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Biodiversity and Management as Central Players in the Network of Relationships Underlying Forest Resilience

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ABSTRACT

Global change is threatening the integrity of forest ecosystems worldwide, amplifying the need for resilience-based management to ensure their conservation and sustain the services they provide. Yet, current efforts are still limited by the lack of implementation of clear frameworks for operationalizing resilience in decision-making processes. To overcome this limitation, we aim to identify reliable and effective drivers of forest resilience, considering their synergies and trade-offs. From a comprehensive review of 342 scientific articles addressing resilience in forests globally, we identified factors shaping forest resilience. We recognized them into two categories that influence forest responses to disturbances: resilience predictors, which can be modified through management, and codrivers, which are measurable but largely unmanageable (e.g., climate). We then performed network analyses based on predictors and codrivers underlying forest resilience. In total, we recognized 5332 such relationships linking predictors or codrivers with forest attributes resilience. Our findings support the central role of biodiversity, with mixed, non-planted, or functionally diverse forests promoting resilience across all contexts and biomes. While management also enhanced resilience, the success of specific interventions was highly context-dependent, suggesting that its application requires a careful analysis of trade-offs. Specifically, practices like cutting and prescribed burning generally enhanced resilience in terms of tree growth, plant diversity, landscape vegetation cover, and stand structure. In contrast, pest and herbivore control reduced the resilience of plant taxonomic diversity while offering only minimal gains for other variables. Even long-term restoration projects showed clear trade-offs in the resilience of different forest attributes, highlighting the need for careful consideration of these effects in practical management decisions. Overall, we emphasize that a reduced number of predictors can be used to effectively promote forest resilience across most attributes. Particularly, enhancing biodiversity and implementing targeted management strategies when biodiversity is impoverished emerge as powerful tools to promote forest resilience.

1 | Introduction

Forests cover about 30% of the Earth's land surface and play a crucial role in ensuring human well-being by providing a wide variety of ecosystem services, including climate and water regulation, wood provisioning, and recreational and cultural use (Thompson et al. 2011; Felipe-Lucía et al. 2018). Therefore, the potential ability of forests to cope with the threats associated with a changing climate (Dale et al. 2001; Canadell and Raupach 2008; Senf and Seidl 2021; Forzieri et al. 2022) is mobilizing the interest of academics, managers, and policymakers (Millar and Stephenson 2015; McDowell et al. 2020; Nikinmaa et al. 2020). The resilience concept, understood here broadly as the ability of a system to absorb or withstand disturbance impacts (Holling 1973), offers a well-recognized basis for assessing forest responses to global change and incorporating them in forest management and decision-making (Suding and Hobbs 2009; Dudney et al. 2018; Elmqvist et al. 2019; Grafton et al. 2019; Girardin et al. 2021). However, resilience is a somewhat puzzling concept often lacking a clear framework for operational implementation (Pimm et al. 2019; Lloret et al. 2024). This is due to the variety of resilience conceptualizations—from the ability of a system to recover after disturbance to the capacity to maintain a dynamic equilibrium state and avoid shifting to alternative states–, the scale of application—from individuals to forest stands, landscapes, or entire social-ecological systems, and the multiplicity of approaches to measure it (Scheffer et al. 2001; Walker et al. 2004; Folke 2006; Brand and Jax 2007; Moser et al. 2019; Van Meerbeek et al. 2021). Since resilience is not an inherent fixed property but an emerging and dynamic feature of ecosystems, implementing management actions that restore connectivity, promote biodiversity, or alleviate pressures on key species and interactions can play a crucial role in shaping forest resilience (Messier et al. 2019; Anderson et al. 2023). By targeting specific drivers of forest resilience, management can proactively reinforce the adaptive capacity of ecosystems, improving their ability to withstand and recover from pressures related to climate change, pest outbreaks, and land-use changes, while fostering long-term forest sustainability (Lloret et al. 2024).

