

CWD decay stages and carbon-nitrogen dynamics in Hyrcanian forests

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Research Article

Keywords: coarse woody debris, deadwood decomposition, nutrient cycling, Hyrcanian forests, soil properties, carbon dynamics, temperate forests, forest ecology

Posted Date: June 30th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10178991/v1>

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Additional Declarations: The authors declare no competing interests.

Abstract

Coarse woody debris (CWD) represents a critical structural and functional component of temperate forest ecosystems, contributing to carbon storage, nutrient cycling, microbial activity, and microsite heterogeneity. However, the relationships among deadwood decomposition, structural attributes, and associated soil nutrient dynamics remain insufficiently understood in Hyrcanian temperate forests. This study investigated the effects of CWD decay stage, diameter class, and deadwood type (snag versus log) on nutrient concentrations and adjacent soil physicochemical properties within a 50 ha mixed beech–hornbeam forest in northern Iran. A complete inventory of standing and downed CWD was conducted, and both soil and wood samples were collected across six decay classes and three diameter classes. Soil organic carbon, total nitrogen, available phosphorus, exchangeable potassium, moisture content, bulk density, and texture were quantified using standard laboratory procedures. Carbon and nutrient concentrations in CWD were determined by elemental and chemical analyses. Linear mixed-effects models, regression analyses, and principal component analysis (PCA) were used to evaluate decomposition-mediated biogeochemical relationships. The results demonstrated that decomposition stage exerted a strong influence on both deadwood chemistry and adjacent soil properties. Nitrogen concentrations increased significantly with advancing decay, whereas C/N ratios declined progressively, indicating intensified microbial immobilization and biochemical transformation of woody tissues during decomposition. Medium-diameter CWD exhibited the strongest localized effects on soil moisture and nutrient enrichment, suggesting that intermediate-sized substrates provide optimal conditions for microbial activity and nutrient transfer. Logs generally showed stronger nutrient coupling with surrounding soils than snags, likely because of greater stem–soil contact and enhanced moisture retention. Principal component analysis further revealed that soil moisture, bulk density, and nutrient availability represented major environmental gradients associated with deadwood decomposition patterns. These findings demonstrate that structurally diverse coarse woody debris functions as a long-term biogeochemical regulator within Hyrcanian forests by mediating localized carbon persistence, nutrient redistribution, and soil heterogeneity. The study highlights the ecological importance of retaining multiple deadwood forms, diameter classes, and decay stages in close-to-nature forest management and provides new insights into deadwood-mediated ecosystem functioning in temperate broadleaved forests under changing environmental conditions.

Introduction

Coarse woody debris (CWD), including standing dead trees (snags) and downed logs, represents a fundamental structural and functional component of forest ecosystems. Beyond its role as residual biomass, CWD regulates multiple ecological processes associated with biodiversity conservation, carbon sequestration, nutrient cycling, soil development, and long-term ecosystem resilience (Harmon et al., 1986; Russell et al., 2015; Thom & Seidl, 2016). In natural and unmanaged forests, deadwood constitutes a major organic matter reservoir and contributes substantially to forest carbon and nutrient budgets over decadal timescales (Pan et al., 2011; Köster et al., 2021). Consequently, the ecological importance of CWD has increasingly been recognized in sustainable forest management, retention

forestry, and climate-change mitigation strategies (Müller & Bütler, 2010; Stokland et al., 2012; Lindenmayer et al., 2020).

The ecological functions of CWD are strongly mediated by decomposition processes. During decay, physical and chemical transformations in woody tissues regulate the release, immobilization, and redistribution of nutrients between deadwood and surrounding soils (Berg & McClaugherty, 2020). These processes influence microbial activity, moisture retention, soil organic matter formation, and regeneration microsites (Fukasawa et al., 2021; Bradford et al., 2022). At the same time, decomposition dynamics determine the residence time of carbon in deadwood pools and therefore affect forest carbon balance and long-term carbon storage capacity (Russell et al., 2015; Harris et al., 2021). Because decomposition rates vary widely among tree species, wood sizes, climatic conditions, and decay stages, CWD contributes to pronounced spatial and temporal heterogeneity within forest ecosystems (Zhou et al., 2022).

Previous studies have shown that deadwood decomposition is controlled by interacting biotic and abiotic drivers, including substrate quality, wood density, temperature, moisture conditions, fungal colonization, and decomposer communities (Boddy & Heilmann-Clausen, 2008; Herrmann & Bauhus, 2013; Purahong et al., 2018). In particular, decay stage has been identified as a key determinant of carbon loss and nutrient dynamics in decomposing wood (Kahl et al., 2017; Köster et al., 2021). As decomposition progresses, carbon concentrations generally decline due to respiratory losses, whereas nitrogen may accumulate through microbial immobilization and external nutrient inputs (Berg & McClaugherty, 2020). These shifts frequently result in decreasing C/N ratios in advanced decay stages, reflecting progressive biochemical transformation of woody tissues (Fukasawa et al., 2021). However, the magnitude and direction of these processes remain highly variable among forest ecosystems and species, suggesting that deadwood-mediated biogeochemical dynamics are context dependent (Bradford et al., 2022).

The ecological effects of CWD are also influenced by structural attributes such as diameter and deadwood type. Large logs often persist longer and store greater quantities of carbon, whereas smaller and intermediate-sized debris may decompose more rapidly because of greater surface-to-volume ratios and enhanced microbial accessibility (Woodall & Nagel, 2006; Russell et al., 2015). Similarly, standing and downed deadwood create distinct microenvironmental conditions through differences in aeration, stem–soil contact, moisture retention, and decomposer colonization pathways (Angers et al., 2010; Heilmann-Clausen et al., 2021). These structural differences may produce contrasting effects on adjacent soil properties and nutrient availability, yet comparative evidence regarding snag–log interactions remains limited in many temperate forest ecosystems.

