Received: 13 October 2019 | Accepted: 23 January 2020

DOI: 10.1111/1365-2664.13599

FORESTS UNDERGOING NOVEL DISTURBANCES

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities

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Funding information
Ministry of Science and Technology; Gregor Louisoder Environmental Foundation

Handling Editor: Jos Barlow

Abstract

1. Salvage logging following natural disturbances may alter the natural successional trajectories of biological communities by affecting the occurrences of species, functional groups and evolutionary lineages. However, few studies have examined whether dissimilarities between bird communities of salvaged and unsalvaged forests are more pronounced for rare species, functional groups and evolutionary lineages than for their more common counterparts.
2. We compiled data on breeding bird assemblages from nine study areas in North America, Europe and Asia, covering a 17-year period following wildfire or windstorm disturbances and subsequent salvage logging. We tested whether dissimilarities based on non-shared species, functional groups and evolutionary lineages (a) decreased or increased over time and (b) the responses of rare, common and dominant species varied, by using a unified statistical framework based on Hill numbers and null models.
3. We found that dissimilarities between bird communities caused by salvage logging persisted over time for rare, common and dominant species, evolutionary lineages and for rare functional groups. Dissimilarities of common and dominant functional groups increased 14 years post disturbance.
4. Salvage logging led to significantly larger dissimilarities than expected by chance. Functional dissimilarities between salvaged and unsalvaged sites were lower compared to taxonomic and phylogenetic dissimilarities. In general, dissimilarities were highest for rare, followed by common and dominant species.
5. *Synthesis and applications*. Our research demonstrates that salvage logging did not decrease dissimilarities of bird communities over time and taxonomic, functional and phylogenetic dissimilarities persisted for over a decade. We recommend

resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

KEYWORDS
biodiversity, breeding season, forest management, harvesting, Hill numbers, natural disturbance, successional trajectory

1 | INTRODUCTION

Naturally occurring disturbances (i.e. wildfires, windthrows and insect outbreaks) are an integral part of natural forest dynamics (Pickett & White, 1985). Disturbances can cause abrupt but long-lasting changes in forests by altering biophysical and environmental features, resource availability and ecosystem processes (Turner, 2010). Generally, forests are resilient to historic disturbance regimes and, given sufficient time, typically recover their pre-disturbance state (Gunderson, 2000). Within disturbance-affected communities, taxonomic diversity, that is, the identity and richness of species, can gradually recover to a pre-disturbance state (Purvis & Hector, 2000). However, the extent, frequency and intensity of natural disturbances have increased globally and are expected to continue to increase in the near future (Seidl et al., 2017), with possible effects on community recovery. Functionally and phylogenetically diverse species communities may hence be necessary for the provision of ecosystem services and for maintaining ecosystem stability (Cadotte, Dinnage, & Tilman, 2012; Loreau & de Mazancourt, 2013). Also, evolutionarily distinct avian species are more likely to become extinct in anthropogenically disturbed forests (Frishkoff et al., 2014). While the loss of a single species could lead to a negligible reduction of taxonomic diversity, it might represent the loss of an entire evolutionary lineage or distinct functional group (Cadotte et al., 2010; Faith, 2015). The increasing amount of natural disturbances has also led to an increase of salvage logging, that is, the removal of trees affected by disturbances, conducted in managed and protected forests worldwide (Leverkus, Lindenmayer, Thorn, & Gustafsson, 2018). It has hence become increasingly important to understand whether and how the recovery of forest biodiversity is altered by the combined effects of natural and anthropogenic disturbances.

Besides economic reasons, salvage logging is commonly justified on the basis that it contributes to forest structural restoration (reviewed in Müller et al., 2019). For instance, following a major drought and bark beetle outbreak in 2018/19, the Federal Ministry for Food and Agriculture of Germany called for a 'clear-up followed by reforestation strategy' to support the recovery of disturbed forest stands (Thorn, Müller, & Leverkus, 2019). Because salvage logging immediately follows the natural disturbance (i.e. up to 3 years), it acts as an additional disturbance (Lindenmayer, McBurney, Blair, Wood, & Banks, 2018; Morissette, Cobb, Brigham, & James, 2002), with possible negative effects on species richness, community recovery of various species groups (Thorn et al., 2018) and ecosystem services (Leverkus et al., 2020).

