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Controls of Initial Wood Decomposition on and in Forest Soils Using Standard Material

Anita C. Risch[1]*, Deborah S. Page-Dumroese[2], Anna K. Schweiger[3], James R. Beattie[4], Mike P. Curran[5], Leena Finér[6], Mike D. Hyslop[7], Yong Liu[8], Martin Schütz[1], Tom A. Terry[9], Weiwei Wang[8,10] and Martin F. Jurgensen[7]

[1] Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland, [2] USDA Forest Service, Rocky Mountain Research Station, Moscow, ID, United States, [3] Remote Sensing Laboratories, Department of Geography, University of Zurich, Zurich, Switzerland, [4] Research School of Astronomy and Astrophysics, Australian National University, Canberra, ACT, Australia, [5] British Columbia Ministry of Forests, Lands and Natural Resource Operations, Victoria, BC, Canada, [6] Natural Resources Institute Finland (Luke), Joensuu, Finland, [7] College of Forest Resources and Environmental Sciences, Michigan Technological University, Houghton, MI, United States, [8] The Key Laboratory for Silviculture and Conservation of Ministry of Education, Beijing Forestry University, Beijing, China, [9] Retired, Olympia, WA, United States, [10] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China

Forest ecosystems sequester approximately half of the world's organic carbon (C), most of it in the soil. The amount of soil C stored depends on the input and decomposition rate of soil organic matter (OM), which is controlled by the abundance and composition of the microbial and invertebrate communities, soil physico-chemical properties, and (micro)-climatic conditions. Although many studies have assessed how these site-specific climatic and soil properties affect the decomposition of fresh OM, differences in the type and quality of the OM substrate used, make it difficult to compare and extrapolate results across larger scales. Here, we used standard wood stakes made from aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.) to explore how climate and abiotic soil properties affect wood decomposition across 44 unharvested forest stands located across the northern hemisphere. Stakes were placed in three locations: (i) on top of the surface organic horizons (surface), (ii) at the interface between the surface organic horizons and mineral soil (interface), and (iii) into the mineral soil (mineral). Decomposition rates of both wood species was greatest for mineral stakes and lowest for stakes placed on the surface organic horizons, but aspen stakes decomposed faster than pine stakes. Our models explained 44 and 36% of the total variation in decomposition for aspen surface and interface stakes, but only 0.1% (surface), 12% (interface), 7% (mineral) for pine, and 7% for mineral aspen stakes. Generally, air temperature was positively, precipitation negatively related to wood stake decomposition. Climatic variables were stronger predictors of decomposition than soil properties (surface C:nitrogen ratio, mineral C concentration, and pH), regardless of stake location or wood species. However, climate-only models failed in explaining wood decomposition, pointing toward the importance of including local-site properties when predicting wood decomposition. The difficulties we had in explaining the variability in wood decomposition, especially

for pine and mineral soil stakes, highlight the need to continue assessing drivers of decomposition across large global scales to better understand and estimate surface and belowground C cycling, and understand the drivers and mechanisms that affect C pools, CO_2 emissions, and nutrient cycles.

INTRODUCTION

Forest ecosystems play an important role in the global carbon (C) cycle (Schimel, 1995; Pan et al., 2011) and sequester approximately half of the world's organic C, most of which is stored in the soil (Dixon et al., 1994; Wei et al., 2014; Nave et al., 2019). Soil C storage represents the balance between input of fresh organic matter (OM) and turnover of labile and recalcitrant soil C through decomposition, leaching, and erosion (Mayer et al., 2020). Fresh OM, mostly dead plant litter or woody material from above- or belowground sources, is decomposed by soil fauna and microorganisms at a rate that is related to soil physical, chemical, and biological properties, vegetation composition, topography, climate, and land use, which interact to determine the fertility or productivity of a site (Jackson et al., 2017; Wiesmeier et al., 2019).

Many studies have documented the influence of climate and soil properties on fresh OM decomposition rates (e.g., Tóth et al., 2007; Goebel et al., 2011; Juhos et al., 2021), but differences in the type and quality of OM substrate used in these studies makes it challenging to compare and extrapolate results to other forest sites (Parton et al., 2007; Talbot and Treseder, 2012). By holding the quality [e.g., lignin, cellulose content, C:nitrogen (N) ratio] of the decomposing OM material constant across sites, decomposition becomes a function of soil abiotic (micro-climate, soil physical, and chemical properties) and biotic (microbial and invertebrate communities) properties (Parton et al., 2007; Zhou et al., 2007; Cornwell et al., 2009; Weedon et al., 2009; Russell et al., 2015; Zhang and Wang, 2015; MagnússonI, Tietema et al., 2016; Wang et al., 2018; Hu et al., 2021; Seibold et al., 2021). Therefore, using standard materials allows us to compare and better understand decomposition processes across different climatic regions, forest, and soil types (e.g., Gholz et al., 2000; Parton et al., 2007; Djukic et al., 2018; Fanin et al., 2019).

Many different types of standard materials, such as tea bags, filter paper, cotton cloth (e.g., Latter and Howson, 1977; Latter and Walton, 1988; Keuskamp et al., 2013; Djukic et al., 2018; Fanin et al., 2019), or plant material [leaf litter, fine roots (e.g., Berg, 2000; Gholz et al., 2000; Parton et al., 2007)] have been used in decomposition studies to date. However, standardized woody material, e.g., wood blocks, dowels, chop sticks, tongue depressors, or wood stakes (e.g., Jurgensen et al., 2006; Mackenzie et al., 2006; Bradford et al., 2014) are likely better suited to explore decomposition processes in forested ecosystems, as wood is a "normal" component of forest soils (surface residue, stumps, roots), important for forest soil C sequestration (e.g., Dixon et al., 1994) and its slow decomposition integrates soil abiotic and biotic conditions over longer time periods (Smyth et al., 2016;

Oberle et al., 2020). Here, we use standard aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.) stakes to assess decomposition. Aspen wood generally decomposes faster than pine wood as it has lower wood density, lignin content and N:lignin ratio, but higher N concentration (Cornwell et al., 2009; Weedon et al., 2009; Bani et al., 2018; Wang et al., 2018, 2020; Seibold et al., 2021).