To operationalize resilience-based management, it is necessary to identify, at a given spatiotemporal scale, resilience drivers that could be manipulated (i.e., *resilience predictors*, hereafter) for maintaining a set of relevant forest attributes (i.e., *system variables*, hereafter) within a range that defines a reference state (Carpenter et al. 2001; Lloret et al. 2024). Moreover, there may also exist a set of hardly manageable factors determining resilience (i.e., *codrivers*, hereafter). These codrivers provide the context in which resilience operates and inform on factors that determine exposure to hazards and intrinsic sensitivity to them (e.g., geographical location and climatic conditions). Conversely, resilience predictors will allow us to actively promote forest resilience through policy and management actions, such as selecting silvicultural practices, land use planning, or favoring key elements of the forest-related value chain (Standish et al. 2014; Lloret et al. 2024). Resilience predictors and codrivers may affect different system variables, determining trade-offs or, alternatively, defining bundles of predictors that may consistently affect bundles of system variables, thus facilitating synergistic actions. These bundles of predictors or system variables are akin to the concept of ecosystem services bundles, which are essential for effective forest management (Spake et al. 2017). Thus, identifying the existence and generality of potential modules within the complex network of relationships between system variable responses, resilience predictors, and codrivers will contribute to operationalizing forest resilience (Messier et al. 2019). Ultimately, identifying these modules will foster better-informed strategies for conserving and enhancing forest resilience and functioning while also unveiling the potential existence of trade-offs and synergies. In this context, network analysis offers a promising approach by detecting clusters of strongly interconnected nodes (Rosvall and Bergstrom 2008), i.e., key drivers (predictors and codrivers) of the system behavior. This analysis is particularly valuable for operationalizing resilience, as it reveals the connectivity and compartmentalization of the system components, providing insights into how disturbances can be buffered. For instance, by limiting the spread of their impact to the whole system and thereby preserving overall system resilience (Messier et al. 2013; Gao et al. 2016).

Here, we applied network modularity analysis (Rosvall and Bergstrom 2008) to assess the existence of modules and pinpoint which bundles of resilience predictors or codrivers have a more consistent tendency to influence the resilience of certain bundles of system variables (i.e., modules), considering the spatiotemporal scale at which these relationships occur (see Tables S1–S3). This network assessment enables addressing the resilience of specific system variables while keeping a more comprehensive perspective of the resilience of the whole system. Therefore, this approach scales up the focus from deterministic methods that target specific predictors and system variables to more integrative and holistic strategies that consider the resilience of the entire forest ecosystem. To understand the key factors shaping forest resilience, we built networks to identify the resilience predictors and codrivers that could exert the most consistent effect on forest resilience (i.e., highest centrality), considering the evidence supporting their impact on system variables (i.e., weighted degree) (Janssen et al. 2006). We mainly focused on those resilience predictors which potentially can be managed to promote resilience, together with those codrivers which tend to threaten resilience. Specifically, we explored how the modular structure of resilience drivers is organized, the extent to which resilience predictors and codrivers are spatiotemporally coupled, and the role of biodiversity and active management in enhancing resilience. To that end, we examined a total of 5332 relationships between resilience predictors or codrivers and system variables, derived from a comprehensive review of 342 articles covering forests worldwide. Recognizing potential biases due to variations in study approaches, we thoroughly reviewed each article and consistently applied the operational resilience framework proposed by Lloret et al. (2024) to ensure a uniform interpretation of resilience across sources.

2 | Materials and Methods

2.1 | Literature Search and Data Categorization

We conducted a systematic literature review focused on forest resilience following the PRISMA guidelines (Page et al. 2021). Our search was performed in the Scopus database (Relx Group 2018) using the search string TITLE–ABSTRACT–KEYWORDS (“resilience” AND “forest”) ALL (“measur*” OR “manag*”) PUBYEAR > 1999. We included studies published between 2000 and February 2nd, 2022, yielding an initial dataset of 5035 articles in total. Following PRISMA's systematic screening approach and adapting the methodology of Nikinmaa et al. (2020), we applied a two-step selection process. In the first step, we screened abstracts to retain articles that met the following inclusion criteria: (1) publication in a peer-reviewed scientific journal written in English, (2) inclusion of the word “resilience” in conjunction with an active verb, and (3) focus on forest-related systems, natural resource management, landscape management, or non-specified ecosystems that could also be applicable to forests. After the first screening, 3728 records were excluded. In the second step, we conducted a full-text review of the 1307 selected articles, applying additional criteria: (4) the study provided a clear definition of resilience, (5) the assessment of resilience had an ecological focus, excluding purely sociological studies, and (6) the study applied a qualitative or quantitative method to assess resilience. After applying these criteria, a final set of 342 articles was retained for data extraction and analysis (Hurtado et al. 2025).

