomic dissimilarity), non-shared lineages (phylogenetic dissimilarity), and non-shared functional groups (functional dissimilarity) in the logged and unlogged plots (Fig. 2). The Jaccard-type dissimilarity was used to quantify the corresponding non-shared proportions in the pooled logged and unlogged plots (Appendix S1: Fig. S1). A linear model was then fitted on the mean dissimilarities during each year using R version 3.4.4 (R Development Core Team 2008), to test whether the dissimilarity between logged and unlogged plots changed over the course of the succession. Additionally, we used rank frequency curves and scatter plots to visualize differences in the frequency of species occurrence (Appendix S1: Figs. S2 and S3) and two measures (species-based coverage and incidence-based coverage) to inspect sample completeness (Appendix S1: Table S2).

RESULTS

Our final data set consisted of 501 species, with saproxylic beetles as the most species-rich group (179), followed by wood-inhabiting fungi (110), vascular plants and birds (52 each), epigeal bryophytes (41), epixylic bryophytes (34), epixylic lichens (26), and epigeal lichens (7). In general, the dissimilarities (δ) of communities were mainly driven by rare species, with $\delta_{q=0} > \delta_{q=1} > \delta_{q=2}$ (Fig. 2).

All investigated species groups showed initial dissimilarities between logged and unlogged plots ranging from 0.2 in the case of epixylic lichens and saproxylic beetles up to 0.6 in the case of wood-inhabiting fungi (Fig. 2). Initial dissimilarities for functional groups were in mean lower than those found for taxonomic diversity but could also reach 0.15 as in the case of wood-inhabiting fungi. Dissimilarities in evolutionary lineages had large

confidence intervals for different levels of q and ranged in mean between 0.1 and 0.4 (Fig. 2).

Dissimilarities between salvage logged and unlogged plots showed that, for rare species ($q = 0$) of all species groups, convergence occurred more often than divergence during the early stages of succession. Here, vascular plants, epixylic bryophytes, and epixylic lichens showed significant convergence (Fig. 2 a, c,e). Thus, rare species played a major role in driving decreasing taxonomic dissimilarities between logged and unlogged plots. However, most groups showed neither community convergence nor divergence. Trends in taxonomic dissimilarity were generally higher and only partially matched the trends in functional and/or phylogenetic dissimilarities, with little significant changes in successional trajectories. For instance, there was no convergence or divergence in taxonomic dissimilarities of wood-inhabiting fungi, whereas a significant convergence was found for rare functional groups and evolutionary lineages (Fig. 2f).

Common ($q = 1$) species contributed to a convergence over time only in the case of the functional dissimilarities of wood-inhabiting fungi. In addition, as shown in Fig. 2, the confidence intervals of the different q parameters largely overlapped.

DISCUSSION

Our study showed that all investigated species groups showed initial dissimilarities between logged and unlogged plots. Furthermore, community convergence or divergence caused by experimental salvage logging is most visible when measured based on taxonomic diversity. Significant convergences in the studied forest plots were predominantly driven by the dissimilarities of rare species ($q = 0$). However, in some cases, such as the phylogenetic diversity of wood-inhabiting fungi, the dissimilarity measures revealed the equal contributions of rare and dominant species (Fig. 2f). The dissimilarities of common ($q = 1$) and dominant ($q = 2$) species were less pronounced but, in general, they showed little variation over time (i.e., few successional trends). Accordingly, the logging-induced dissimilarities of common and dominant species persist over succession. However, remarkable differences in the responses of the different taxonomic groups and in taxonomic, functional and phylogenetic diversity were also revealed (Fig. 2).

Dissimilarities between logged and unlogged plots differed less among the different q parameters (evidenced by the overlapping confidence bands) for both functional and phylogenetic dissimilarities (Fig. 2). Earlier studies found little variation in species traits despite increasing disturbance. For example, Gerisch et al. (2012) demonstrated that a higher flooding frequency in floodplains resulted in an increasing functional redundancy among carabid beetle assemblages, probably because these species adapted such that they were able to handle flooding-induced disturbances. The functional