Naturally occurring disturbance and salvage logging can have long-lasting effects on forest structures (Donato, Campbell, & Franklin, 2012) and forest bird communities (Thorn et al., 2018). For instance, the species richness and community composition of birds in boreal stands affected by wildfire or green-tree harvesting differed significantly during the first years after these disturbances, and differences may persist for more than 25 years (Hobson & Schieck, 1999), or even 60–70 years (Zhao, Azeria, Le Blanc, Lemaître, & Fortin, 2013). However, in contrast to the many studies investigating community convergence in disturbed versus green-tree-logged stands, there have been very few comparisons of disturbed and salvage-logged stands (reviewed in Thorn et al., 2018).

Anthropogenic disturbances, such as salvage logging, may result in the reduction of specialized species and/or increases of generalist species (Gossner et al., 2016) but also the potential extinction or extirpation of rare species (Leitão et al., 2016). Specialist bird species often respond more negatively to landscape fragmentation and disturbance than generalists (Devictor, Julliard, & Jiguet, 2008). These changes in specialist and generalist species may also apply to rare functional groups or rare evolutionary lineages (Olden, 2006). However, empirical tests of whether the strength of community response to salvage logging varies depending on the relative contribution of dominant versus rare (for abundance data) or common versus rare (for occurrence data) species are lacking (but see Thorn et al., 2020).

We compiled a large dataset of breeding bird assemblages sampled in salvaged and unsalvaged naturally disturbed forests in North America, Europe and Asia. 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) to test: (a) whether compositional differences between communities of salvage-logged and unsalvaged forests decrease or increase over time and (b) whether those trends differ for rare, common and dominant species. We expected that dissimilarities of non-shared species, functional groups and evolutionary lineages would decline with increasing time after the disturbance and that dissimilarities would be more pronounced for rare than for common and dominant species.

2 | MATERIALS AND METHODS

2.1 | Bird data

Data on breeding bird assemblages were compiled from nine study areas in North America (n = 3), Europe (n = 4) and Asia (n = 2; Figure 1; Table 1), by extending the databases compiled by two reviews on the effect of salvage logging on biodiversity and ecosystem services (Leverkus, Rey Benayas, et al., 2018; Thorn et al., 2018). The data compilation followed a systematic review protocol to warrant high standards in data selection (Leverkus, Gustafsson, Benayas, & Castro, 2015). We retained only datasets based on field surveys and excluded modelling studies. Studies provided comparisons between completely salvage-logged plots and completely unsalvaged control plots, that is, more than 75% of the trees were affected by a natural disturbance and then completely salvage logged. Salvage-logged plots were of similar size, surveyed with the same sampling effort as unsalvaged control plots (Thorn et al., 2018). In addition to the use of the raw data from published studies (see Table 1 and *Data sources* section), the time series for the present work was extended by expanding three of the studies (Hutto & Young, 2002; Thorn et al., 2016; Zmihorski, 2010) by additional surveys, adhering in each case to the original sampling design.

The forests in the studied areas were affected first by wildfires or windstorms and then by salvage logging. Bird surveys were standardized to a specific plot area by using standardized fixed-radius point counts or fixed-width transect counts (Bibby, Burgess, Hill, & Mustoe, 2000). Bird surveys were conducted only on days without rain, with low wind speed and with clear or slightly overcast skies (Bibby et al., 2000). Our final dataset consisted of 668 salvage-logged

