



Poleward migration of the destructive effects of tropical cyclones during the 20th century

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Determination of long-term tropical cyclone (TC) variability is of enormous importance to society; however, changes in TC activity are poorly understood owing to discrepancies among various datasets and limited span of instrumental records. While the increasing intensity and frequency of TCs have been previously documented on a long-term scale using various proxy records, determination of their poleward migration has been based mostly on short-term instrumental data. Here we present a unique tree-ring-based approach for determination of long-term variability in TC activity via forest disturbance rates in northeast Asia (33–45°N). Our results indicate significant long-term changes in TC activity, with increased rates of disturbances in the northern latitudes over the past century. The disturbance frequency was stable over time in the southern latitudes, however. Our findings of increasing disturbance frequency in the areas formerly situated at the edge of TC activity provide evidence supporting the broad relevance of poleward migration of TCs. Our results significantly enhance our understanding of the effects of climate change on TCs and emphasize the need for determination of long-term variation of past TC activity to improve future TC projections.

North Pacific | tropical cyclones | natural hazard | poleward migration | dendrochronology

Tropical cyclones (TCs) have significant social and economic impacts (1, 2) that are expected to strengthen further (3, 4) in tandem with the globally observed trend of their increasing intensity over the last few decades (5, 6). The current understanding of past variation and future changes in global TC activity (especially frequency, intensity, and track directions) is of relatively higher confidence; however, the region-specific changes are not yet well quantified (7). Regional changes in TC activity are poorly understood due to differences among datasets, with lower confidence in basin-specific projections and particularly in frequency projections within individual basins (7–10). The detection of past trends in region-specific TC activity can improve our understanding of multiple climatic factors determining changes in TC genesis, for example, spatial changes in sea surface temperature (11, 12) or large-scale circulation (13, 14), and thus improve projections of future changes in TC activity.

The western North Pacific is the world's most active ocean basin in terms of TC occurrence, where projections show the most prominent increase in both the frequency and intensity of TCs (2, 15). In addition, the most pronounced trends in poleward migration of the lifetime-maximum intensity and tracks of TCs have recently been identified here (16–18). Opinions on the past variability of the TC land interaction in the western North Pacific are conflicting, with some studies detecting a decrease (19), others detecting an increase (9), and still others showing no trend (20) in the destructive potential of TCs. However, most of the previous studies investigating the changes in TC activity were

based on precise, short-term instrumental data, with a focus on basin-integrated metrics regardless of whether or not a TC made landfall. In addition, northern latitude regions not affected by the strongest TCs (categories 4 and 5 on the Saffir–Simpson Hurricane Scale) were often ignored, even though TCs may have an increasing impact there as changes in large-scale circulation favor formation of TCs in the western North Pacific (16–18, 21, 22).

The impacts of potential changes in TC activity on both human society and the environment are difficult to quantify and compare over decades, as different areas with different levels of settlement and infrastructure have been affected (23). Instrumental records are too short to satisfactorily determine whether detected trends in TC activity are within the range of long-term natural variability or are associated with climate change (24, 25). Thus, unified and high-resolution proxy records from multiple locations are essential for understanding the long-term trends in TC activity over a wider area (16, 26).

TCs cause severe damage when they make landfall with high wind speeds, torrential rains, and floods (2, 3, 27). For example, Hurricane Katrina killed or severely damaged approximately 320 million large trees (28). The severity of forest damage generally increases in tandem with TC intensity (29), with TCs inducing tree mortality mainly in large canopy trees rather than small, understory trees (30). Consequently, newly emerged canopy gaps

Significance

Long-term variability in tropical cyclone (TC) activity is of high relevance for the development of adaptation and mitigation strategies; however, our current knowledge is based mostly on short-term records, with strong discrepancies among various datasets. We used tree-ring records of past forest disturbances to show rapid increases in the destructive effects of TCs during the 20th century. Long-term changes in TC activity imply that the recent poleward migration of TCs is not within the range of long-term natural variability and may be associated with climate change. Our findings are important, as affected regions were formerly situated at the edge of areas affected by TCs, and these areas are more sensitive to TC hazards because of a lack of experience-based adaptation strategies.