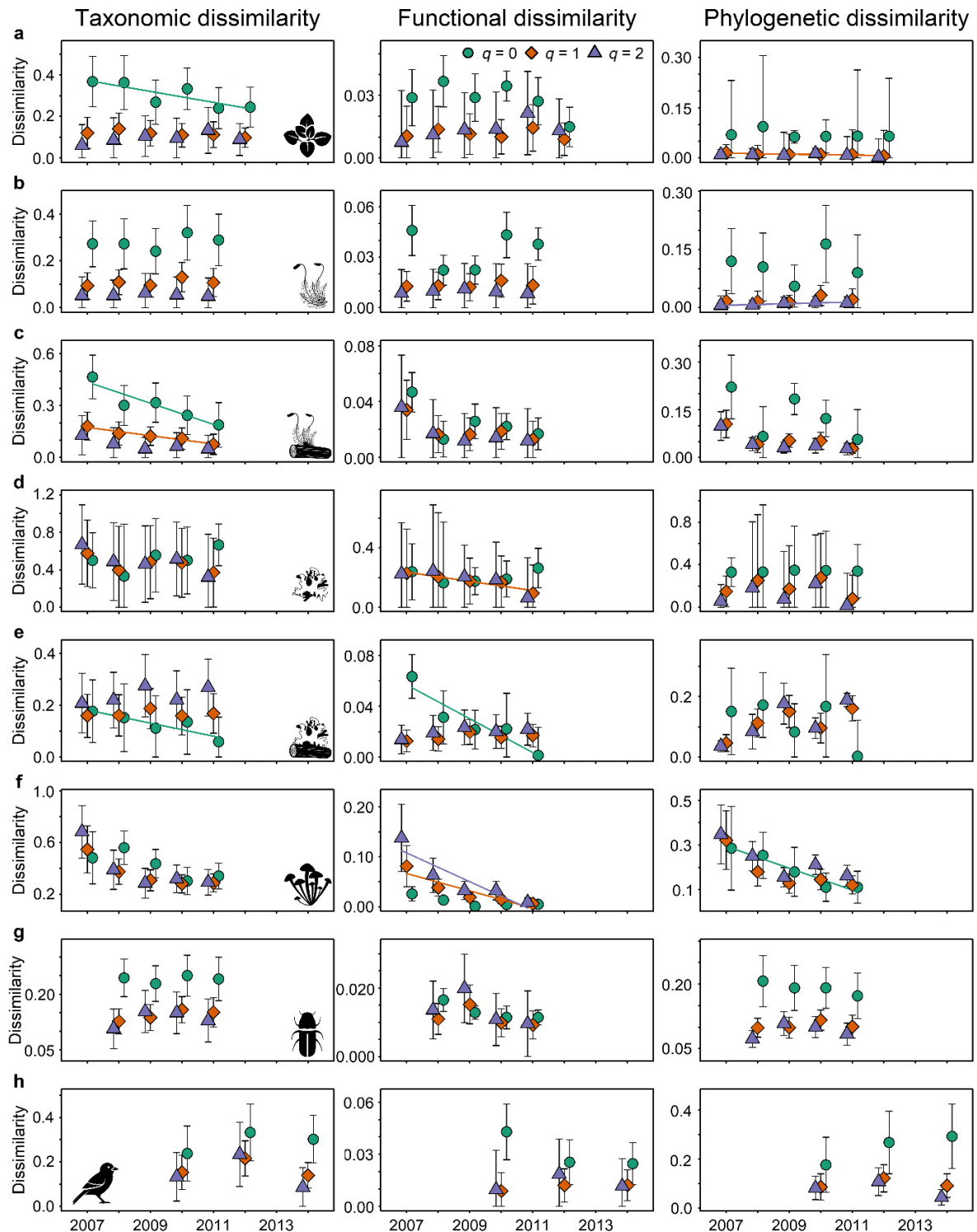


Fig. 2. Sørensen-type dissimilarity changes in logged vs. unlogged, storm-disturbed forest plots between 2007 and 2014 for (a) vascular plants, (b) epigeal bryophytes, (c) epixylic bryophytes, (d) epigeal lichens, (e) epixylic lichens, (f) wood-inhabiting fungi, (g) saproxylic beetles, and (h) birds. The three columns show taxonomic dissimilarities (based on the effective average proportion of non-shared species), phylogenetic dissimilarity (effective non-shared evolutionary lineages), and functional dissimilarity (effective non-shared virtual functional groups). Different colors indicate different q parameters, in which the weight of rare species decreases with increasing values of q . The colored regression line indicates significant changes. Error bars show 95% confidence intervals based on a bootstrap method. Note the different scales of the y-axis.