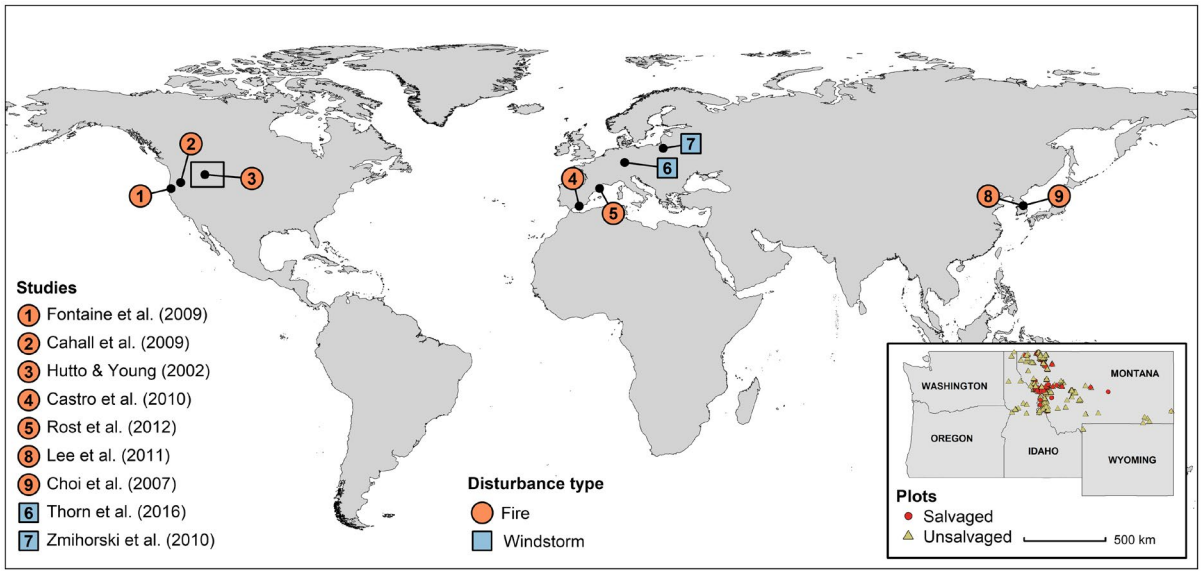

FIGURE 1 General locations of the breeding birds surveyed to investigate the effects of salvage logging on bird communities. The inset map shows the extent of the sampling plots in the study of Hutto and Young (2002)

TABLE 1 Datasets used to investigate the effect of additional disturbance on the successional trajectories of bird communities

No.	Country	Disturbance type	Number of years sampled	Study plots	Recorded species	Recorded individuals	Reference
1	USA	Wildfire	1	122	49	979	Fontaine et al. (2009)
2	USA	Wildfire	2	20	34	363	Cahall and Hayes (2009)
3	USA	Wildfire	17	4,100	145	42,091	Hutto and Young (2002)
4	Spain	Wildfire	2	27	44	724	Castro, Moreno-Rueda, and Hódar (2010)
5	Spain	Wildfire	3	58	55	971	Rost, Clavero, Brotons, and Pons (2012)
6	South Korea	Wildfire	1	38	24	105	Choi, Lee, Nam, and Lee (2007)
7	South Korea	Wildfire	2	48	42	689	Lee, Lee, Son, and Rhim (2011)
8	Germany	Windstorm	4	42	52	1,912	Thorn et al. (2016)
9	Poland	Windstorm	3	109	76	4,225	Zmihorski (2010)

plots (hereafter salvaged plots) and 3,896 disturbed (control) plots without post-disturbance logging (hereafter unsalvaged plots) and covered studies with survey duration ranging from one to 17 consecutive sampling years after the natural disturbance (Table 1).

2.2 | Functional traits and phylogeny

We followed Calba, Maris, and Devictor (2014) in the selection of 22 ecological traits reflecting avian resource and habitat use. Body mass and clutch size were continuous variables. Binary classifications were used for the main dietary component (plants, vertebrates, invertebrates), the main foraging method (pursuit, gleaning, pouncing, grazing, digging, scavenging, probing), the main foraging substrate (water, mud, ground, vegetation, air), the main foraging period (nocturnal) and the migratory status. Nest location was classified as one categorical variable (canopy, ground and hole). All traits were classified using the Cornell Laboratory of Ornithology (www.allaboutbirds.org) and the Handbook of Birds of the World (www.hbw.com). For a full list of the traits, see Table S2. We did not account for possible regional differences in the species migratory status, since the majority of our studies were located on a similar latitude in the Northern Hemisphere (Figure 1).

Phylogenetic trees were constructed separately for the species pool in each study area by combining a relaxed molecular clock of trees containing well-supported avian clades and a fossil-calibrated backbone that included representatives from each clade (Hackett et al., 2008). For each study area, 4,000 bootstrap replicate trees were mined from the online tool at www.birdtree.org, which first trims to a subset and then samples trees from a chosen pseudo-posterior distribution (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). The bootstrap replicates were then condensed into a dated consensus tree using TreeAnnotator 1.8.2 (http://beast.community/treeannotator). All subsequent analyses were based on these consensus trees (phylogenetic trees may be found in Figures S9–S17).

2.3 | Quantifying dissimilarity

Dissimilarities between the bird communities of salvaged and unsalvaged plots were quantified by treating each sampled plot within each year as a sampling unit and then extracting the species incidence (presence/absence) to obtain a count of the occurrences (i.e. the incidence-based frequency) for each species. This procedure yielded a species-incidence-based frequency vector for salvaged and unsalvaged plots for each sampling year. The number of occurrences among multiple plots of each species was treated as a proxy of the abundance of that species. As shown by Colwell et al. (2012), such incidence-based occurrence records are able to account for spatial aggregation or clustering in the data. Moreover, incidence-based data support statistical approaches to diversity inferences that are just as powerful as the corresponding abundance-based approaches.