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caused by uprooting or stem breakage of canopy trees provide suitable microhabitats for seed germination and/or the possibility of understory trees to reach the canopy (31). However, current knowledge of the impact of TCs on forest ecosystems is based largely on short-term observations of the immediate aftermath of individual events and the subsequent forest response (32). Nevertheless, the long-term effects (29) and the impact of the recent changes in TC activity on forest ecosystems remains unclear. Thus, long-term detection of past TCs and the determination of their synergistic effects on forest ecosystems (29, 32) are urgently needed. Tree rings have previously proven their potential to detect previous canopy disturbances and to provide insight into past TC activity and the impact of TCs on forest ecosystems (27, 33). Thus, tree rings could serve as a large-scale proxy and reduce the current uncertainties induced by the short length and inconsistency of instrumental data.

We developed and analyzed a large tree-ring network covering a >1,300-km latitudinal span in coastal northeast Asia to detect the past variability of TC-induced canopy disturbances. We especially sought to determine whether past TC activities along the latitudinal gradient have been stable, or whether any variability induced by the poleward migration of the TC's maximum intensity could be identified. For this purpose, we analyzed raw tree-ring width series to detect past canopy disturbances in natural forests where TCs are the main disturbance agent (34).

Results and Discussion

Studied Gradient of Decreasing TC Activity. The latitudinal distribution of our study sites along a unique gradient of gradually decreasing TC activity from south to north was significantly correlated with decreases in both the intensity ($R = 0.998$; $P < 0.001$) and frequency ($R = 0.843$; $P < 0.05$) of the TCs (Fig. 1 and

SI Appendix, Figs. S1 and S2). We identified high correlations between canopy disturbance chronologies for individual sites and maximum wind speeds during TCs (*SI Appendix, Table S1*), while climate-growth relationships were only weak and mostly non-significant, with no systematic change along the gradient (*SI Appendix, Fig. S3*). These results confirm that TCs are the main disturbance agent in our study area, making our study area a natural laboratory for exploring the impact of TCs on forests.

Disturbance Frequency Along the Gradient. We found a markedly decreasing trend ($P < 0.001$) of canopy disturbances during the early stage of tree life (≤ 15 y) from south to north, while the opposite trend was found for trees exposed to canopy disturbance between their 15th and 50th years ($P < 0.001$) and after their 50th year ($P < 0.001$) (Fig. 2 and *SI Appendix, Table S2*). Similar trends in the frequency of canopy disturbances identified for the full dataset were also found for four dominant species, including two conifers and two broadleaves (Fig. 3 and *SI Appendix, Table S3*). From these trends, we inferred that the observed variability in the frequency of canopy disturbances along the latitudinal gradient reflects the conjoined effects of regionally distinct TC activity. Thus, we can conclude that the detected changes are not induced simply by the turnover of community composition in space and time, as the impact of TCs was also reflected in species-specific responses.

The overall higher occurrence of canopy disturbances during the early stage of tree life in the southern areas mirrored higher activity of TCs. In contrast, the higher incidence of trees exposed to canopy disturbance in later stages of life (after their 15th or even 50th year) in the northern areas reflected the lower activity of TCs. We suggest that using growth trends to determine species shade tolerance in further studies should be done at more sites with contrasting disturbance regimes. Thus, our application of a