The majority of wood decomposition studies have been conducted by placing the woody material aboveground, i.e., on top of the soil surface organic horizon (González et al., 2008; Weedon et al., 2009; Bradford et al., 2014; Liu et al., 2015; Hu et al., 2018; Lustenhouwer et al., 2020). Considerably less is known about decomposition processes of standard wood material buried belowground (e.g., Smyth et al., 2016; Erdenebileg et al., 2020; Jurgensen et al., 2020), although the volume of buried wood can contribute up to 935 m^3 ha^{-1} in temperate forests (Weedon et al., 2009; Moroni et al., 2015). In addition, only a few studies used standardized woody material across widely different sites to allow for a direct comparison of decomposition processes across larger scales (e.g., Reed et al., 2003; Adams et al., 2021; Page-Dumroese et al., 2021). Therefore, we initiated a large-scale study using standard wood stakes to assess the effect of climate, soil properties, and ecosystem disturbance (e.g., fire, drainage, timber harvesting) on above- and belowground decomposition processes in forested ecosystem across the northern hemisphere in 1998 (Jurgensen et al., 2006).

Subsequent results from individual studies or regional sites showed that buried wood stakes generally decomposed faster than when put on the soil surface (Risch et al., 2013; Page-Dumroese et al., 2019; Wang et al., 2019; Jurgensen et al., 2020). Climatic properties, more specifically, higher soil temperatures, and to a lower degree higher precipitation, but not air temperature, were found to be the drivers of these differences in decomposition in Swiss subalpine forests (Risch et al., 2013). Similarly, higher soil temperatures explained higher decomposition rates in boreal forests in Finland (Finér et al., 2016) and after wildfires in Montana, United States (Page-Dumroese et al., 2019). However, average annual air temperature and precipitation did not affect decomposition of wood stakes placed into the mineral soil along a transect from southern British Columbia to southern Oregon (Page-Dumroese et al., 2021), while higher moisture of mineral stakes explained their faster decomposition compared to the stakes placed on the soils surface in a Chinese pine plantation (Wang et al., 2019). This latter result may suggest that actual evapotranspiration might also be a predictor for wood stake decomposition as it includes the amount of water removed from the soil surface (Meentemeyer, 1978; Aerts, 2006). Soil phosphorus was found to be positively related to

decomposition in Swiss subalpine forests (Risch et al., 2013), but differences in soil N, OM, and pH did effect on decomposition in China (Wang et al., 2019). Clay type, rather than the amount of clay, in combination with temperature, also had a positive effect on wood decomposition, although this study was conducted in microcosms rather than *in situ* (Fissore et al., 2016).

While the results from these local and regional studies provide a general understanding on how wood decomposition of standard material is influenced by environmental and climatic properties, an integrated understanding of the long-term and large-scale processes that drive wood decomposition processes across forest ecosystems is still missing. Such knowledge is, however, needed to improve soil decomposition models and better estimate C cycling across large scales (Smyth et al., 2011). In this paper, we therefore, combined wood stake decomposition data from 44 unharvested forest sites distributed across the northern hemisphere. The sites spanned a relevant range of climatic and edaphic conditions and cover all major forest biomes, except for tropical forests (**Figure 1**). Standard aspen and loblolly pine stakes were placed horizontally on top of the surface organic horizons (surface), at the interface between the surface organic horizons and the mineral soil (interface), and vertically in the mineral soil (mineral) for 1–7 years, depending on local climatic and soil conditions (**Supplementary Table 1**).

Our study objectives were to: (1) assess large-scale patterns in decomposition of wood stakes at different incubation locations (surface, interface, mineral) over time within unharvested forest stands, and (2) determine the impact of climate (air temperature, soil temperature, precipitation, actual evapotranspiration) and soil properties (surface organic horizon and mineral soil C and N concentrations, mineral soil pH, bulk density) on decomposition at these different incubation locations. We expected that stakes placed into the mineral soil would decompose faster than stakes placed on the soil surface or at the interface (Busse, 1994; Trofymow, 1998; Risch et al., 2013; Wang et al., 2019; Erdenebileg et al., 2020). We also anticipated that higher air temperature would generally lead to greater decomposition of stakes regardless of where the wood stakes are placed (Brischke and Rapp, 2008; Risch et al., 2013; Finér et al., 2016; Fissore et al., 2016), but that soil temperature would be an even better predictor than air temperature for the mineral stakes. We expected precipitation to interact with air temperature as a controlling factor for decomposition, in particular, for stakes placed at the soil surface where high precipitation and warm temperatures should speed up decomposition (Jurgensen et al., 2020). However, we also expected higher mineral stake decomposition at sites with lower precipitation, as water retention by the mineral soil becomes much more important for decomposition processes at drier sites. Consequently, we also expected that actual evapotranspiration is a better predictor for wood stake decomposition than temperature and precipitation, as it includes the amount of water removed from the soil surface (Meentemeyer, 1978; Aerts, 2006). Sites with higher N levels in the surface organic horizons or mineral soil (Van Der Wal et al., 2007) and, therefore, smaller C:N ratios (Scott and Binkley, 1997; Kielak et al., 2016; Hu et al., 2021), should also have higher decomposition rates at all incubation

locations. In addition, we expected that changes in soil physical properties (e.g., bulk density) will affect decomposition *via* soil C accumulation and microbial activity (Federer et al., 1993; Ruehlmann and Körschens, 2009). Finally, we expected that local climate (Bradford et al., 2014) and soil properties (Adams et al., 2021; Page-Dumroese et al., 2021) would interact to influence decomposition rates across sites.