We used Hill numbers (i.e. the effective number of species; Hill, 1973), based on species proportional incidence frequencies, to quantify and decompose diversity measures. Hill numbers differ by a parameter q that reflects their respective sensitivity to the relative frequency of a species. A main advantage of using Hill numbers is that they obey the replication principle (Chao, Gotelli, et al., 2014) and can thus be decomposed into independent components of alpha- and beta-diversity. The resulting beta-diversity is then transformed to obtain two general classes of dissimilarity measures, the Jaccard-type and the Sørensen-type (Chao, Chiu, & Jost, 2014). The Jaccard-type taxonomic dissimilarity index quantifies the effective proportion of non-shared species in salvaged and unsalvaged plots pooled, whereas the Sørensen-type index quantifies the effective average proportion of non-shared species in individual plots. These two types of dissimilarity measures include most of the commonly used dissimilarity indices.

We used Jaccard-type taxonomic dissimilarity measures (Chao, Chiu, et al., 2014) to quantify the temporal change in the dissimilarity of unsalvaged versus salvaged plots. Figures S1–S8 show that the dissimilarity patterns for the Sørensen-type indices were generally consistent except for differences in magnitude. Setting $q = 0$ in the class of Jaccard-type measures yields the classic richness-based Jaccard index, which weights all species equally; setting $q = 1$ yields the Shannon-entropy-based Horn index, which weights all incidences equally, thats is each species is weighted according to its incidence frequency; setting $q = 2$ yields the regional non-overlap index, which is very sensitive to dominant species but gives little weight to rare species (Chiu, Jost, & Chao, 2014). Special cases of Sørensen-type measures are described in Chao, Gotelli, et al. (2014). Because of the different weighting of the species, dissimilarity measure of $q = 0$ is disproportionally sensitive to rare species (i.e. infrequently detected species for incidence data), $q = 1$ to common species (i.e. frequently detected species for incidence data) and $q = 2$ to dominant species (i.e. highly frequently detected species for incidence data). Since our analysis is based on incidence frequencies, the classification of the species as rare ($q = 0$), common ($q = 1$) or dominant ($q = 2$) was based on each local dataset and was not linked to their global abundance. Here, 'rare' species refer to those species whose occurrence rates are relatively low in any plot.

Another advantage of using Hill numbers is that they enable a unified approach to generalizing the Jaccard- and Sørensen-type taxonomic dissimilarity measures to include species differences based on species evolutionary ancestries (i.e. phylogenetic trees; Chiu et al., 2014) or on species traits (Chao et al., 2019). In our study, the dendrogram-based approach of Chao, Gotelli, et al. (2014) was applied to quantify phylogenetic dissimilarity between salvaged and unsalvaged plots. This approach takes all species inter-relations into account, incorporating species relations not only for species pairs but also for every possible combination of any subset of species. For functional dissimilarity, we followed the approach of Chao et al. (2019), which is based on species pairwise-distances. For species traits, these distances were obtained by Gower distances (Gower, 1971). All plausible threshold levels of functional distinctiveness between any two species were considered. Interpretation of the Jaccard- and Sørensen-type phylogenetic and functional

dissimilarity indices is similar to that of their taxonomic versions. For example, the Jaccard-type phylogenetic and functional dissimilarity measures quantified, respectively, the effective proportion of non-shared evolutionary lineages (for phylogenetic dissimilarity) and non-shared functional groups (for functional dissimilarity) in salvaged and unsalvaged plots.

2.4 | Data analysis

All analyses were carried out in R 3.4.2 (R Development Core Team, 2017). Null models were used to compare the expected dissimilarities within unsalvaged plots (i.e. within the control treatment), to the dissimilarities between salvaged and unsalvaged plots (i.e. among treatments). Therefore, the dissimilarities of 999 randomly assembled communities ('simulated dissimilarities') recruited from unsalvaged plots were calculated and compared to the observed dissimilarities between salvaged and unsalvaged plots. Randomization was achieved using the independent swap algorithm (function *randomizeMatrix* from PICANTE package; Kembel et al., 2010), in which species occurrences, frequencies and species richness of the sample are held constant during the randomization process (Gotelli, 2000). Since, during randomization, every species can be randomly assigned to any unsalvaged plot, the results from the null model depicted the mean dissimilarities between any pair of unsalvaged plots occurring by chance.