Interest in deadwood ecology has intensified in recent decades because climate change, drought stress, windthrow, insect outbreaks, and increasing tree mortality are rapidly altering forest carbon dynamics worldwide (Seidl et al., 2017; Anderegg et al., 2020). Mortality-driven increases in deadwood inputs can substantially modify nutrient cycling pathways and carbon storage patterns, particularly in unmanaged

and old-growth forests (Pastore et al., 2020; Harris et al., 2021). As a result, understanding the mechanisms governing carbon persistence and nutrient redistribution in CWD has become increasingly important for predicting forest ecosystem responses to environmental change and for improving ecosystem-based forest management approaches (Lindenmayer et al., 2020).

Despite growing international attention to deadwood ecology, substantial knowledge gaps remain regarding the relationships among decay stage, CWD structure, nutrient dynamics, and adjacent soil properties, especially in temperate broadleaved forests of the Hyrcanian region. Most previous studies in Hyrcanian forests have primarily focused on deadwood quantity, spatial distribution, or structural characteristics (Amanzadeh et al., 2013; Mataji et al., 2014), while comparatively little attention has been paid to biogeochemical interactions between decomposing wood and surrounding soils. Moreover, empirical evidence simultaneously evaluating the effects of decay stage, diameter class, and CWD type (snag versus log) on both wood chemistry and soil properties remains scarce.

The Hyrcanian forests of northern Iran constitute one of the oldest temperate forest ecosystems in the world and are recognized as a global biodiversity hotspot (Sagheb-Talebi et al., 2014). These uneven-aged broadleaved forests are characterized by high structural complexity, substantial deadwood accumulation, and humid environmental conditions that potentially favor active decomposition processes and nutrient turnover. Nevertheless, the ecological role of deadwood in regulating localized carbon and nutrient dynamics within these forests remains insufficiently understood.

Therefore, this study investigated the relationships among CWD decay stage, diameter class, deadwood type, and associated soil physicochemical properties in a natural beech–hornbeam forest of the Hyrcanian region. Specifically, the study aimed to: (i) evaluate how soil properties vary in relation to CWD diameter classes and deadwood type; (ii) compare carbon and nutrient concentrations between CWD and adjacent soils across decay stages; and (iii) identify the main edaphic factors associated with deadwood distribution and decomposition patterns.

We hypothesized that: (1) advanced decay stages would exhibit increased nitrogen accumulation and reduced C/N ratios due to progressive microbial immobilization during decomposition;

(2) medium-diameter CWD would exert the strongest localized effects on soil moisture and nutrient availability because of optimal balance between substrate persistence and decomposer accessibility; and (3) snags and logs would generate distinct biogeochemical microenvironments owing to differences in moisture regime, aeration, and soil contact.

By integrating deadwood characteristics, nutrient dynamics, and soil responses, this study provides new insights into the ecological role of coarse woody debris in regulating carbon and nutrient cycling processes in temperate Hyrcanian forests and contributes to the broader understanding of deadwood-mediated ecosystem functioning in natural forest landscapes.

Materials and methods

Site description

The study was conducted within the Gorazbon district of the Kheyroud Educational and Experimental Forest, located in the Hyrcanian temperate forests of northern Iran, Mazandaran Province, Nowshahr County (36°27'–36°40' N, 51°32'–51°45' E). The Hyrcanian forests represent one of the oldest temperate broadleaved forest ecosystems in the world and are recognized as a global biodiversity hotspot because of their high floristic diversity, structural complexity, and long ecological continuity.

The study area is characterized by humid temperate climatic conditions with mean annual precipitation ranging from approximately 1,600 to 2,200 mm and mean annual temperature between 10 and 16°C. Elevation varies from approximately 1150 to 1350 m above sea level. The topography is mountainous with steep slopes and highly heterogeneous terrain. Soils are predominantly derived from limestone and marl parent materials and are generally classified as forest brown soils with variable texture and drainage conditions.

The over-story vegetation is dominated by oriental beech (*Fagus orientalis* Lipsky) and European hornbeam (*Carpinus betulus* L.), accompanied by several associated broadleaved tree species. The investigated stands are uneven-aged and structurally complex, containing substantial amounts of coarse woody debris (CWD) generated through natural mortality, canopy dynamics, and small-scale disturbances. A total study area of 50 ha was selected to encompass a representative range of deadwood structures, decomposition stages, and microsite conditions within unmanaged and semi-managed forest stands.

Experimental design and coarse woody debris inventory

A complete (100%) inventory of coarse woody debris (CWD), including both standing deadwood (snags) and downed deadwood (logs), was conducted across the entire 50 ha study area. Only CWD originating from oriental beech and European hornbeam with a minimum diameter ≥ 7.5 cm was included in the inventory. This threshold was selected because it represents the lower size limit commonly used to distinguish ecologically functional coarse woody debris from fine woody debris in temperate forest ecosystems.

For standing deadwood (snags), species identity and diameter at breast height (DBH; 1.3 m above ground level) were recorded. For downed deadwood (logs), species identity, total length, and mean diameter were measured. Diameter classes were stratified into small (7.5–32.5 cm), medium (32.5–57.5 cm), and large (> 57.5 cm) categories. These classes were selected to represent ecologically meaningful differences in substrate persistence, moisture retention capacity, and decomposition environment.

The spatial position of each CWD element was determined using the distance–azimuth method. Three fixed reference points located along the forest road network were geo-referenced using a high-precision differential global positioning system (DGPS) receiver. From each reference point, the horizontal distance

and azimuth to individual CWD elements were measured using a laser rangefinder equipped with an electronic compass. Geographic coordinates (latitude and longitude) of each CWD element were subsequently calculated from reference-point coordinates using standard trigonometric relationships. All field measurements were conducted during leaf-off conditions to maximize visibility and minimize measurement uncertainty.

CWD decay status for both snags and logs was classified into six decay classes following the criteria proposed by Christensen and Vesterdal (2003), (Table 1). Classification was based on structural integrity, bark persistence, wood hardness, branch retention, stem shape, and degree of decomposition. Lower decay classes represented recently dead material with relatively intact structural characteristics, whereas higher decay classes represented advanced decomposition stages characterized by substantial softening, fragmentation, and loss of original woody structure.