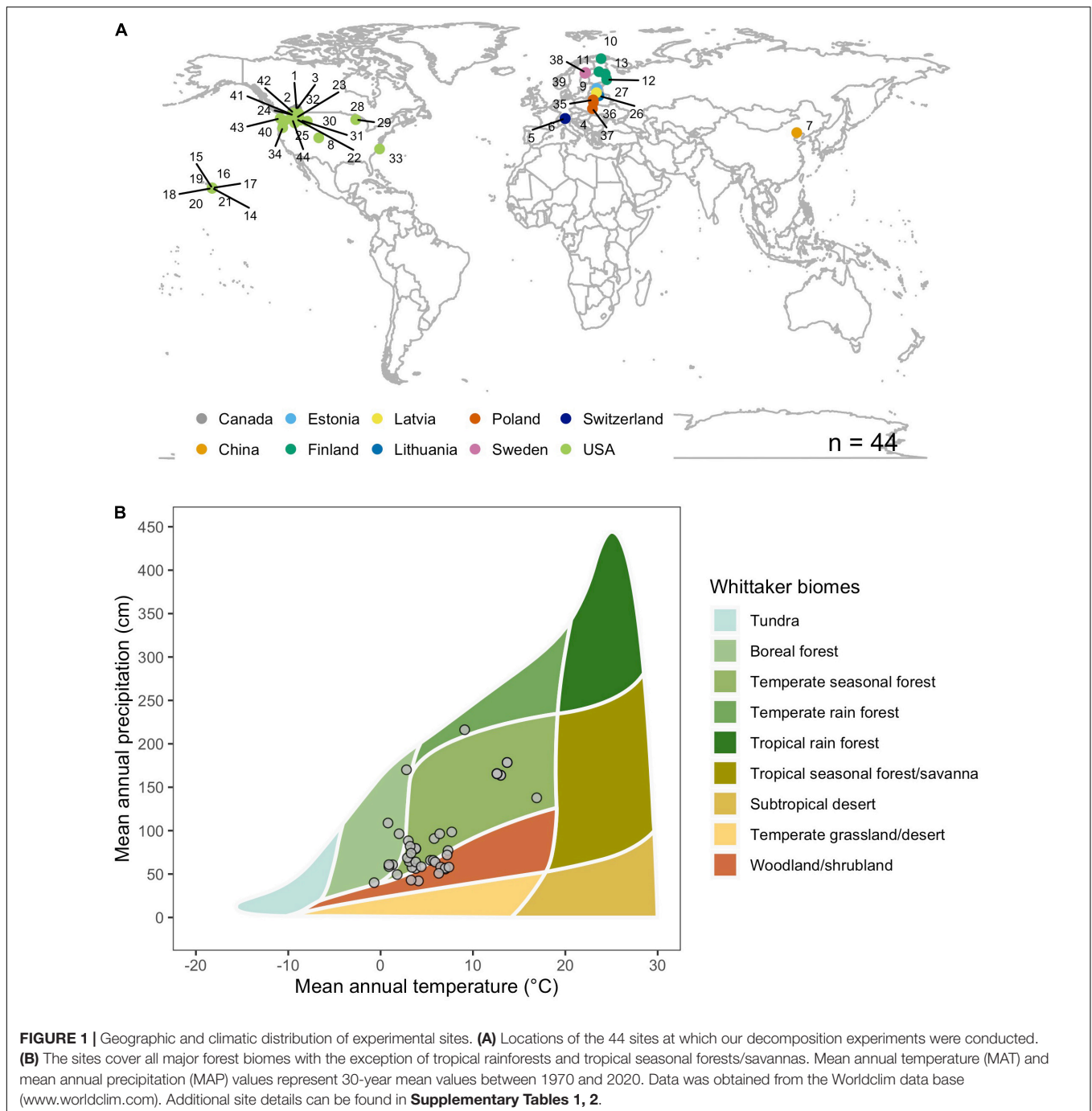## MATERIALS AND METHODS

Study Sites
Between 1998 and 2015 we field incubated 7,277 standard wood stakes at 44 sites located in North America, Europe and Asia (**Figure 1A**). Site elevations ranged from 35 to 2,451 m above sea level, and the sites featured mean annual temperature (MAT) and mean annual precipitation (MAP) of −0.7 to 16.9°C and 401 to 2162 mm, respectively (**Figure 1B** and **Supplementary Table 1**). The 44 sites covered boreal and temperate forest biomes, but did not include tropical rain forests or tropical seasonal forest/savannas (**Figure 1B**). All sites were part of a larger study to investigate the impact of different forest ecosystems, surface topography, soil types, climatic conditions, and disturbance regimes (e.g., forest management activities, fire) on wood stake decomposition (**Supplementary Table 2**). However, for this study we only used data from undisturbed forest stands. For site characteristics and tree species composition see **Supplementary Table 2**.