For every study region and year after the disturbance, the mean dissimilarity value for every q = {0, 1, 2} and every respective dissimilarity (taxonomic, functional and phylogenetic) was calculated. Changes in the mean dissimilarity in a given year between salvaged and unsalvaged plots over the course of succession were identified by fitting general additive mixed-effects models (Gaussian error distribution, function *gamm4* from GAMM4 package; Wood & Scheipl, 2017). Separate models were fitted for all types of dissimilarities (taxonomic, functional and phylogenetic) and q numbers (q = 0, q = 1, q = 2), resulting in nine models (Table S1). To each of those models, we included the year after the disturbance as smoothed effect, fitted for observed and simulated communities separately, to test if successional trends in dissimilarities differ. Additionally, the null model (observed vs. simulated) was included as a fixed effect to test for differences between the observed and simulated dissimilarities. The study identity was specified as random effect to account for differences across the study sites and repetitive sampling within these sites.

The data provided by Hutto and Young (2002) covered 90% of all studied plots and 81% of all surveyed individuals in our final dataset (Table 1). To assess the effect of this study on the overall results, we repeated our analysis by excluding the data of Hutto and Young (2002). However, our results and trends were mostly similar, with overall few exceptions (Figures S5–S8). Also, we repeated the analysis by excluding the year 17, to evaluate the robustness of our results to this possible outlier. We found the same significant trends as in Figure 3 and Figure S2, with the exception that the increasing trends in dissimilarity after year 14 either disappeared or became very small (Figures S3 and S4).

3 | RESULTS

Our final dataset consisted of 299 species, represented by 51,813 individuals. The analysis showed that observed and simulated bird communities differed significantly for non-shared species (taxonomic dissimilarity), evolutionary lineages (phylogenetic dissimilarity) and functional groups (functional dissimilarity; Figure 2; Figure S1). The dissimilarities varied when the species

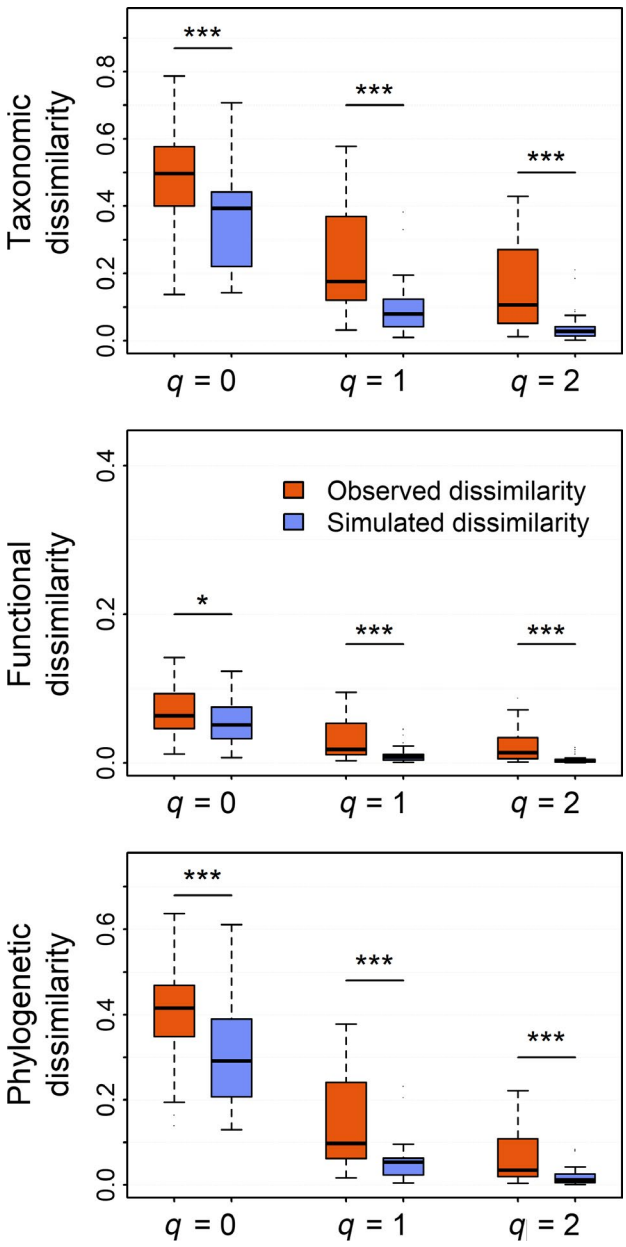

FIGURE 2 Effective proportion (Jaccard-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). Boxplots show the dissimilarity for rare (q = 0), common (q = 1) and dominant (q = 2) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. *0.05, ***0.001