Table 1
Characteristics of CWDs decay stages (Christensen and Vesterdal 2003)

Decay stages	Bark	Twigs branches	Softness	Surface	Shape
1	intact or missing only in small patches, more than 50%	present	hard or knife penetrate 1–2 mm	covered by bark, outline intact	circle
2	missing or less than 50%	only branches (> 3 cm) present	hard or knife penetrate less than 1 c	smooth, outline intact	circle
3	missing	missing	begin to be soft, knife penetrate 1–5 cm	smooth or crevices present, outline intact	circle
4	missing	missing	soft, knife penetrate more than 5 cm	large crevices, small pieces missing, outline intact	circle or elliptic
5	missing	missing	soft, knife penetrate more than 5 cm	large pieces missing, outline partly deformed	flat elliptic
6	missing	missing	soft, partly reduced to mould, only core of wood	outline hard to define	flat elliptic covered by soil

Species identification and ethical considerations

The investigated species, oriental beech (*Fagus orientalis* Lipsky) and European hornbeam (*Carpinus betulus* L.), were identified in the field by a professional botanist affiliated with the Department of Forestry, University of Tehran. Voucher specimens were deposited in the herbarium of the University of Tehran, Tehran, Iran, under accession numbers 135 (beech) and 141 (hornbeam), respectively, to confirm taxonomic identity and ensure long-term reproducibility of species identification.

All plant material used in this study was collected from Hyrcanian forest ecosystems under permits issued by the relevant Natural Resources authorities prior to fieldwork. Neither investigated species is listed as threatened under the IUCN Red List or included in the CITES appendices. All field activities and sample collection procedures were conducted in full compliance with institutional, national, and international regulations and in accordance with IUCN and CITES guidelines.

Soil sampling and laboratory analyses

Soil samples were collected adjacent to each CWD element at a depth of 0–30 cm, corresponding to the biologically active mineral soil layer where most fine-root activity, microbial processes, and nutrient transformations occur in Hyrcanian forest ecosystems. Sampling was conducted at two distances from each CWD element (0.5 m and 1 m) to capture localized soil responses associated with deadwood influence zones. Subsamples obtained from both distances were homogenized to produce one composite sample per CWD element.

Control soil samples were collected from nearby areas lacking visible coarse woody debris influence while maintaining comparable topographic and vegetation conditions. Soil sampling was stratified according to CWD diameter classes (small, medium, and large) and the six decomposition classes to ensure representation of both structural and decomposition gradients.

All soil samples were transported to the laboratory in sealed polyethylene bags to minimize moisture loss and contamination during transport. In the laboratory, samples were air-dried at room temperature, gently crushed, and passed through a 2-mm sieve to remove coarse fragments, roots, and undecomposed organic residues. Subsamples were subsequently prepared for physicochemical analyses following standard soil analytical protocols.

Soil organic carbon (SOC) was determined using the Walkley–Black wet oxidation method (Walkley and Black 1934), in which oxidizable organic carbon is digested with potassium dichromate ($K_2Cr_2O_7$) and concentrated sulfuric acid followed by titration with ferrous ammonium sulfate. Total nitrogen (TN) was measured using the Kjeldahl digestion method (Jackson 1967). Available phosphorus (P) was extracted using an acid extractant appropriate for acidic forest soils and quantified colorimetrically by the molybdenum blue method. Exchangeable potassium (K) was extracted using neutral ammonium acetate and quantified by flame photometry.

Soil bulk density was determined using the core method. Undisturbed soil cores were collected in the field, oven-dried at 105°C to constant mass, and bulk density was calculated as the ratio of oven-dry

mass to core volume. Soil texture (sand, silt, and clay fractions) was analyzed using the hydrometer method following dispersion with sodium hexametaphosphate.

Gravimetric soil moisture content was determined by oven drying fresh soil at 105°C for 24 h and expressing moisture content as percentage mass loss relative to oven-dry weight. This measurement provided an estimate of localized soil water conditions associated with different deadwood structures and decomposition stages.

All laboratory analyses included analytical blanks, calibration standards, and replicate measurements for quality assurance and quality control (QA/QC). Final values are reported on an oven-dry soil basis.

Coarse woody debris sampling and chemical analyses

Wood samples were collected from representative portions of each snag and log to quantify nutrient concentrations in coarse woody debris. For downed logs, samples were obtained from the stump and terminal sections to capture representative decomposition characteristics along the stem profile. Sampling was stratified according to both diameter class and decay class to encompass structural and decomposition variability.

For each decay class, four beech and four hornbeam samples were collected whenever available. Hornbeam material was absent from decay class I, resulting in a total of 60 CWD samples across all species and decomposition classes.

Immediately after collection, wood samples were sealed in polyethylene bags to minimize contamination and moisture loss during transport. In the laboratory, samples were air-dried at room temperature and mechanically ground into a fine homogeneous powder suitable for elemental analyses.

Carbon (C) and nitrogen (N) concentrations were quantified by dry combustion using a CHN elemental analyzer following standard analytical protocols. Phosphorus (P) concentrations were determined after wet digestion using concentrated sulfuric acid and hydrogen peroxide followed by colorimetric analysis with the molybdenum blue method. Potassium (K) concentrations were quantified after nitric acid digestion using flame photometry or atomic absorption spectrophotometry.

All analyses were performed in triplicate to ensure analytical precision and reproducibility. Laboratory blanks, calibration standards, and replicated reference materials were included within each analytical batch for quality control. Final nutrient concentrations are expressed on a dry-mass basis.

Statistical analyses

All statistical analyses were performed in R version 4.3.1 (R Core Team, 2024) and PC-ORD version 7. Prior to analysis, all variables were evaluated for normality and homogeneity of variance using the

Shapiro–Wilk test, Levene’s test, quantile–quantile plots, and residual diagnostics. Variables failing to satisfy parametric assumptions were log- or square-root transformed when appropriate.

Differences in soil physicochemical properties among CWD diameter classes, decay classes, deadwood types (snag versus log), and species were analyzed using linear mixed-effects models (LMMs). Diameter class, decay class, deadwood type, and species identity were treated as fixed effects, while sampling unit was treated as a random effect to account for hierarchical dependence and localized spatial variability.

Post hoc pairwise comparisons among factor levels were conducted using Tukey-adjusted estimated marginal means. Effect sizes were quantified using partial eta squared (η^2) to evaluate the relative contribution of explanatory variables to observed variation.