Wood Stakes
We used trembling aspen and loblolly pine as standard wood materials for our study, which are commonly used as test materials in wood decomposition studies (Jurgensen et al., 2006; González et al., 2008; Woodward et al., 2011). These stakes have different wood properties (see **Supplementary Table 3**). Two field surface or interface (2.5 × 2.5 × 15 cm) and two mineral soil (2.5 × 2.5 × 20 cm or 2.5 × 2.5 × 30 cm) stakes were cut from a longer, sapwood stake of each tree species. Stakes were kiln-dried at 75–80°C for 24 h resulting in a stake moisture content of approximately 15% (±5%). The remaining roughly 10 cm "center section" of the same stake was used as a laboratory control (time = 0) to calculate mass loss of the field stakes. The top of each mineral soil stake was treated with a wood sealer to prevent water wicking through the stake. For additional details on wood stake properties and fabrication see Jurgensen et al. (2006).

Experimental Design and Wood Stake Placement
One to eight replicate plots (2.5 × 2.5 m to 20 × 20 m in size) were established at each of the 44 study sites (**Supplementary Table 1**) depending on site conditions. All stakes were installed at the beginning of the growing season when soils were moist and the stakes therefore easier to insert into the soil. Wood stakes were placed horizontally on top of the surface organic horizons (surface), and at the interface between surface organic horizons and the mineral soil (interface). Mineral soil stakes were inserted

FIGURE 1 | Geographic and climatic distribution of experimental sites. **(A)** Locations of the 44 sites at which our decomposition experiments were conducted. **(B)** The sites cover all major forest biomes with the exception of tropical rainforests and tropical seasonal forests/savannas. Mean annual temperature (MAT) and mean annual precipitation (MAP) values represent 30-year mean values between 1970 and 2020. Data was obtained from the Worldclim data base (www.worldclim.com). Additional site details can be found in **Supplementary Tables 1, 2**.

vertically into the mineral soil to a depth of 20 or 30 cm (mineral), depending on site conditions such as the depth to bedrock or the presence of an impenetrable layer (Jurgensen et al., 2020). Individual mineral stakes were placed roughly 40–50 cm apart. Note that some sites had no surface organic horizon, consequently they did not receive surface or interface stakes. When surface and interface stakes were placed, they were secured with stainless steel landscape staples (Forestry Suppliers, Inc., Jackson, MS, United States). To reduce soil compaction and damage to the mineral stakes during installation, the surface

organic horizons were removed, and a hole was made with a square 2.5 × 2.5 cm coring tool. Stakes were gently inserted into the mineral soil so that the top was level with the soil surface and all sides were in contact with the mineral soil. Once the stakes were inserted, the organic layer was restored, where present. Wood stake moisture content at the time of installation was <20%.

Twenty-five stakes of each species (aspen, pine) were installed per plot for each soil available location. Five randomly selected stakes per species, soil location, and replicate were extracted at

regular intervals (6, 12, or 24 months) depending on climatic and soil conditions and initial number of replicates available (**Supplementary Table 1**). Total stake incubation times across the 44 sites varied from 1 to 7 years (**Supplementary Table 1**). A total of 2,337 surface, 2,036 interface, and 2,904 mineral aspen and pine stakes were used across the 44 sites. After the stakes were extracted, they were brushed clean of adhering soil, immediately weighed in the field and air-dried before sending them to the College of Forest Resources and Environmental Science at Michigan Technological University (United States) for processing.

In the laboratory, stakes were further cleaned of any remaining soil, dried at 105°C for 48 h, and weighed. The 10 cm laboratory "control" center section from each stake was used to determine initial weight of the field-deployed surface, interface, and mineral stakes (time = 0), and to calculate wood stake mass loss during the study [for details see Jurgensen et al. (2006)]. Soil depth effects on decomposition were assessed by cutting 2.5 × 2.5 cm blocks at 3.8 and 15.2 cm from the top of the 20 cm long mineral soil stakes, and an additional block at 27.5 cm from 30 cm long stakes.

Climate and Soil Properties

Although it is desirable to collect site-specific air and soil temperature, precipitation and soil moisture data in decomposition studies (Bradford et al., 2016), this is often not feasible due to resource constraints when sites are spread across different continents. Therefore, we sourced high resolution (1 km grid) site-specific monthly air temperature and precipitation data from the CHELSEA climate model (Version 1.2, Karger et al., 2017, 2018) for the specific duration during which the wood stakes were incubated at each site. For example, at site CAN1, all wood stakes were buried in 2001 and were retrieved at yearly intervals until 2005. Hence, for wood stakes incubated from 2001 to 2002, we averaged monthly air temperature and precipitation data for 2001 and 2002. For the wood stakes incubated from 2001 to 2003, we averaged the 2001–2003 monthly air temperature and precipitation data, and so forth for the other years. We also sourced yearly actual evapotranspiration (AET) from the MODIS Global Evapotranspiration Project,[1] and calculated AET for the site-specific incubation times. Note that for AET we only had data from 2000 to 2014, so we used the average of all available years (2000–2014) for the years that did not fall within this range (1998, 1999, 2015). Finally, we also sourced high-resolution (1 km grid) mean annual soil temperature (20-year average from 2000 to 2020) data (hereafter MATs) for the 0–5 cm and 5–15 cm soil layer (Lembrechts et al., 2022). We used the average of the 0–5 cm and 1–15 cm soil layer for each site.