were weighted according to their relative abundance. The largest dissimilarities occurred when all species, all evolutionary lineages and all functional groups were weighted equally (q = 0). The mean dissimilarity decreased when weighting of the species was shifted towards common (q = 1) and dominant (q = 2) species (Figure 2; Figure S1).

Over the course of 17 years, there was no significant increase or decrease in the observed community dissimilarity between salvaged and unsalvaged plots (Figure 3; Figure S2). Significant non-linear trends in the observed community dissimilarity were found only for: (a) common (q = 1) and dominant (q = 2) functional groups (Jaccard-type; Figure 3b); and (b) for dominant (q = 2) non-shared species (Sørensen-type; Figure S2a), as well as for common (q = 1) and dominant (q = 2) functional groups (Sørensen-type; Figure S2b). For all of these trends, the observed community dissimilarity followed a decrease between year 1 and year 12, followed by an increase after year 14 (Figure 3; Figure S2).

For simulated communities we found a significant trend of slight decrease followed by a slight increase only for dominant species (q = 2; taxonomic dissimilarity; Figure 3a). However, the magnitude of changes in dissimilarities was very small (<5%).

The average dissimilarity of simulated communities was significantly lower (p < 0.001) than the observed dissimilarities (Table S1). Thus, the average dissimilarities between salvaged and unsalvaged