Given our aim to provide a general overview of the most promising resilience predictors and contextual factors to guide decision-making for promoting forest resilience, we included studies that addressed resilience regardless of the specific metric used. In our effort to synthesize and integrate insights from existing literature, we systematically applied the operational resilience framework proposed by Lloret et al. (2024) across each selected study (Hurtado et al. 2025). Recognizing that resilience interpretations can differ across sources, we mitigated this variability by thoroughly analyzing each article and consistently applying the operational resilience framework-ORF based on each study's design and findings, thus extracting information about six key concepts (Lloret et al. 2024). Rooted on the “resilience of what to what” approach (Carpenter et al. 2001), we first identified *system variables* that describe specific characteristics of the system, which respond to disturbances or stressors and whose resilience is analyzed in relation to values characterizing a *reference state* representing pre-disturbed, undisturbed, or desired conditions. We identified a total of 16 categories for system variables encompassing diverse attributes such as aesthetic/recreational services, biogeochemical cycles, soil enzymatic activity, landscape vegetation cover, dominant vegetation type, plant taxonomic diversity, plant functional diversity, non-plant taxonomic diversity, non-plant functional diversity, stand structure, canopy characteristics, height, stand biomass, stand primary production, demographic rates, and tree growth (see Table S1 for a full description).

Then, we searched for reliable factors that exert a significant effect on the resilience of particular system variables to specific disturbances within a given context. In this regard, we distinguished between two types of factors: (1) *resilience predictors* (*RP*) that are factors that have an effect on system resilience and can be modified through management actions (Table S2), and (2) *codrivers* (*CD*) that are measurable variables that influence the response of the system to disturbances but are hardly manageable to promote resilience at the spatiotemporal scale at which resilience is assessed (e.g., climate) (Table S3) (Lloret et al. 2024). The resilience predictors and codrivers identified from the selected articles were classified into two hierarchical levels: a broader, general categorization and a more detailed classification. The general categorization encompassed six resilience predictors (i.e., biodiversity, tree species identity, biotic pressure, forest structure, active management, and silvicultural regime) and six codriver categories (i.e., geographical features, climate, ecosystem characteristics, soil, disturbance severity, and disturbance regime). The detailed classification included 22 resilience predictors and 20 codrivers established within the aforementioned broad categories (Tables S2 and S3). For each resilience predictor and codriver identified at both levels of detail, we gathered information about their significant effects on the resilience of specific system variables and whether this effect promoted (i.e., positive effect) or threatened resilience (i.e., negative effect).

Recognizing that resilience is a concept that requires explicit consideration of the spatiotemporal extent at which recovery from disturbances occurs or system properties persist in the face of stressors (Standish et al. 2014; Lloret et al. 2024), we identified the relevant *spatial* and *temporal scales* that reflect where and when resilience operates in each study. Specifically, spatial and temporal scales were defined based on the extent and resolution of data reported in the selected studies. We categorized spatial scales into six levels according to Pearson and Dawson (2003): site (10–1000 m), local (1–10 km), landscape (10–200 km), regional (200–2000 km), continental (2000–10,000 km), and global (> 10,000 km). For the temporal scale, we used five categories including days, months, years, decades, and centuries. The choice of scales ensured alignment with the main ecological processes governing resilience, such as spatial connectivity among forest patches or recovery times following disturbances.

Finally, to assess potential variations and commonalities of the relationships between system variables with resilience predictors and codrivers across biomes worldwide, we also gathered information about the specific biome evaluated in each study (i.e., boreal, Mediterranean, temperate, and tropical/subtropical).

2.2 | Network Analysis

2.2.1 | Identifying Modular Patterns in Forest Resilience Networks

To identify the main factors that influence forest resilience, we first characterized bundles of system variables whose resilience is preferentially affected by the same resilience predictors or codrivers (i.e., modules). Running the Infomap algorithm 1000 times (Rosvall and Bergstrom 2008), we identified modules within networks linking system variables to resilience predictors (or codrivers). These networks encompassed all system variables together with resilience predictors or codrivers, regardless of the biome. Since we were interested in assessing the resilience predictors able to promote resilience (i.e., positive effects) and the codrivers that shape the context where the resilience of system variables is most threatened (i.e., negative effects), we constructed two separate networks. The first network corresponded to links between system variables and resilience predictors which were identified as statistically significant in the respective studies (with 1018 significant relationships out of 2433 total relationships evaluated in 275 papers). The second network related system variables and codrivers reported as statistically significant in the respective studies (with 1122 significant relationships out of 2914 total relationships evaluated in 288 papers). To ensure the robustness of our main findings regardless of how resilience predictors and codrivers were categorized, we applied the same approach to construct networks using both broad and detailed categorizations.