To assess the effect of soil chemical and physical properties on decomposition, we collected three replicate samples from both the surface organic horizons (inclusive of fibric, hemic, and sapric layers) and the mineral soil to the same depth as the wood stakes were incubated (0–20 or 0–30 cm). Mineral soil samples were collected using either the soil excavation/foam core method (Page-Dumroese et al., 1999) or a slide hammer (AMS samplers, American Falls, ID, United States). All samples were sent to the USDA Forest Service, Rocky Mountain Research

Station Soil Analytical Lab (Moscow, ID, United States). Organic samples were dried at 60°C for 24 h, weighed, and then ground to pass a 0.4 mm sieve. Mineral soil was dried at 105°C for 24 h and weighed to determine total bulk density (weight/unit volume). A subsample of the mineral soil was then ground to pass a 0.4 mm sieve. Both organic and mineral soil samples were analyzed for C and N concentration (Leco, Corp., St. Joseph, MI, United States). Soil pH was determined on a 2:1 water to dry soil paste. Mineral soil and organic horizon properties were averaged by site (**Supplementary Table 2**).

Calculations and Statistical Analyses

We used linear mixed effects model (LMM) as implemented in the R package nlme (Pinheiro et al., 2021) to assess the effects of incubation location (location), incubation time (time), and wood types (wood type) on wood stake decomposition. Location, time, wood type, and all their interactions were included as fixed effects, plots nested in sites were included as random effects. As all our fixed effects were found to be highly significant (see Section "Results"), we separated our further analyses by location and wood type [see description of structural equation models (SEM) below].

We developed *a priori* main and alternative causal conceptual models for surface, interface, and mineral stakes (see **Supplementary Figures 1–4**) and tested how climate and soil properties affect wood decomposition with structural equation modeling (SEM). To avoid collinearity in the predictor variables, we used Spearman's correlation analysis (**Supplementary Figure 5**) and dropped variables with Spearman's rho > |0.70| (Dormann et al., 2013), i.e., we dropped mineral soil N concentration. Spearman correlation coefficients for all pairs of variables were calculated with the R function "cor" and the correlogram displayed using the R library "corrplot.mixed."

The variables included in the main surface stake models were air temperature, precipitation, and surface organic horizon C:N ratio (**Supplementary Figure 1A**). In addition, we calculated several alternative models. In one, we used AET instead of air temperature and precipitation (**Supplementary Figure 1B**), and to test whether surface organic C concentration was a better predictor than surface horizon C:N ratio, we calculated a SEM where we replaced the surface organic horizon C:N ratio with surface organic C concentration (**Supplementary Figure 1A**). The main and alternative models were hierarchical, with climate variables directly affecting wood decomposition and indirectly *via* soil properties (**Supplementary Figure 1**).

For the interface stakes, we increased the level of complexity and included mineral soil properties (**Supplementary Figure 2**). Again, we calculated a main and several alternative models for both aspen and pine wood stakes. In the two main models, air temperature and precipitation were allowed to affect decomposition directly and indirectly *via* organic surface C:N ratio, or mineral soil C concentration and mineral soil pH. All soil properties were allowed to directly affect decomposition (**Supplementary Figure 2A**). Surface horizon C:N ratio was allowed to have an indirect effect on decomposition *via* the mineral soil properties, and the mineral soil properties were allowed to interact with one

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[1] https://www.ntsg.umt.edu/project/modis/mod16.php

another (**Supplementary Figure 2A**). The same structure was used for all alternative models. In one, we replaced the surface organic horizon C:N ratio with surface organic C concentration (**Supplementary Figure 2A**). As soil bulk density was not significantly correlated with soil C concentration (**Supplementary Figure 5**), we also calculated an alternative model where we included bulk density as an additional mineral soil property (**Supplementary Figure 2B**). A third alternative model used AET instead of air temperature and precipitation (**Supplementary Figure 2C**).

For the mineral stakes we calculated the same main and alternative models as for the interface stakes (**Supplementary Figures 3A–C**), but also added a fourth alternative model in which we used soil temperature (MATs) instead of air temperature (**Supplementary Figure 3D**), as well as a fifth alternative model in which we omitted the surface organic horizon C:N ratio for simplicity (**Supplementary Figure 3E**). Finally, to assess if climate properties alone could explain wood stake decomposition without including soil properties, we also calculated another series of alternative models ("climate-only models") in which air temperature and precipitation or AET were allowed to directly affect surface, interface and mineral aspen and wood stake decomposition, respectively (**Supplementary Figure 4**).

We tested our conceptual models (**Supplementary Figures 1–4**) for aspen and pine wood stakes separately using a d-sep approach (Shipley, 2009; Lefcheck, 2016). We used the piecewiseSEM package (version 2.0.2; Lefcheck, 2016) in R 3.4.0 in which a structured set of linear models are fitted individually. This approach allowed us to account for the nested experimental design (Shipley, 2009; Lefcheck, 2016). We used the lme function of the nlme package (Pinheiro et al., 2021) to model response variables, including plots nested in sites as a random factors. For the mineral stakes we averaged the mass loss of wood blocks across soil depths (see methods described in "Wood stake incubation experiment"). However, we also calculated a model in which stake ID was included as an additional random effect. In this case all individual wood blocks per stake were included and provided a measure of decomposition at different mineral soil depth.