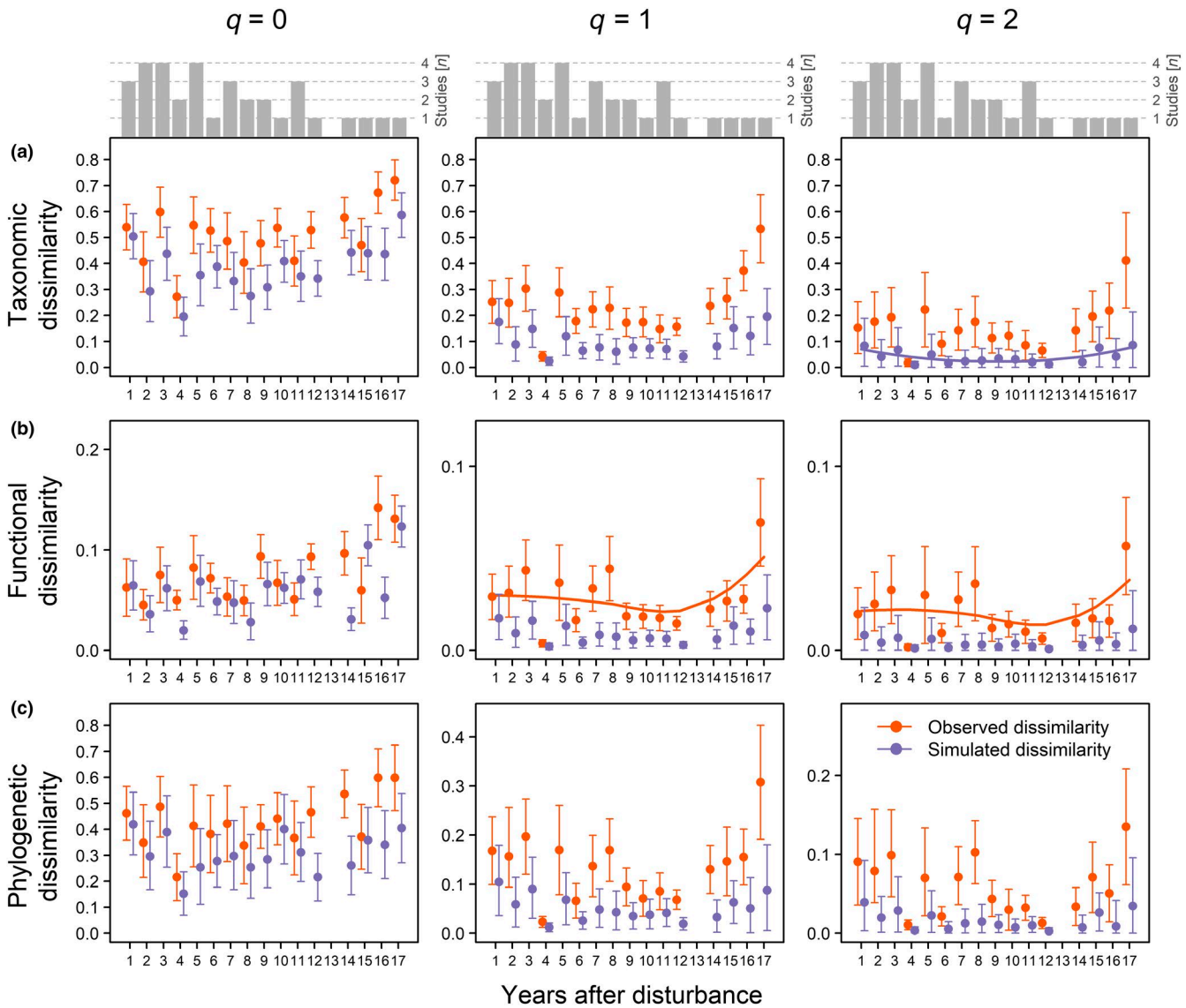

FIGURE 3 Effective proportion (Jaccard-type; mean ± *SD*) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (a) Taxonomic dissimilarity, (b) functional dissimilarity and (c) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare (q = 0), common (q = 1) and dominant (q = 2) species. Significant (p < 0.05) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the *y*-axes

plots were higher than the average dissimilarity that occurred within the unsalvaged plots by chance during the course of post-disturbance forest succession.

4 | DISCUSSION

Analysing data from nine studies covering a post-disturbance period of 17 years, we demonstrated that dissimilarities persisted or showed a u-shaped pattern. These differences exceeded the changes expected by chance, that is, without salvage logging, and were strongest for taxonomic, followed by phylogenetic and functional dissimilarity.

Comparisons of observed and simulated dissimilarities revealed that dissimilarities caused by salvage logging were higher than expected by chance (Table S1; Figure 2; Figure S1). Bird communities following naturally occurring disturbances are thought to undergo a gradual recovery, from disturbed-forest to mature-forest communities (Fontaine, Donato, Robinson, Law, & Kauffman, 2009). Our results suggested that the differences between the bird communities of salvaged and unsalvaged sites persisted within the first 17 years after a natural disturbance. It may be that 17 years are much shorter than the time required by a disturbed forest to recover. For example, differences in species richness and community composition can be detected for >60–70 years in the bird communities of boreal forests affected by wildfire and clear cutting (Zhao et al., 2013). Hence, it may be that the differences in bird communities caused by salvage logging also last for several decades.

Our results showed that dissimilarities between bird communities of salvaged and unsalvaged plots were larger for rare (q = 0) than for common (q = 1) or dominant (q = 2) species (Figure 2; Figure S1). Moreover, the highest taxonomic, functional and phylogenetic dissimilarities for observed and simulated communities were those of rare species (Figure 3; Figure S2). These results confirm the findings of Magurran and Henderson (2003), who in temporal studies showed that species with a low relative abundance persist only few years in the assemblage. Rare species (q = 0) can be habitat specialists that rely on ephemeral resources and thus occur only on a limited number of plots for short periods. A main characteristic of salvage logging is that it diminishes the structural heterogeneity caused by the natural disturbance (Swanson et al., 2011). In our case, this reduction in heterogeneity resulted in the short occurrence of rare and/or specialist species on either salvaged or unsalvaged plots, increasing the dissimilarity for rare (q = 0) species. For example, the corn crake *Crex crex* likely benefited from grass-dominated post-storm salvaged stands and was found only on few salvaged plots in Poland. In contrast, the common redstart *Phoenicurus phoenicurus*, which preferred remnant snags with cavities, was almost exclusively found on unsalvaged wind-disturbed plots in Germany. Conversely, common (q = 1) and dominant (q = 2) species consisted mainly of generalists that because of their broad habitat requirements and higher abundances were able to colonize salvaged and unsalvaged plots with similar success, resulting in a lower dissimilarity between the two site types.