Since the consistency of relationships between system variables and resilience predictors or codrivers in each study can vary depending on the specific system studied, a semi-quantitative approach is expected to be more suitable when working with a wide range of diverse sources. Thus, the strength of the links between system variables and resilience predictors or codrivers were weighted as: $strength = \frac{(a-b)*(a+b)}{c} = \frac{a^2-b^2}{c}$, where a = number of times that the resilience predictor or codriver had a significant positive effect on the resilience of the system variable (i.e., resilience promotion), b = number of times that had a significant negative effect (i.e., resilience reduction), c = total number of times that this relationship has been evaluated without finding a significant effect on resilience. When dealing with categorical resilience predictors or codrivers, we considered the category that most frequently promoted system resilience as having a positive effect (see Tables S2 and S3). Therefore, the weighted links used for computing the networks provided information about the resilience predictors or codrivers that significantly influenced the resilience of system variables. Higher strengths indicate both higher consistency in significant effects on forest resilience and higher credibility, as they are supported by a greater number of studies proving this effect. Using the resulting weighted relationships, we built four networks: two based on the broad categorization and two on the detailed categorization of resilience predictors and codrivers. We also used the positive subnetwork for resilience predictors-system variables and the negative subnetwork for codrivers-system variables since we aimed to assess the modular structure of resilience predictors that promoted system variables' resilience and the modular structure of codrivers that threatened system variables' resilience, respectively.

Based on the resulting networks, we calculated a centrality index (i.e., importance of the effect) for each system variable, resilience predictor, and codriver. Specifically, we computed the weighted degree by summing the strengths of all links that a given resilience predictor or codriver has with the different system variables it affects. To this end, we used the *bipartite* function (Dormann et al. 2008) in R software version 4.3.1.

Finally, we conducted additional biome-specific network analyses to identify context-dependent predictors and codrivers that influence forest resilience across boreal, Mediterranean, temperate, and tropical/subtropical biomes. The number of papers included for these networks ranged from 32 to 153 (boreal = 32 papers, Mediterranean = 79 papers, temperate = 153 papers, tropical/subtropical = 57 papers). We built networks by subsetting the entire database for each biome, using both the general and detailed categorization of resilience predictors and codrivers. In each case, we built the positive subnetworks for resilience predictors-system variables relationships and the negative subnetworks for codrivers-system variables relationships. In this way, we generated four networks per categorization level relating system variables and resilience predictors (boreal: 66 significant relationships out of 157 total relationships evaluated; Mediterranean: 232 significant relationships out of 472 total relationships; temperate: 486 significant relationships out of 1191 total relationships; tropical/subtropical: 115 significant relationships out of 328 total relationships), as well as four networks per categorization level relating system variables and codrivers (boreal: 81 significant relationships out of 184 total relationships evaluated; Mediterranean: 329 significant relationships out of 760 total relationships; temperate: 441 significant relationships out of 1066 total relationships; tropical/subtropical: 93 significant relationships out of 375 total relationships).

2.2.2 | Combining Positive and Negative Effects in Forest Resilience Networks

To evaluate potential trade-offs and cascading effects of each resilience predictor, we further identified modules within the negative subnetwork of resilience predictors-system variables. We followed the same approach as for the positive subnetwork, for both the broad and detailed categorizations of resilience predictors (see "Identifying modular patterns in forest resilience networks"). Then, we assessed the existence of both positive (i.e., resilience promotion) and negative (i.e., resilience reduction) effects of resilience predictors on the resilience of different system variables, as well as the resulting balance. Additionally, using the detailed categorization of resilience predictors, we assessed those system variables that, while influenced by certain predictors, also act as predictors for the resilience of other variables. These assessments provide information about how the effects of a predictor can expand through the network, beyond the simple directional effects on particular variables (hereafter, cascading effects).

2.2.3 | Assessing Resilience-Based Management Practices

Since active management emerged as the resilience predictor with the highest weighted degree (see Results section), we sought to assess the impact of specific management practices on forest resilience. Thus, we repeated the same network analysis detailed in the previous subsection, focusing only on the relationships between active management and system variables, using a more detailed categorization of management practices (147 significant relationships out of 243 total relationships evaluated in 55 papers). To that end, we classified active management into seven categories: prescribed burning, cutting (i.e., group selection harvest, cut-and-burn, cut-and-leave, shelterwood, clearcutting, harvesting, shrub clearing, biomass reduction), fertilization/liming, biotic control (i.e., pests and herbivores control), implementation of restoration projects (including planting), and water regulation.