redundancy seen in our study might have been caused by the increasing amounts of early-decaying dead wood and/or the increasing insolation resulting from experimental salvage logging (Fontaine et al. 2010, Swanson et al. 2011). The dead-wood resources found in plots of both treatments were relatively uniform such that, for example, early-decay beetle species were able to colonize the recently killed spruce trees during the first years of succession. Roughly two-thirds of the saproxylic beetles on coniferous trees are adapted to early successional stages (Saint-Germain et al. 2007). However, adaptations to early-decaying spruce wood might not have evolved conservatively, which would explain the contrasting convergence of rare evolutionary beetle lineages over time (Fig. 2g). A study from the same area revealed an increasing functional redundancy of saproxylic beetles with increasing amounts of dead wood (Thorn et al. 2018). This finding also suggests that dissimilarities in functional trait composition or phylogenetic clades are less affected by stochastic processes than are dissimilarities based on taxonomic diversity. Nevertheless, low dissimilarities in functional groups could theoretically mean that the analyzed traits are weakly related to the assembly process, which determines species occurrence in our study area. In turn, low dissimilarities in evolutionary lineages could indicate weak phylogenetic conservatism of assembly-relevant traits (reviewed in Cadotte et al. 2013). Mismatches between differences in taxonomic, phylogenetic, and functional dissimilarities differed remarkably between different taxonomic groups. For instance, all measures of dissimilarities were of similar magnitude for wood-inhabiting fungi but differed remarkably among each other in the case of epixylic bryophytes (Fig. 2). Hence, this finding may indicate that the assembly relevance of our selected traits differs among different taxonomic groups.

The relative impact of stochastic vs. niche-based processes is commonly cited to explain the responses of rare and dominant species (Norden et al. 2017). Dominant species occupy key niche positions across communities and are therefore thought to be predominantly affected by deterministic mechanisms, such as environmental filtering (Umaña et al. 2015). By contrast, because of their smaller population sizes, rare species are more likely to be affected by stochastic processes, such as drift (Orrock and Watling 2010). In our study, rare species of vascular plants, epigeal bryophytes, epixylic bryophytes, and saproxylic beetles had significantly higher dissimilarities than did common species and thus may have been more affected by stochasticity. The common and dominant species, i.e., those found with a high frequency in both the experimentally logged and unlogged plots, were presumably able to survive experimental salvage logging. Indeed, the abundance and spatial arrangement of survivors as well as the arrival patterns of colonizers are thought to be major determinants of successional trajectories in areas with varying disturbance intensities (Turner et al. 1998). Our results demonstrate that the

abundance and incidence of species able to survive a natural disturbance and subsequent salvage logging are of major importance for successional trajectories (Johnstone et al. 2016). In our study, several plant species, including Norway spruce (*Picea abies* (L.) H. Karst.) and blueberry (*Vaccinium myrtillus* L.), were frequently found in both the unlogged and experimentally logged plots. Hence, these common and dominant species contributed little to the dissimilarities between plots. However, the large number of colonizing species that differed between the logged and unlogged plots likely contributed to stochasticity-driven dissimilarities. This contribution of rare species, such as vascular plants and epixylic bryophytes, decreased over time (Fig. 2a, b), which suggests that the role of stochasticity, and thus the contribution of rare species to dissimilarities, became progressively smaller. The temporal decline in the dissimilarities between logged and unlogged plots indicates that the early stages of succession were predominantly driven by the initial abiotic conditions whereas the development of more predictable community structures was guided by subsequent deterministic processes, similar to results from a study of abandoned fields (Li et al. 2016).

As in the case of functional traits, dissimilarities based on phylogenetic distances were generally less pronounced than those based on taxonomic diversity (Fig. 2). This finding indicates that the dissimilarities caused by salvage logging were determined not only by species with the same life-history traits, but also by species recruited from the same evolutionary clades. Evidence for this conclusion comes from the similar responses of the functional and phylogenetic dissimilarities of wood-inhabiting fungi, suggesting a highly conserved trait evolution. By contrast, the differences in the responses of the functional and phylogenetic dissimilarities of epigeal bryophytes or saproxylic beetles, particularly for $q = 0$, suggested little conservatism in the trait evolution of species with the largest contributions to the differences (i.e., rare species, since $q = 0$). In the case of epigeal bryophytes, the phylogenetic diversity of dominant species converged over time (Fig. 2b). This implied that the additional disturbance of salvage logging led to the establishment of assemblages in which the dominant species were recruited from distantly related evolutionary clades. A possible explanation is that specific clades of bryophytes are more adapted to persist in habitats with a high level of disturbance, indicative of trait conservatism within a specific lineage. In our study area, this might have reflected the ability of particular species to overcome the increased insolation caused by the experimental salvage logging (Raabe et al. 2010).