Over the studied period, years 1–12 were characterized by a linear decrease in dissimilarity, followed after year 14 by an increase in dissimilarity for functional groups (q = 1 and q = 2; Figure 3). However, a more-detailed analysis of the included studies showed differences in the trends. For instance, after excluding Hutto and Young (2002) from the analysis no trend of increasing or decreasing dissimilarity was found, indicating that compositional differences persisted over the years (Figures S7 and S8). This result might be attributed to the sensitivity of the bird communities to salvage logging among different regions. For example, post-fire salvage logging in the Rocky Mountains can have a greater impact on bird communities than in the Mediterranean Basin because it affects a higher proportion of the bird community that occurs in burned forests (Rost, Hutto, Brotons, & Pons, 2013). Also, in the Rocky Mountains salvage logging has detrimental effects to fire specialists, like the Black-backed Woodpecker *Picoides arcticus* or the American Three-toed Woodpecker *Picoides tridactylus*, while in the Mediterranean Basin salvage logging affects only common forest birds species with wide distributions across European forests (Rost et al., 2013).

The dissimilarities between bird communities of salvaged and unsalvaged plots were lowest for functional groups (Figure 2; Figure S1). This suggests that bird communities of salvaged and unsalvaged plots share most functional groups but relatively smaller proportion of their species and evolutionary lineages. As salvage logging diminishes structural heterogeneity by reducing biological legacies (Swanson et al., 2011), communities of salvaged plots may have a high functional redundancy, in contrast to the low functional redundancy of the communities of unsalvaged plots. Although communities of salvaged plots may consist of functionally different groups (Azeria et al., 2011), we found a high similarity of rare, common and dominant functional groups in bird communities of salvaged and unsalvaged plots (Figure 2; Figure S1). Gerisch, Agostinelli, Henle, and Dziock (2012) showed that a high taxonomic diversity was not associated with a high functional diversity. We suggest that the observed pattern of functional, taxonomic and phylogenetic dissimilarity was driven by common or dominant species from genera like *Sylvia*, *Phylloscopus* and *Setophaga*, which while taxonomically and phylogenetically distant, are functionally similar. These species are mainly generalists that colonize both unsalvaged and salvaged plots. It is thus likely that these genera drive not only the determined taxonomic and phylogenetic dissimilarity but also the high functional redundancy between communities. Indeed, larger difference can be detected when comparing salvaged and unsalvaged plots to undisturbed forests (Thorn et al., 2016; Zmihorski, 2010), where phylogenetic and functionally distantly related genera occur with higher frequency.

Current knowledge about the effects of salvage logging has mainly come from local, short-term (1–5 years) studies (reviewed in Thorn et al., 2018). Our study, conducted at a wider spatial and temporal scale, provides a mid-term comparison of disturbed and salvage-logged forests but it is still relatively short compared to the

time a forest needs to recover. Hence, future studies might address whether initial changes in successional trajectories persist to later stages and how these changes vary across changing and interacting disturbance regimes (Leverkus, Lindenmayer, et al., 2018; Seidl et al., 2017).

5 | CONCLUSIONS

Our study provides evidence that salvage logging leads to short- to mid-term changes in bird community composition that are significantly greater than those occurring over the course of natural succession. Our results therefore demonstrate that salvage logging can lead to changes in community composition for non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity). In addition, because of the reduction of structural heterogeneity that salvage logging causes, it affects rare and/or specialized the most. The global increase in natural disturbances caused by climate change will trigger high levels of salvage logging world-wide. Hence, we argue that salvage logging may lead to widespread changes in the successional trajectories of forest bird community. Therefore, we recommend resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

ACKNOWLEDGEMENTS

S.T. was supported by a MOST (Ministry of Science and Technology) Taiwan Research Fellowship and received funds from the Gregor Louisoder Environmental Foundation. We thank Rebecca E. Cahall for providing bird data from the Eastern Cascades, Oregon (USA). We also thank two anonymous reviewers for their constructive comments.

AUTHORS' CONTRIBUTIONS

K.B.G., J.M. and S.T. conceived the idea and designed the study; A.C., K.B.G., Y.-H.C. and S.T. analysed the data; C.-Y.C., E.-J.L., J.B.F., J.C., J.R., M.Ż., R.L.H., S.T. and K.B.G. collected the data; K.B.G. wrote the first draft of the manuscript. All authors contributed significantly to later drafts and revisions.

DATA AVAILABILITY STATEMENT

All data are from previously published articles, listed in the *Data sources* section. Data from these articles can be made available upon reasonable request to original data owners.

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DATA SOURCES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Georgiev KB, Chao A, Castro J, et al. Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *J Appl Ecol*. 2020;57:1103–1112. https://doi.org/10.1111/1365-2664.13599