RESULTS

As expected, wood stake decomposition differed considerably among the 44 sites (**Supplementary Figure 6**). Overall, location, time, wood type, and their two-way interactions explained 44% of the total variation in decomposition when controlling for site effects in a mixed effects model (**Table 1**). Stakes inserted into the mineral soil generally decomposed more (**Figure 2A** and **Table 1**) and faster (interaction between location * time; **Figure 2C** and **Table 1**) than stakes placed at the interface between the surface organic horizon and mineral soil, and stakes placed on the soil surface. As expected, aspen stakes had greater mass loss (**Figure 2B** and **Table 1**) over time than pine stakes (interaction between wood type * time) across our 44 forested sites (**Figure 2D** and **Table 1**).
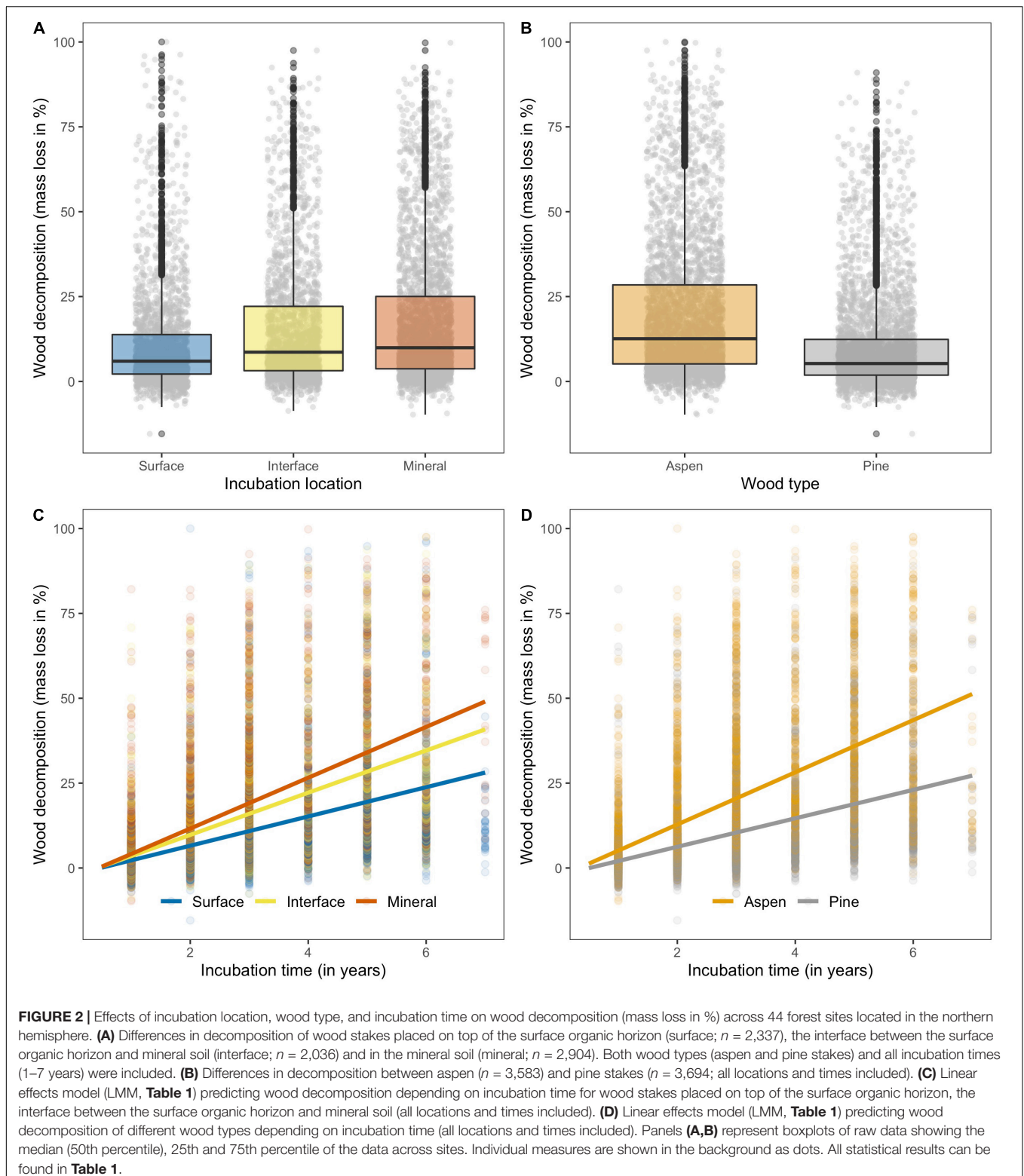
Looking at wood stake decomposition from a processed-based perspective with our structural equation models (SEMs), our main model for surface aspen stakes explained 44% (marginal R^2) of the variation in the decomposition across the 44 forest sites (**Figure 3A**). Air temperature (positive) and precipitation (negative) influenced the decomposition directly; hence, decomposition was higher at sites with higher air temperatures, but lower at sites with higher precipitation. Although we found no significant direct or indirect effect of the surface organic horizon C:N ratio on decomposition (**Figure 3A**), the C:N ratio contributed to the total explanatory power of the model. When removing the surface organic horizon C:N ratio completely (climate-only model), the total variation in decomposition explained dropped from 44 to just 1% (**Supplementary Figure 7A**). When replacing surface C:N ratio with surface C concentration in one of our alternative models, the total variation in decomposition explained dropped from 44 to 12% (**Supplementary Figure 8A**). Using AET instead of air temperature and precipitation also failed to explain decomposition differences in our surface aspen stakes (only 1 and 0.1% of variation explained; **Supplementary Figures 7B, 8B**). Neither our main nor alternative models explained any of the variation in surface pine stake decomposition (all marginal R^2 values between 0.1 and 1%; **Figure 3B** and **Supplementary Figures 7C,D, 8C,D**).

Our main SEM for aspen interface stakes explained 36% of the total variation in decomposition across our sites (**Figure 3C**). As with aspen surface stakes, air temperature had a positive effect on decomposition and precipitation a negative one. Air temperature was positively correlated with the surface organic horizon C:N ratio, which was positively associated with mineral soil pH. Soil pH, in turn, had a negative relationship with decomposition. Precipitation had a positive relationship with mineral soil C concentrations and a higher C concentration was positively related to decomposition of the interface aspen stakes across sites (**Figure 3C**). Again, replacing the surface organic horizon C:N ratio with C concentration in our alternative model resulted in less total variation in decomposition explained (31% instead of 36%; **Supplementary Figure 9A**).