Paired comparisons between CWD-associated soils and corresponding control soils were evaluated using paired t-tests. Relationships between nutrient concentrations in CWD and adjacent soils were further examined using linear regression analyses with 95% confidence intervals.

To explore multivariate relationships among soil properties, deadwood characteristics, and decomposition gradients, principal component analysis (PCA) was performed using centered and standardized environmental variables. Environmental vectors were fitted to the ordination space to identify the principal soil variables associated with CWD distribution patterns and decomposition status. Variance inflation factors (VIFs) were evaluated prior to ordination analyses to minimize multicollinearity among explanatory variables.

All statistical tests were evaluated at a significance level of $p < 0.05$. Unless otherwise stated, results are presented as mean $\pm$ standard error (SE).

Results

The structural attributes of coarse woody debris differed substantially between snag and log components and among tree species. Downed logs contributed a greater proportion of total deadwood volume than standing snags in both beech and hornbeam stands, whereas snag density was generally higher than log density. Violin-boxplot distributions further demonstrated significant differences in deadwood structure between deadwood types, particularly in beech stands where logs exhibited substantially greater volume accumulation.

The distribution of deadwood across decay classes indicated that intermediate and advanced decay stages represented the dominant components of the deadwood pool. Logs exhibited a greater proportion of advanced decay classes relative to snags, suggesting longer persistence and prolonged decomposition trajectories after stem collapse. In contrast, snag components were more strongly represented in earlier decay stages, reflecting standing persistence prior to structural breakdown (Fig. 2).

The heatmap revealed clear decomposition-mediated shifts in nutrient concentrations within both deadwood and adjacent soils. Carbon concentrations generally declined with increasing decay stage in CWD, whereas nitrogen concentrations progressively increased, particularly in intermediate and advanced decay classes. Consequently, C/N ratios consistently decreased along the decomposition gradient, indicating progressive biochemical transformation of woody tissues during decay.

Nutrient responses also varied among diameter classes. Medium- and large-diameter deadwood exhibited stronger nitrogen enrichment and lower C/N ratios than smaller debris, suggesting enhanced microbial immobilization and prolonged nutrient retention within larger substrates. Adjacent soils similarly showed elevated nitrogen concentrations and moisture-associated nutrient accumulation near advanced decay classes.

Phosphorus and potassium displayed more variable patterns across decomposition stages, although localized enrichment was frequently associated with intermediate and advanced decay classes. Species-specific differences were comparatively smaller than the effects of decay stage and deadwood structure, emphasizing the dominant role of decomposition status in regulating nutrient redistribution (Fig. 3).

Regression analyses demonstrated significant positive relationships between nutrient concentrations in coarse woody debris and adjacent soils for nitrogen, phosphorus, potassium, and carbon. Nitrogen and potassium exhibited the strongest coupling patterns, indicating active nutrient exchange and localized enrichment processes associated with deadwood decomposition.

The positive relationships observed between CWD and soil nutrient concentrations suggest that decomposing wood functions as an important source of nutrient redistribution within the forest floor environment. Stronger nutrient coupling in advanced decay stages likely reflects intensified microbial activity, enhanced fungal colonization, and increased transfer of dissolved organic compounds from decomposing wood into surrounding soils.

Differences between snag and log regression trajectories further indicate that deadwood structural type influences nutrient transfer pathways. Logs generally exhibited stronger nutrient–soil coupling than snags, likely because of direct contact with the mineral soil and greater moisture retention capacity (Fig. 4).

The principal component analysis explained a substantial proportion of the total environmental variation associated with coarse woody debris decomposition and soil properties. PC1 primarily represented a gradient associated with nutrient-rich, moist soil conditions and was positively correlated with soil nitrogen, potassium, moisture content, and bulk density. In contrast, negative PC1 scores were associated with coarser soil texture and lower nutrient availability.

Distinct clustering patterns were observed among deadwood types and species. Beech logs were primarily associated with nutrient-rich and moisture-dominated environments, whereas hornbeam snags were more strongly associated with lower nutrient conditions and greater electrical conductivity. These

patterns indicate that both species identity and deadwood structure influence localized decomposition environments.

The ordination further demonstrated that advanced decay stages were associated with elevated soil moisture and nutrient concentrations, supporting the hypothesis that decomposition intensity strongly regulates localized biogeochemical conditions. The strong alignment of environmental vectors with decomposition-related clusters suggests that moisture availability and soil nutrient status represent key controls over deadwood-mediated ecosystem processes in Hyrcanian forests (Fig. 5).

The structural equation model revealed that decay stage exerted strong positive effects on wood moisture content, microbial activity, decomposition rate, and nitrogen accumulation within coarse woody debris. Increased decomposition intensity subsequently reduced C/N ratios in deadwood while enhancing nutrient availability in adjacent soils.

Nitrogen accumulation within decomposing wood showed one of the strongest positive effects on soil nutrient availability, indicating that microbial immobilization and nutrient retention within CWD play important roles in regulating localized nutrient enrichment processes. Soil nutrient availability further contributed positively to carbon stabilization and ecosystem resilience, highlighting the broader ecological significance of deadwood-mediated nutrient dynamics.

Diameter class and deadwood type exerted additional indirect effects on decomposition pathways through their influence on moisture retention and aeration conditions. Logs generally promoted stronger soil nutrient responses than snags because of greater stem–soil contact and enhanced moisture exchange.

Discussion

The patterns observed in this study are broadly consistent with previous investigations conducted in temperate and boreal forests, while also revealing several region-specific characteristics of Hyrcanian forest ecosystems. In particular, the strong influence of decay stage and deadwood structure on localized nutrient dynamics supports the growing consensus that coarse woody debris functions as a key regulator of spatial biogeochemical heterogeneity in forest ecosystems.

The relatively greater contribution of logs to total deadwood volume compared with snags agrees with findings from unmanaged European beech forests and old-growth temperate ecosystems, where fallen deadwood often dominates long-term carbon storage because of prolonged decomposition trajectories and greater physical persistence (Christensen & Vesterdal, 2003; Russell et al., 2015). Similar patterns were reported by Sagheb-Talebi and Schütz (2002) and Amanzadeh et al. (2013) in unmanaged Hyrcanian forests, suggesting that humid temperate conditions favor the accumulation and gradual decomposition of large downed stems. However, total deadwood volumes observed in the present study were lower than those reported from some Central European old-growth forests, which may reflect differences in forest productivity, disturbance history, and climatic controls on decomposition rates.