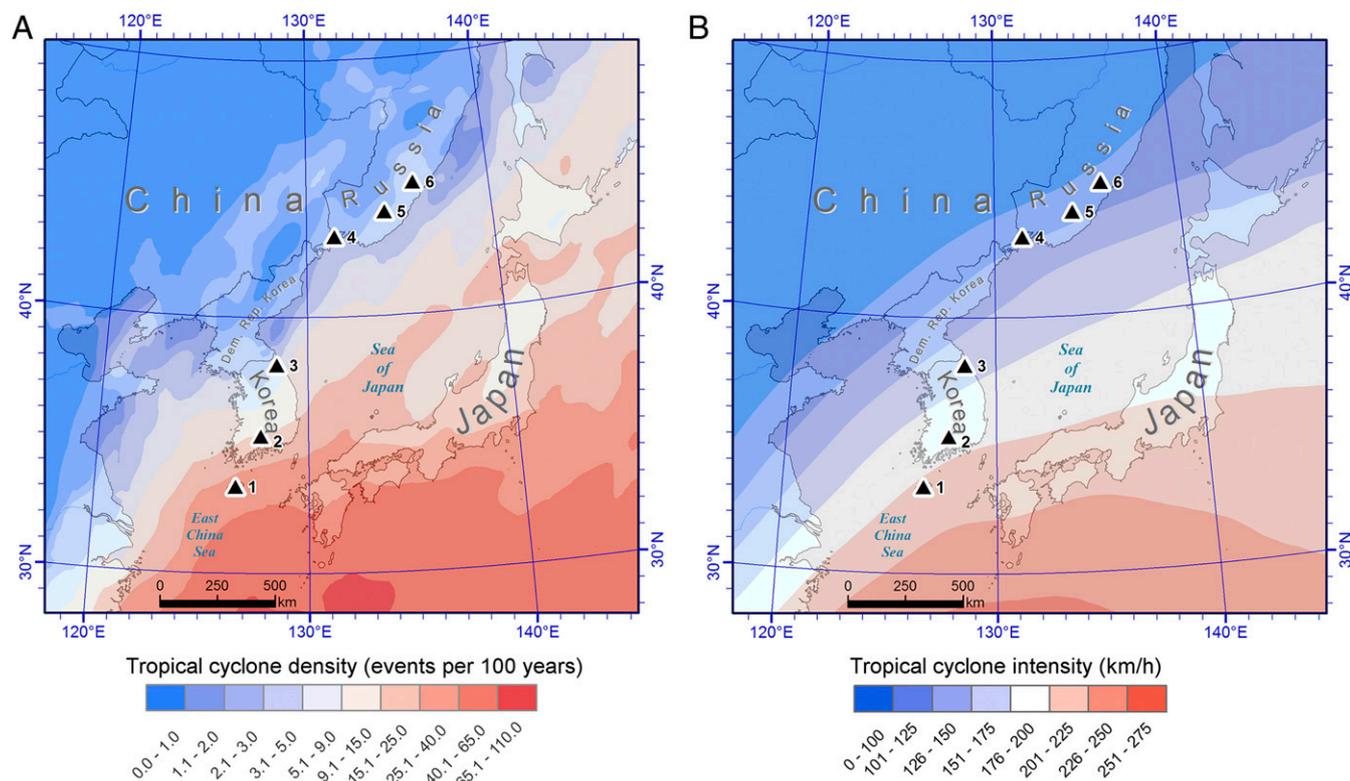


Fig. 1. Location of our study sites together with mean states of overall TC density and intensity of strong TCs across northeastern Asia. Decreasing gradients of TC frequency (A) and intensity (B) from south to north across our study sites (black triangles). TC frequency was derived from the "Tropical cyclones best tracks 1970-2011" dataset, showing the number of TC events scaled to 100 y. TC intensity shows 50-y return period windspeeds based on "Cyclone wind 50-y return period" dataset. Both datasets were compiled by UNEP/GRID-Geneva based on IBTrACS source data (74). Study site numbering refers to *SI Appendix, Table S4*.