TABLE 1 | Linear mixed effects model explaining wood decomposition based on incubation location (location), incubation time (time), wood type (wood type), and their interactions as fixed effects ($R^2 = 0.44$, $p < 0.0001$).

	numDF	denDF	*F*-value	*p*-value
Intercept	1	7170	46941.28	<0.0001
Location	2	7170	257.62	<0.0001
Time	1	7170	4632.52	<0.0001
Wood type	1	7170	1260.65	<0.0001
Location * Wood type	2	7170	14.53	<0.0001
Location * Time	2	7170	52.17	<0.0001
Time * Wood type	1	7170	132.04	<0.0001

Plot nested within site was included as a random effect. numDF, numerator degree of freedom; denDF, denumerator degrees of freedom. Note that the three-way interaction was not significant [$F_{(2,7168)} = 2.88$, $p = 0.06$] and therefore dropped from the model.

FIGURE 2 | Effects of incubation location, wood type, and incubation time on wood decomposition (mass loss in %) across 44 forest sites located in the northern hemisphere. **(A)** Differences in decomposition of wood stakes placed on top of the surface organic horizon (surface; n = 2,337), the interface between the surface organic horizon and mineral soil (interface; n = 2,036) and in the mineral soil (mineral; n = 2,904). Both wood types (aspen and pine stakes) and all incubation times (1–7 years) were included. **(B)** Differences in decomposition between aspen (n = 3,583) and pine stakes (n = 3,694; all locations and times included). **(C)** Linear effects model (LMM, **Table 1**) predicting wood decomposition depending on incubation time for wood stakes placed on top of the surface organic horizon, the interface between the surface organic horizon and mineral soil (all locations and times included). **(D)** Linear effects model (LMM, **Table 1**) predicting wood decomposition of different wood types depending on incubation time (all locations and times included). Panels **(A,B)** represent boxplots of raw data showing the median (50th percentile), 25th and 75th percentile of the data across sites. Individual measures are shown in the background as dots. All statistical results can be found in **Table 1**.

The explanatory power dropped even more for our other alternative models, i.e., including total soil bulk density (total amount of variation explained dropped from 36 to 25%; **Supplementary Figure 9B**) or replacing temperature and precipitation with AET (36–3%; **Supplementary Figure 9C**). The same was true for the climate-only models [from 36 to 3% (temperature/precipitation) and 36% to 0.1% (AET); **Supplementary Figures 7E,F**].

FIGURE 3 | Influence of local environmental conditions on the wood decomposition (mass loss in %) in forested ecosystems. Structural equation model (SEM) diagrams illustrate climatic and soil properties found to affect decomposition of **(A)** surface aspen stakes, **(B)** surface pine stakes, **(C)** interface aspen stakes, **(D)** interface pine stakes, **(E)** mineral aspen stakes, **(F)** mineral pine stakes. Blue, solid lines represent positive relationships, red, dashed lines negative relationships. Line width corresponds to differences in significance levels (thick = $p < 0.001$, medium = $p < 0.005$, thin = $p < 0.05$). Non-significant connections were removed. Temp, average air temperature per site for the individual incubation time per wood stake; Precip, average precipitation per site for the individual incubation time per wood stake; Surf CN, surface organic horizon C:N ratio; Min C, mineral soil C concentration; Min pH, mineral soil pH. Decomposition values were log-transformed. Total number of sites included for surface aspen and pine = 19, interface aspen and pine = 10, mineral soil aspen and pine = 23. For alternative models see **Supplementary Figures 7–10**.

Our main SEM for interface pine stakes explained 12% of the total variation in decomposition (**Figure 3D**). Precipitation had a direct, negative relationship with decomposition rates. When we replaced the surface organic horizon C:N ratio with C concentration (**Supplementary Figure 9D**) or included BD as an additional predictor (**Supplementary Figure 9E**) in our alternative models, we explained a similar amount of variation (11 and 14% instead of 12%). When we replaced temperature and precipitation with AET (**Supplementary Figure 9F**) or when we calculated the climate-only models (**Supplementary Figures 7G,H**) we only explained 3, 1, and 0.1% of the variability in the decomposition of interface pine stakes, respectively.

The main SEMs for both aspen and pine mineral stakes explained only 7% of the total variation in wood stake decomposition (**Figures 3E,F**). Again, precipitation was directly and negatively related to decomposition. All our alternative models lead to small in- or decreases in the explanatory power compared to the main models (**Supplementary Figures 10A–J**): i.e., replacing surface organic horizon C:N ratio with C concentration (aspen: 7%, pine 4% of the variation explained; **Supplementary Figures 10A,F**), including mineral BD (aspen: 8%, pine 9%; **Supplementary Figures 10B,G**), replacing air temperature and precipitation with AET (aspen: 4%, pine 2%; **Supplementary Figures 10C,H**), replacing air temperature with soil temperature (aspen: 5%, pine 5%; **Supplementary Figures 10D,I**) or dropping the surface organic horizon C:N ratio from the models (aspen: 3%, pine 2%; **Supplementary Figures 10E,J**). Also, calculating models with only climate variables did not improve the prediction of mineral soil wood stake decomposition (aspen: 3% and 1%, pine: 2% and 0.1%; **Supplementary Figures 7I–L**). The same was true when we used the decomposition rates of individual wood blocks from different depths instead of averaging the individual values per stake (stake ID included as a random factor; results not shown).