The pronounced effects of medium-diameter CWD on soil moisture and nitrogen concentration are consistent with observations by Spears and Lajtha (2004), Kim et al. (2017), and Fukasawa et al. (2021), who reported enhanced microbial activity and nutrient availability in soils associated with intermediate-sized decomposing wood. These studies proposed that medium-sized debris may provide optimal conditions for fungal colonization and moisture retention because of favorable surface-area-to-volume relationships. Our findings support this interpretation and further suggest that such effects may be particularly important in humid Hyrcanian forests, where moisture availability strongly regulates decomposition processes.

In contrast, some studies from colder boreal ecosystems have reported stronger nutrient accumulation in larger diameter deadwood because of slower decomposition and prolonged nutrient retention (Köster et al., 2015; Olajuyigbe et al., 2011). The discrepancy between those findings and the present results may reflect climatic differences influencing microbial activity and wood decay kinetics. Under humid temperate conditions, intermediate-sized deadwood may decompose rapidly enough to stimulate nutrient transfer while still persisting sufficiently long to maintain localized soil effects. This highlights the context dependency of deadwood-mediated nutrient dynamics and suggests that relationships between wood size and ecosystem functioning may vary substantially across climatic gradients.

The observed differences between snags and logs also align with previous studies demonstrating that standing and downed deadwood follow distinct decomposition pathways. Angers et al. (2010) and Heilmann-Clausen et al. (2021) emphasized that differences in aeration, moisture exposure, and stem-soil contact can produce contrasting fungal communities and nutrient dynamics between deadwood types. In the present study, stronger effects of logs on soil moisture and nutrient concentrations likely resulted from their direct contact with mineral soil and greater capacity to transfer dissolved organic compounds into adjacent substrates. Comparable findings were reported by Spears et al. (2003) and Holub et al. (2001), who observed enhanced nitrogen and potassium enrichment in soils beneath decomposing logs.

Nitrogen enrichment in advanced decay stages observed in this study strongly agrees with the decomposition trajectories described by Berg and McClaugherty (2020) and Kahl et al. (2017). Increasing nitrogen concentrations and declining C/N ratios during decomposition have been widely attributed to microbial immobilization, fungal biomass accumulation, and preferential carbon loss through respiration. Similar patterns have been documented in temperate forests of Europe, North America, and East Asia (Noh et al., 2017; Klockow et al., 2014), indicating that nitrogen accumulation during advanced decomposition may represent a relatively universal feature of deadwood biogeochemistry.

However, the persistence of relatively high nitrogen concentrations within advanced decay classes in the Hyrcanian forests may also reflect the humid climatic conditions and high microbial activity characteristic of this region. Fukasawa et al. (2021) suggested that moisture-rich environments can accelerate fungal colonization and nutrient immobilization processes, thereby intensifying nitrogen

retention within decomposing wood. Consequently, the observed nutrient patterns may indicate that Hyrcanian forests possess particularly active wood-decay dynamics relative to drier temperate ecosystems.

The contrasting trajectories between deadwood and soil C/N ratios observed in this study are also comparable to results reported by Prescott (2010) and Bradford et al. (2022), who argued that nutrient transfer from deadwood to mineral soil is typically gradual and asynchronous. Rather than acting as an immediate nutrient source, decomposing wood may initially function as a transient nutrient sink in which nutrients are retained within microbial biomass before eventual release to surrounding soils. This delayed transfer mechanism may explain why adjacent soils exhibited increasing C/N ratios despite progressive nitrogen enrichment within the deadwood itself.

The multivariate relationships identified through principal component analysis further support findings from previous studies emphasizing the importance of edaphic conditions in regulating decomposition. Soil moisture and bulk density have consistently been identified as major drivers of microbial respiration and wood decay rates across temperate ecosystems (Herrmann & Bauhus, 2013; Bradford et al., 2022). Similarly, Fierer et al. (2001) and Bantle et al. (2014) demonstrated that soil texture and nutrient availability can substantially influence microbial processing of woody substrates. The strong correlations observed in the present study therefore reinforce the concept that decomposition dynamics emerge from interactions between intrinsic wood properties and surrounding environmental conditions.

From a broader ecological perspective, the findings of this study support the growing body of evidence that deadwood contributes to forest resilience through slow but persistent regulation of carbon and nutrient cycling. Similar conclusions were reached by Thom and Seidl (2016) and Lindenmayer et al. (2020), who argued that structurally diverse deadwood pools enhance ecological stability, biodiversity conservation, and long-term ecosystem functioning under increasing climatic stress. In this context, the present study extends previous knowledge by providing rare empirical evidence from Hyrcanian temperate forests, a globally important but comparatively understudied forest ecosystem.

Overall, comparison with previous studies indicates that many of the decomposition-mediated nutrient processes observed in Hyrcanian forests are consistent with broader ecological patterns reported worldwide. Nevertheless, the magnitude and spatial expression of these effects appear strongly influenced by the humid temperate conditions, structural complexity, and decomposition environment characteristic of the Hyrcanian region. These findings therefore emphasize both the generality and ecosystem-specificity of deadwood-mediated biogeochemical processes in natural forests.

Declarations

Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Funding

This research was supported by Islamic Azad University. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Author Contributions

First Author: Conceptualization, Methodology, Field data collection, Formal analysis, Writing - Original draft preparation.

Data Availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. The raw data (Excel files) and R scripts used for statistical analysis can be accessed upon request.