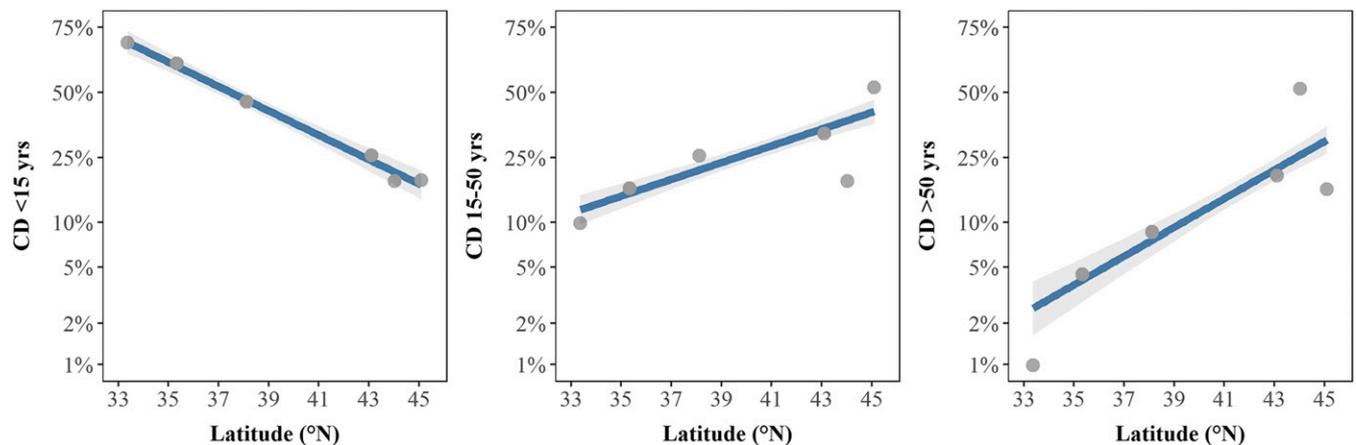


Fig. 2. Variability in canopy disturbances (CD) along the latitudinal gradient for the whole dataset. Shown are the proportions of trees experiencing CD in the first 15 y, between the 15th and 50th years, and after the 50th year along the latitudinal gradient. The trends for all three investigated groups were significant (*SI Appendix, Table S2*). The proportions of trees at individual localities (dots) were fitted by binomial generalized linear mixed-effect models. Regression lines and 95% two-sided confidence intervals are shown. The y axis is logit-transformed.

commonly used method seems appropriate for the determination of spatiotemporal changes of TC activity and could be applicable for other large-scale systems.

Spatiotemporal Stability of Disturbance Frequency. To investigate the temporal stability of TC-induced disturbances along our latitudinal gradient and to consequently confirm/refute the poleward migration of TCs, we divided our dataset into two groups: (i) younger trees with their first tree ring on or after 1920 and (ii) older trees with their first tree ring before 1920 (*Materials and Methods* and *SI Appendix, Methods*). We did not find any significant differences between the proportion of younger and older trees experiencing canopy disturbance during their first 15 y along the studied gradient (Fig. 4A and *SI Appendix, Table S2*). On the other hand, we found significant differences ($P < 0.001$) between younger and older trees in both the latitudinal trends and the proportion of trees experiencing canopy disturbance between their 15th and 50th year (Fig. 4B and *SI Appendix, Table S2*). Similar latitudinal trends ($P < 0.1$) were identified for younger and older trees experiencing canopy disturbance after their 50th year. More importantly, the proportion of canopy disturbances differed significantly ($P < 0.001$) between younger and older trees experiencing canopy disturbance after their 50th year (Fig. 4C and *SI Appendix, Table S2*). Linear mixed-effect models identified that differences between younger and older trees were more pronounced at the northern latitudes (Fig. 4B and C). Such significant changes in the canopy disturbance frequency are most likely caused by variations in TC activity throughout the 20th century. Thus, the high proportion of younger trees (>1920) experiencing canopy disturbance between their 15th and 50th years at the northern sites seems to reflect increased TC activity. Likewise, the lower proportion of younger trees than older trees exposed to canopy disturbance after their 50th year reflects increased TC activity at northern latitudes, as most of the trees could already reach the canopy during the first 50 y of life. Interestingly, no prominent changes in canopy disturbance frequency were identified for the southern latitudes (33–36°N; overlap in confidence intervals).

Here we report a tree-ring-based, large-scale analysis on the impact of landfalling TCs on forests, documenting shifts in TC activity. The broad spatial coverage of our network enabled us to demonstrate that the impact of TC activity and its poleward migration extends further to the north than reported in some previous studies that did not cover northern regions affected by TCs (35, 36). The significant increase in disturbance frequency at

the northern latitudes is in line with enhanced poleward propagation of TCs under climate change (16, 37). Unchanged canopy disturbance frequency in the southern latitudes is most likely caused by high TC activity, with frequent canopy disturbances already before 1920, and thus the further increase had only a low potential to affect forests even more strongly here.

Our study provides evidence that observed changes in TC activity, specifically northward TC track migration (17), caused more frequent forest disturbances during the last century in the western North Pacific. Detailed analyses of tree-ring-based measurements have provided insight into past TC activity and have proven to be a valuable proxy for detection of past TC activity. The presented analyses enabled accurate determination of how the poleward migration of TCs influenced the disturbance frequency and, consequently, the dynamics of whole forest ecosystems. Although the detection of other than TC-induced disturbances cannot be fully excluded, the highly significant correlations between tree-ring-based disturbance reconstructions and TC activity suggest little impact of other disturbance agents (27, 31) (*SI Appendix, Supporting Information*). Our findings are critical, as we have identified major changes at sites located at the very edge of TC impacts and facing rising TC activity in recent decades (2, 22, 38).