DISCUSSION

As we expected, our results showed that wood stakes incubated in the mineral soil decomposed faster than the stakes placed on the interface and the soil surface across our 44 sites. These findings confirm other results from local studies (Risch et al., 2013; Smyth et al., 2016; Page-Dumroese et al., 2019; Wang et al., 2019; Jurgensen et al., 2020). A similar result was found using tea bags across forest types in France (Fanin et al., 2020). Generally, at relatively dry sites, buried wood decomposes faster compared to wood placed on the soil surface as soil moisture conditions are more favorable for decomposition in the mineral soil compared to the soil surface (Busse, 1994; Brischke and Rapp, 2008; Smyth et al., 2016). In contrast, at cool or wet sites or at sites with compacted subsoils, buried wood can decompose slower than wood placed on the soil surface, as the buried wood might be saturated and conditions might become anaerobic (Smyth et al., 2016) or temperatures might be too cold to allow for microbial activity (Aerts, 2006). The latter most likely was the case for faster

surface compared to mineral aspen and pine stake decomposition in our uncut boreal forest stands located in northern Finland (Finér et al., 2016).

As we expected, aspen stakes decomposed faster than pine stakes across all sites due to their lower wood density, lower lignin content, and higher N content as previously found for local-site studies (e.g., Risch et al., 2013; Finér et al., 2016; Page-Dumroese et al., 2019; Wang et al., 2019; Jurgensen et al., 2020). Decomposing aspen stakes also had lower fungal species richness than pine stakes (Wang et al., 2020), which also might explain their faster decomposition: general observations revealed that low fungal species richness generally is associated with rapid wood decomposition (Toljander et al., 2006; Fukami et al., 2010).

In our study, climatic conditions were stronger predictors of wood decomposition than soil properties, but climatic properties alone (climate only models) failed to explain decomposition (total amount of variation explained between 0.1 and 3% only). These findings contrast, to some extent, with Bradford et al. (2014), who suggested that local-scale soil properties or soil moisture data would be stronger predictors of soil biotic activity and wood decomposition than larger-scale climate properties, especially air temperature. This was not the case for the factors we included in our study, but the failure of our climate-only models to explain decomposition across our forest sites also points toward the strong effect of local site properties in controlling decomposition. Similar to Bradford et al. (2014), air temperature was not an important driver for surface (and interface) pine wood stake decomposition, but it was for our aspen stakes.

Even though we had similar numbers of data points for aspen and pine wood stakes, our SEMs explained decomposition of aspen surface and interface stakes better than the one of pine stakes (surface: 44 vs. 0.001% of variation explained with the model; interface: 36 vs. 12%), while explanation power was similarly low for mineral stakes of both wood types (7%). These findings indicate that we likely did not include the most important drivers of pine decomposition in our study. These missing properties could be the composition, abundance and diversity of the soil microbial community (Bani et al., 2018; Wang et al., 2020), macro-invertebrates such as termites, ants or other insects (Bradford et al., 2014; Jurgensen et al., 2020; Seibold et al., 2021) or the number of days above a threshold temperature for microbial activity (Page-Dumroese et al., 2019).

The performance for our two models for wood stake decomposition in the mineral soil was rather low, and further decreased when we replaced air with soil temperature. These findings contrast with findings in the Swiss Alps, where soil temperatures were much better predictors for decomposition than air temperature (Risch et al., 2013). However, it is worth noting that the soil temperature data we had available here originated from a global soil temperature data product (Lembrechts et al., 2022) that was highly correlated to air temperature (**Supplementary Figure 11**), and do not represent values obtained at each single site. If we would have had local-site soil temperature values we would still expect them to be better predictors than air temperature for decomposition rates in the mineral soil.

Despite the large number of wood stakes that decomposed under a wide range of soil and climatic conditions in our study, developing a universal model that explains wood stake decomposition remains challenging, especially for the mineral soil. However, the positive effect of air temperature and the negative effect of precipitation on decomposition remained relatively stable across our decomposition models, including the alternative models. Given the expected increases in temperature as a result of global climate change (IPCC, 2014, 2018), we would expect higher wood decomposition in all locations and, therefore, greater C fluxes from the soil to the atmosphere in the future (Davidson and Janssens, 2006; Bond-Lamberty et al., 2018). However, increased heavy precipitation events (Fischer and Knutti, 2014) might potentially counteract these C losses. If mineral soils remain saturated for longer periods of time, decomposition would likely decrease, especially at colder high-elevation or boreal sites. Our results make it clear that global models of OM decomposition need to also include local-site soil properties mentioned by Bradford et al. (2014), rather than only using readily available data of global air/soil temperature and precipitation. Ideally, such models would also include information on the composition and abundance of the soil micro- and macro-fauna as drivers of OM decomposition. The difficulties we had in explaining the variability in wood decomposition across the 44 northern hemisphere forest sites, highlight the need to continue assessing wood decomposition from local to regional and continental scales to better understand and predict C losses and gains in a changing world.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. R code and data are availabe at github Doi: 10.5281/zenodo.6355363.

AUTHOR CONTRIBUTIONS

MJ and DP-D developed the overall research idea, coordinated data collection, and laboratory analyses. AR developed and framed the research question. DP-D, MJ, AR, LF, MS, WW, TT, and MC collected the data. MH and JB assembled and calculated the climate data. AS, AR, and JB analyzed the data. AR wrote the manuscript with contributions from DP-D, MJ, AS, LF, MH, MS, WW, TT, MC, and YL. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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