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Figures

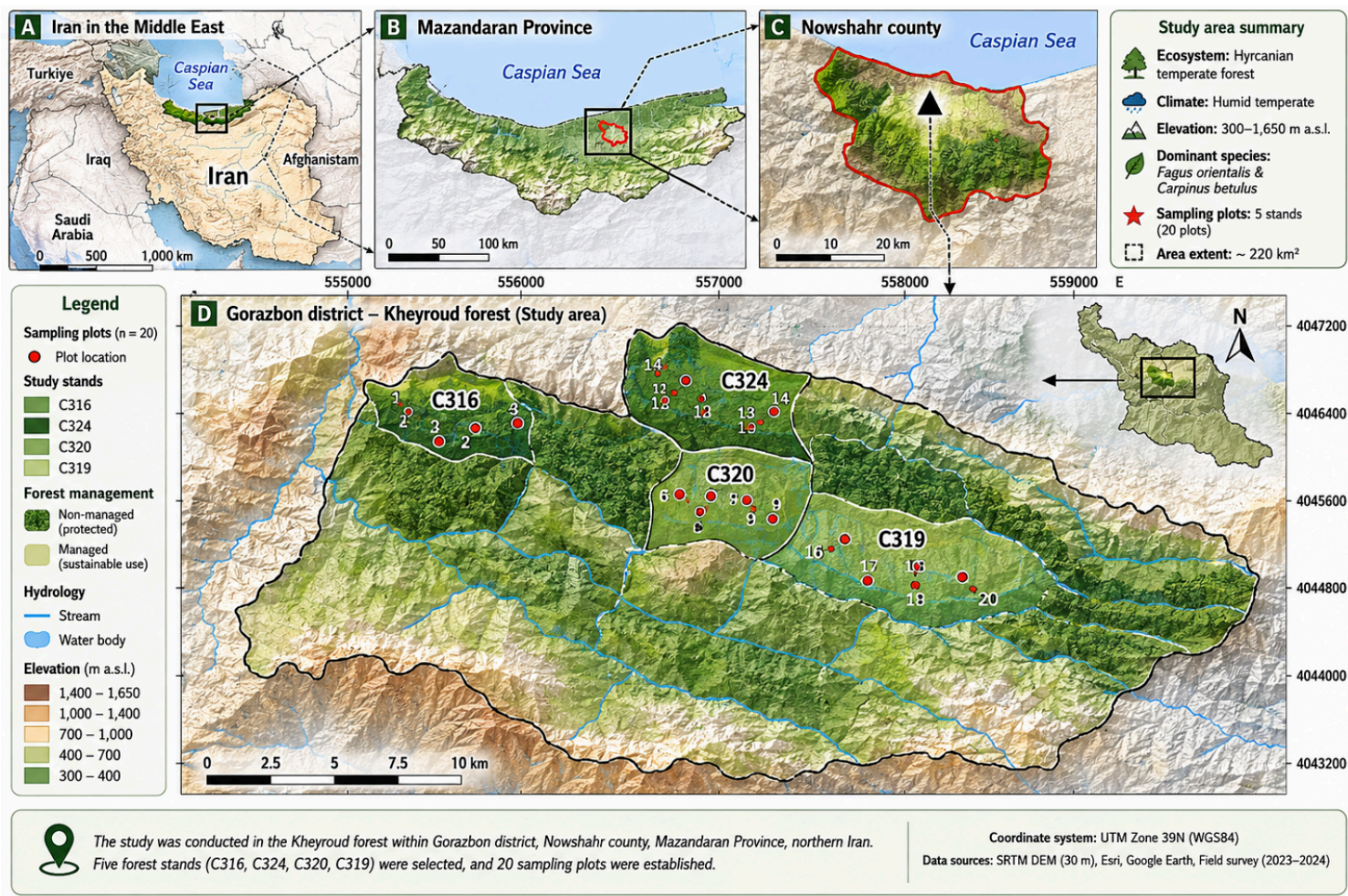


Figure 1

Location of the Kheyroud Educational-Research Forest

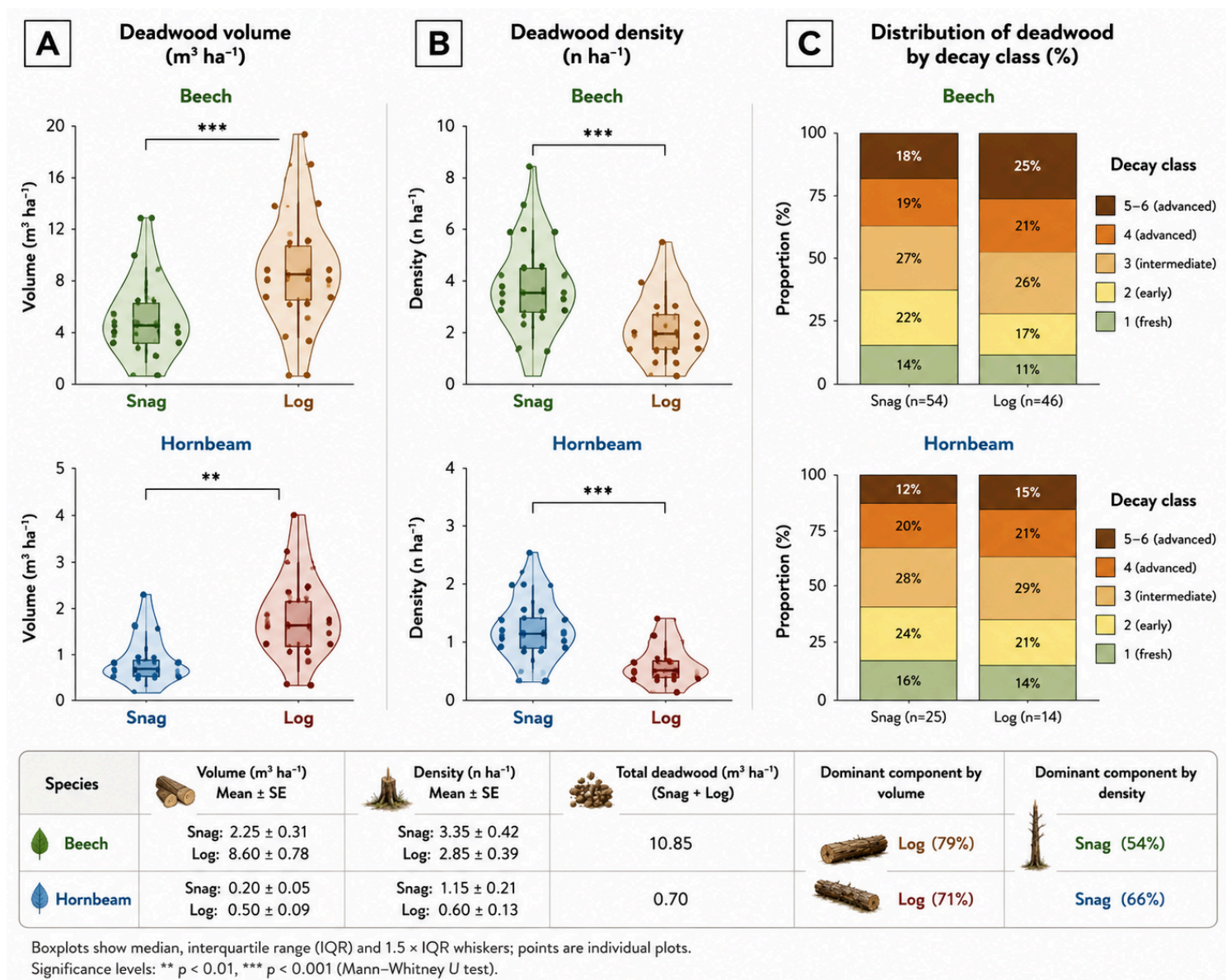


Figure 2

Structural characteristics, density, and decay-class distribution of coarse woody debris in Hyrcanian forests.

Nutrient dynamics in coarse woody debris (CWD) and adjacent soil across decay and diameter classes