Increasing threats in these areas can be expected in the future (21), and local authorities and foresters should develop mitigation and preparedness activities to reduce TC impacts (39). This is especially important because regions exposed to low TC activity are more sensitive to TC hazards, owing to a lack of experience-based adaptation strategies (40). Although we did not identify an increase in TC disturbances at southern latitudes, future alterations of disturbance dynamics cannot be ruled out given the projected continuing changes in TC activity. Furthermore, this study shows that ecologists can positively contribute to TC research and that this may improve the understanding of various aspects of global climate change (41).

Our proxy records indicate that poleward migration of TCs in the western North Pacific is a more prolonged process than previously documented on the base of reliable, but short-term, instrumental records of TC activity. Changes in TC activity are determined by complex modes of large-scale natural climate variability as El Niño–Southern Oscillation, sea surface temperature, Pacific Decadal Oscillation or North Pacific Oscillation (22, 42, 43), and climate change (44–46). Although the responses of TCs to these complex processes are not fully comprehended, the observed expansion of the tropics (47, 48) is seen as a major

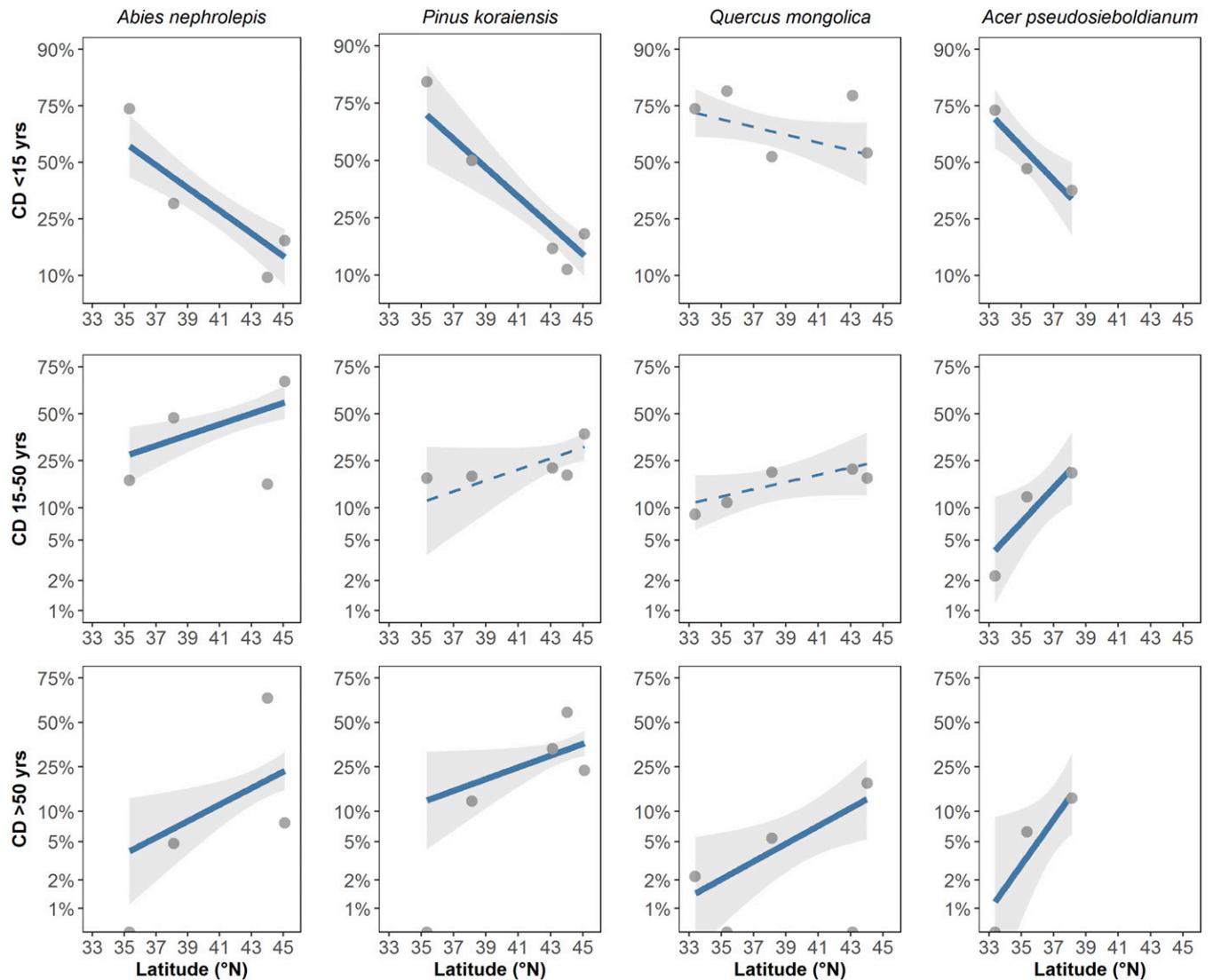


Fig. 3. Species-specific variability in canopy disturbances (CD) along the latitudinal gradient. Shown is the variability in frequency of CDs expressed by the length of the period preceding the canopy disturbance along the latitudinal gradient for four dominant tree species. The proportions of trees at individual localities (dots) were fitted by binomial generalized linear mixed-effect models. Regression lines and 95% two-sided confidence intervals are shown. Solid lines indicate significant ($P < 0.05$) regressions. The y axis is logit-transformed.

mechanism forcing the poleward migration of the lifetime-maximum intensity of TCs (16) via changes in Hadley circulation inducing a poleward shift of TC genesis-favorable climate conditions (49, 50). Specifically, the expansion of the tropics leads to increased sea surface temperatures at higher latitudes, where they trigger TC genesis and hence poleward migration of TC activity. Thus, our results not only contribute to improved understanding of the impact of TCs on forest ecosystems in northeast Asia, but also provide a benchmark for studies of climate forcing of TCs in the western North Pacific. We highlight the importance of performing similar gradient studies for other regions in the world affected by TCs to identify any long-term variability in the activity of landfalling TCs.