Post-disturbance succession can last more than a century in forest ecosystems (Donato et al. 2012), but we investigated only the early stages. Nonetheless, our results revealed a significant convergence, exemplified by the successional trajectories of taxonomic diversity of rare vascular plants and epixylic bryophytes, and divergence, evidenced by the phylogenetic diversity of

dominant epigeal bryophytes. Both findings are in line with earlier investigations of post-disturbance forests, which showed the establishment of colonizing vascular plant species two years after a wildfire (Halpern 1989) as well as the rapid colonization of dead wood by saproxylic beetles (Saint-Germain et al. 2004) and wood-inhabiting fungi (Vogel et al. 2017). However, natural succession, and specifically the transition away from a post-disturbance community, may be determined by different mechanisms acting on different time scales (reviewed in Pulsford et al. 2016).

CONCLUSIONS

Our results depict that experimental logging separates species communities of logged and unlogged plots with most pronounced dissimilarities for rare species, functional groups, and evolutionary lineages. Community convergence occurred more often than divergence during the early stages of succession and was again most prevalent for rare species, while most dissimilarities remain unchanged over the course of early succession. Salvage logging is a common and widespread management strategy in forests affected by a natural disturbance, as it is often thought to foster forest recovery from disturbance (Lindenmayer et al. 2017). However, our findings indicate that salvage logging alters successional pathways underlying altered community composition of multiple taxonomic groups found in storm-disturbed forests, at least in our study system. It seems plausible that these early altered successional trajectories created by salvage logging will finally result in altered forests, but long-term studies are needed to test this hypothesis.

ACKNOWLEDGMENTS

The authors thank the Subject Matter Editor (Daniel Metcalfe) and two anonymous reviewers for providing helpful comments on an earlier manuscript version. S. Thorn was supported by a MOST (Ministry of Science and Technology) Taiwan Research Fellowship and received funds from the Gregor Louisoder Environmental Foundation. We thank numerous helpers in the field, particularly Christoph Hahn, Heinrich Holzer, Oliver Dürhammer, Julia Laube, and Ulrich Bense for the species identifications.

LITERATURE CITED

- Alexander, K. N. A. 2008. Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue D Ecologie-La Terre Et La Vie* 63:9–13.
- Arroyo-Rodríguez, V., F. P. L. Melo, M. Martínez-Ramos, F. Bongers, R. L. Chazdon, J. A. Meave, N. Norden, B. A. Santos, I. R. Leal, and M. Tabarelli. 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews* 92:326–340.
- Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16:1234–1244.
- Chao, A., and R. K. Colwell. 2017. Thirty years of progeny from Chao's inequality: Estimating and comparing richness with incidence data and incomplete sampling. *Sort* 41:3–54.
- Chao, A., C.-H. Chiu, and L. Jost. 2014a. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics* 45:297–324.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014b. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Chao, A., C.-H. Chiu, T. C. Hsieh, T. Davis, and D. A. Nipperess, and D. P. Faith. 2015. Rarefaction and extrapolation of phylogenetic diversity. *Methods in Ecology and Evolution* 6:380–388.
- Chao, A., C.-H. Chiu, S. Villéger, I. F. Sun, S. Thorn, Y. Lin, J. M. Chiang, and W. B. Sherwin. 2019. An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. *Ecological Monographs* 89:e01343.
- Chiu, C.-H., L. Jost, and A. Chao. 2014. Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. *Ecological Monographs* 84:21–44.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington, Washington, D.C., USA.
- Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3–21.
- Dent, D. H., S. J. DeWalt, and J. S. Denslow. 2013. Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *Journal of Vegetation Science* 24:530–542.
- Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science* 23:576–584.
- Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Ellison, A. M. 2010. Partitioning diversity. *Ecology* 91:1962–1963.
- Ferrenberg, S., S. C. Reed, and J. Belnap. 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proceedings of the National Academy of Sciences USA* 112:12116–12121.
- Fontaine, J. B., D. C. Donato, J. L. Campbell, J. G. Martin, and B. E. Law. 2010. Effects of post-fire logging on forest surface air temperatures in the Siskiyou Mountains, Oregon, USA. *Forestry* 83:477–482.
- Fountain-Jones, N. M., G. J. Jordan, T. P. Baker, J. M. Balmer, T. Wardlaw, and S. C. Baker. 2015. Living near the edge: Being close to mature forest increases the rate of succession in beetle communities. *Ecological Applications* 25:800–811.
- Gerisch, M., V. Agostinelli, K. Henle, and F. Dziock. 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121:508–515.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69:1703–1715.

- Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70:704–720.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.
- Holling, C. S. 1996. Engineering resilience versus ecological resilience. Pages 31–44 in P. C. Schulze, editor. *Engineering within ecological constraints*. National Academy Press, Washington, D.C., USA.
- Jean, M., H. D. Alexander, M. C. Mack, and J. F. Johnstone. 2017. Patterns of bryophyte succession in a 160-year chronosequence in deciduous and coniferous forests of boreal Alaska. *Canadian Journal of Forest Research* 47:1021–1032.
- Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369–378.
- Langlands, P. R., K. E. C. Brennan, V. W. Framenau, and B. Y. Main. 2011. Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80:558–568.
- Li, S., M. W. Cadotte, S. J. Meiners, Z. Pu, T. Fukami, and L. Jiang. 2016. Convergence and divergence in a long-term old-field succession: the importance of spatial scale and species abundance. *Ecology Letters* 19:1101–1109.
- Liebsch, D., M. C. M. Marques, and R. Goldenberg. 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biological Conservation* 141:1717–1725.
- Lindenmayer, D.B., C. Messier, and C. Sato. 2016. Avoiding ecosystem collapse in managed forest ecosystems. *Frontiers in Ecology and the Environment* 14:561–568.
- Lindenmayer, D.B., S. Thorn, and S. Banks. 2017. Please do not disturb ecosystems further. *Nature Ecology & Evolution* 1:0031.
- Meiners, S. J., M. W. Cadotte, J. D. Fridley, S. T. A. Pickett, and L. R. Walker. 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. *Functional Ecology* 29:154–164.
- Norden, N., R. L. Chazdon, A. Chao, Y.-H. Jiang, and B. Vilchez-Alvarado. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters* 12:385–394.
- Norden, N., V. Boukili, A. Chao, K. H. Ma, S. G. Letcher, and R. L. Chazdon. 2017. Opposing mechanisms affect taxonomic convergence between tree assemblages during tropical forest succession. *Ecology Letters* 20:1448–1458.
- Orrock, J. L., and J. I. Watling. 2010. Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society B* 277:2185–2191.
- Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2016. A succession of theories: purging redundancy from disturbance theory. *Biological Reviews* 91:148–167.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. ISBN 3-900051-07-0.
- Raabe, S., J. Müller, M. Manthey, O. Dürhammer, U. Teuber, A. Göttlein, B. Förster, R. Brandl, and C. Bässler. 2010. Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. *Forest Ecology and Management* 260:1956–1964.
- Saint-Germain, M., P. Drapeau, and C. Hébert. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. *Canadian Journal of Forest Research* 34:677–685.
- Saint-Germain, M., P. Drapeau, and C. M. Buddle. 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* 30:737–748.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9:117–125.
- Thorn, S., C. Bässler, T. Gottschalk, T. Hothorn, H. Bussler, K. Raffa, and J. Müller. 2014. New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. *PLoS ONE* 9:e101757.
- Thorn, S., C. Bässler, M. Bernhardt-Römermann, M. Cadotte, C. Heibl, H. Schäfer, S. Seibold, and J. Müller. 2016a. Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecology Letters* 19:163–170.
- Thorn, S., S. A. B. Werner, J. Wohlfahrt, C. Bässler, S. Seibold, P. Quillfeldt, and J. Müller. 2016b. Response of bird assemblages to windstorm and salvage logging—insights from analyses of functional guild and indicator species. *Ecological Indicators* 65:142–148.
- Thorn, S., C. Bässler, M. Svoboda, and J. Müller. 2017. Effects of natural disturbances and salvage logging on biodiversity—lessons from the Bohemian Forest. *Forest Ecology and Management* 388:113–119.
- Thorn, S., B. Förster, C. Heibl, J. Müller, and C. Bässler. 2018. Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodiversity and Conservation* 27:3119–3135.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523.
- Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology Letters* 18:1329–1337.
- Vogel, S., B. Alvarez, C. Bässler, J. Müller, and S. Thorn. 2017. The Red-belted Bracket (*Fomitopsis pinicola*) colonizes spruce trees early after bark beetle attack and persists. *Fungal Ecology* 27:182–188.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2949/supinfo>