Values are means for each combination of diameter class and decay class. CWD: coarse woody debris; Inter.: intermediate; Adv.: advanced.

Figure 3

Heatmap of nutrient dynamics in coarse woody debris (CWD) and adjacent soils across decay and diameter classes.

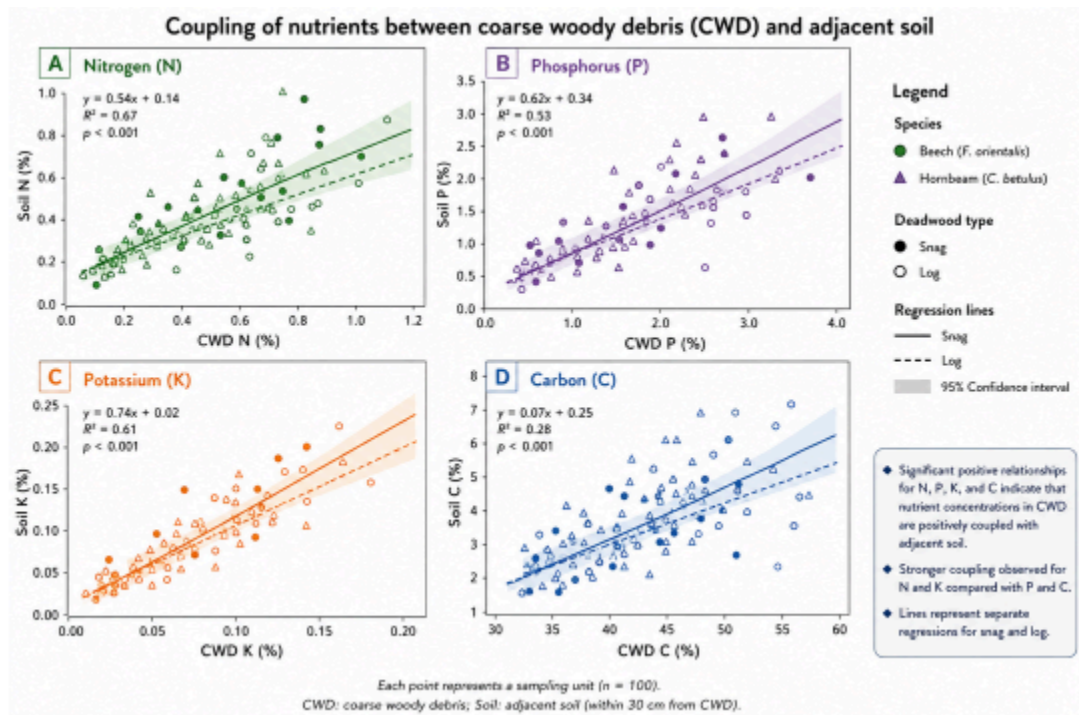


Figure 4

Relationships between nutrient concentrations in coarse woody debris (CWD) and adjacent soils.