Materials and Methods

Tree-Ring Network and Study Sites. We developed a tree-ring width network for northeast Asia containing samples from living individuals of 54 species. Tree rings have a high potential for use as a precise TC proxy record, as documented in previous studies (27, 31, 51). Study sites were placed along a latitudinal gradient (33–45° N) from South Korea to the Russian far east (Fig. 1 and *SI Appendix, Table S4*) and together represent a single type of biome,

temperate broadleaf and mixed forests (52, 53) (*SI Appendix, Fig. S2*). The selected stands were natural old-growth forests located in National Parks (South Korea) or in unpopulated and protected areas (Russia) without evidence of past human impact (e.g., logging, burning, grazing) or other disturbance agents (e.g., fire scars). Thus, they were considered representative of the natural disturbance regimes of the region, i.e., TCs (34, 54). The studied forest ecosystems can potentially also face non-TC disturbances, such as droughts, fires, snow damage, and insect outbreaks (55, 56) and their importance increases with increasing latitude, as the occurrence of TCs is more sporadic (34). However, such disturbances prevail in secondary forests and in forests in the interior regions of Asia (57) but play only a minor role in the natural forests affected by TCs, where our study sites are located. In addition, our study sites are in relatively wet areas, not far from the coast, which also eliminate fire. Charcoal analyses were also made for study sites in Russia (as fires could be more expected there) and carbon dating (if charcoal was found) confirmed that there were no fires during the period covered by the oldest tree in our study (58). More information on study sites and the tree-ring network are provided in *SI Appendix, Methods*.

Identification of Canopy Disturbances. Canopy disturbances were identified based on radial increment patterns of individual tree-ring series. First, the presence/absence of an abrupt and sustained increase in radial growth (i.e., growth release) was detected using the technique of radial-growth averaging

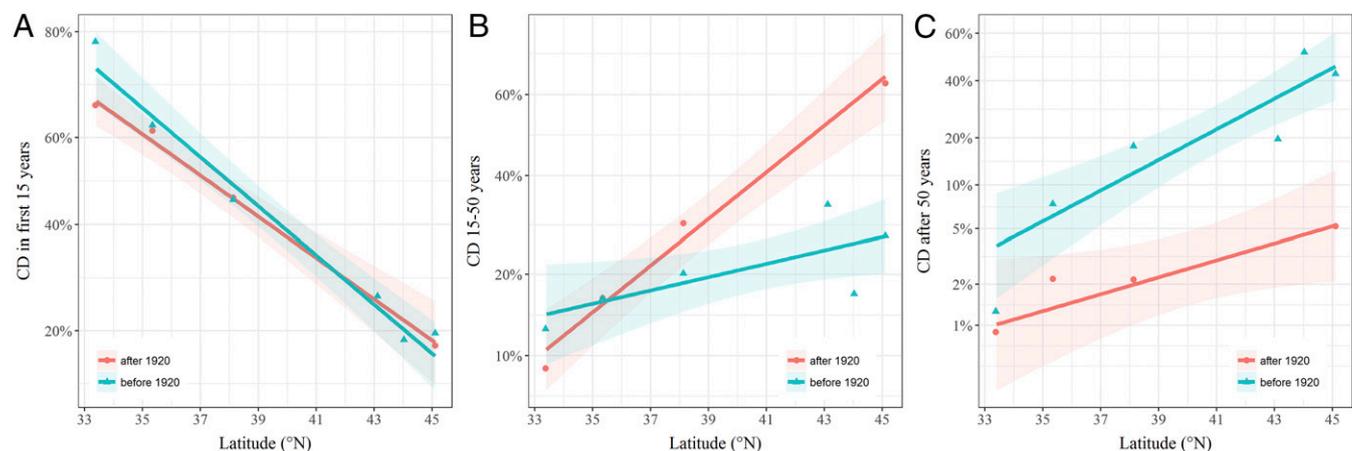


Fig. 4. Temporal analyses of canopy disturbance (CD) frequency along the latitudinal gradient. Shown is the disturbance frequency before (blue triangles and lines) and after 1920 (red dots and lines), expressed as the proportion of trees in individual categories (according to the length of period preceding canopy disturbance): trees experiencing CD in the first 15 y (A), between their 15th and 50th year (B), and after their 50th year (C). The proportions of trees at individual localities (triangles and dots) were fitted by binomial generalized linear mixed-effect models. Regression lines and 95% two-sided confidence intervals are shown. The y axis is logit-transformed.

criteria, as presented by Nowacki and Abrams (59) (*SI Appendix, Methods*). Second, we used gap origin detection, i.e., rapid declining growth pattern (60), to evaluate whether existing canopy trees experienced canopy disturbance already in the sapling stage. This is important, as the current method of growth release detection cannot capture disturbances within first few years and last few years of the tree-ring record (59, 61, 62). A combination of these two approaches provided evidence of past canopy disturbances (63), allowing a retrospective evaluation of the period during the lifespan of individual trees during which they were growing below canopy and “waited” for canopy disturbance to enable them to reach the canopy. Consequently, we can detect the frequency of canopy disturbances along the studied gradient. We distinguished the following categories: (i) trees with canopy disturbance during their first 15 y, including individuals with rapid early growth followed by a long and gradual decline considered as gap origin trees (64, 65); (ii) trees with canopy disturbance after their 15th year and before their 50th year; and (iii) trees with canopy disturbance after their 50th year. Details and examples are provided in *SI Appendix, Methods* and *Figs. S5 and S6*.

Division of the Dataset for Investigation of Temporal Stability. The dataset was divided into two subsets to determine the temporal stability/variability in the proportion of trees according to the duration of the period preceding canopy disturbance for individual trees along the latitudinal gradient. Thus, we divided the dataset according to the calendar year of the first measured tree ring for each individual increment core, with the aim of establishing two subsets in which (i) the breaking year will be before (but not too many years before) commonly documented changes in TC activity, and (ii) both subsets

would contain a comparable number of samples. In a recent study, Barcikowska et al. (66) found a strong increase in intense TC activity since the 1940s over the western North Pacific. This extends significantly beyond the time scale covered by the majority of studies, which have documented the increases in TC activity using shorter climatologic records (38, 67). As there is no clearly determined year/period when the change in TC activity started, we selected the year 1920, which is slightly before the change documented by Barcikowska et al. (66) and splits our dataset into two comparable subsets: 571 trees with the first tree ring before 1920 and 636 trees with the first tree ring after 1920.

Statistical Analyses. We used binomial generalized linear models to analyze latitudinal trends in the proportions of trees according to the length of the period needed for the canopy accession. To test differences between groups of trees established before and after 1920, we used binomial generalized linear mixed-effects models, with locality as a random effect and latitude, establishment period, and their interaction as fixed effects. Latitude was standardized to zero mean for analyses. All analyses were performed and figures prepared using R version 3.4.2 (68) with the “TRADER” (61), “ggplot2” (69), “dplyr” (70), “reshape2” (71), “effects” (72), and “lme4” (73) packages.

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