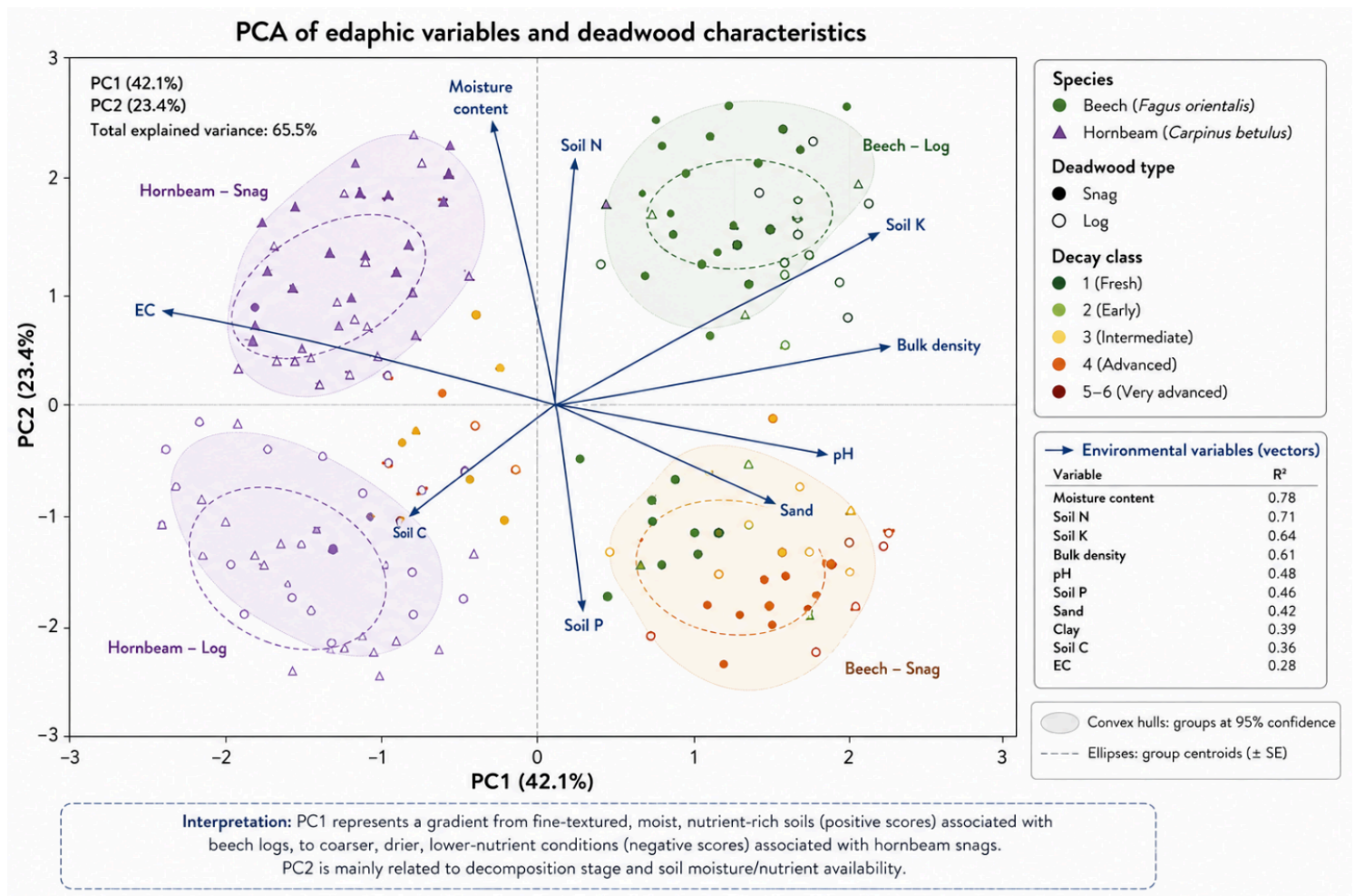


Figure 5

Principal component analysis (PCA) of edaphic variables and deadwood characteristics.

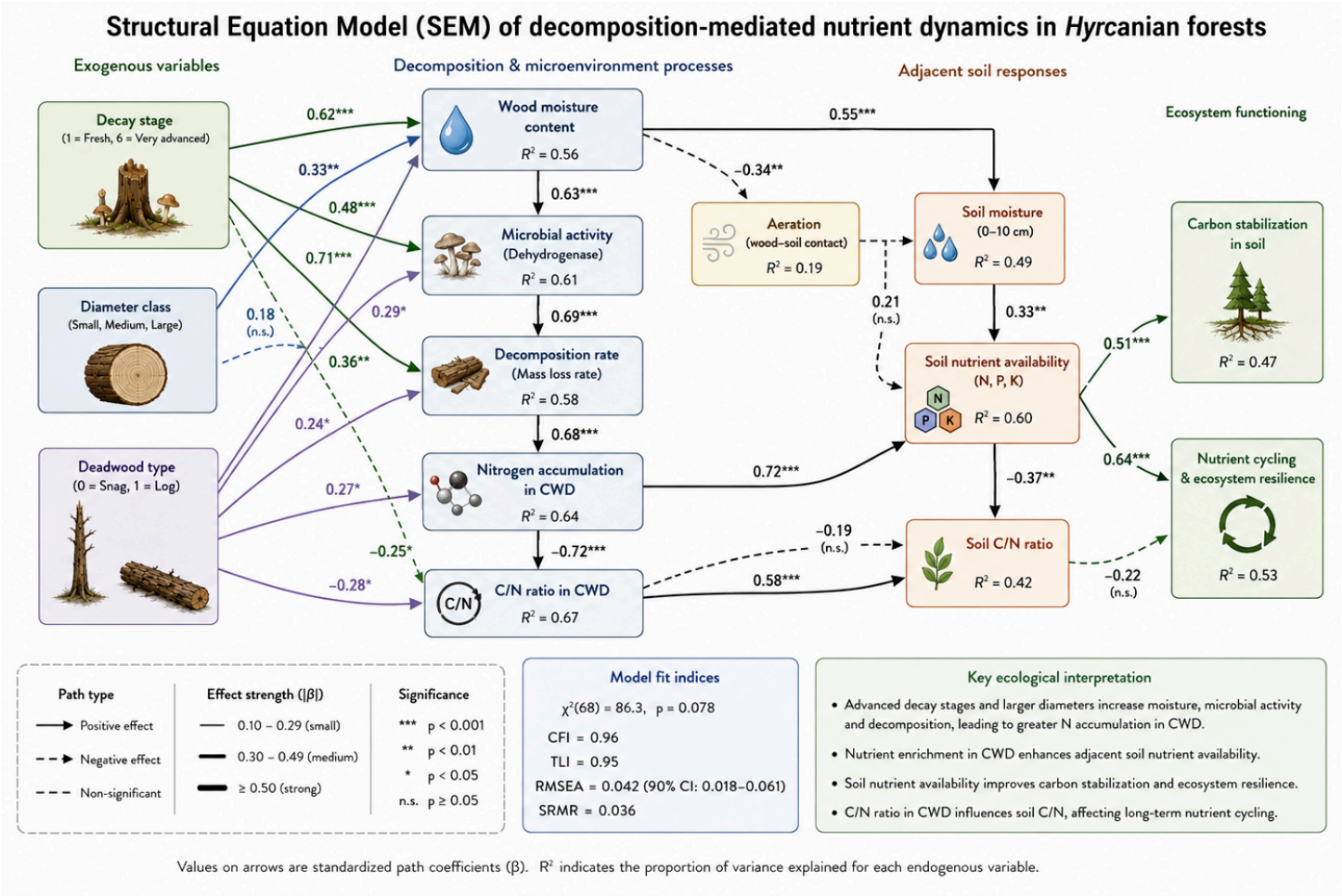


Figure 6

Structural equation model (SEM) illustrating the direct and indirect pathways linking deadwood characteristics, decomposition processes, nutrient dynamics, and ecosystem functioning.