3 | Results

3.1 | Modular Patterns in Forest Resilience Networks

After identifying from the literature those resilience predictors that promoted the resilience of system variables (i.e., with prevalent positive relationships), the network analysis revealed a modular pattern relating them to certain bundles of system variables (Figure 1a). Active management appeared as the most important predictor promoting overall resilience, exhibiting the highest centrality and a positive effect on the resilience of 12 of the 15 system variables affected by resilience predictors (Figure 1a, Table S4). Following active management, biodiversity was ranked as the second most influential predictor able to promote forest resilience (Figure 1a, Table S4). Specifically, for the detailed categorization of resilience predictors, preserving

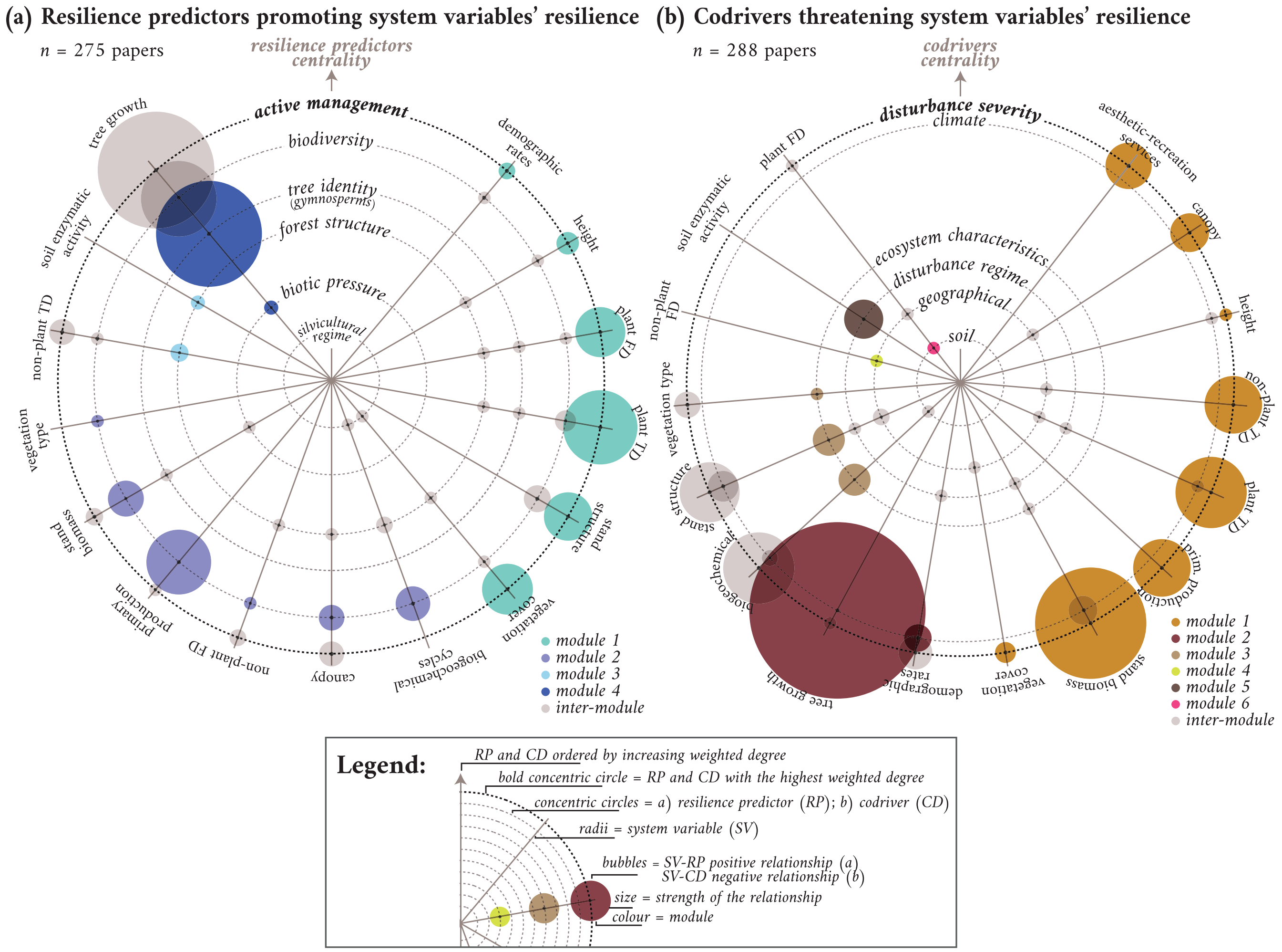

FIGURE 1 | The global network of relationships linking broad categories of resilience predictors (a) and codrivers (b) with the resilience of key forest system variables. Overall, the resilience of specific bundles of forest system variables is promoted by specific bundles of resilience predictors (i.e., with prevalent positive relationships) (a), and threatened by certain bundles of codrivers (i.e., with prevalent negative relationships) (b) (see Materials and Methods; Figure S1 for networks using a detailed categorization of resilience predictors and codrivers, and Figure S2 for networks illustrating resilience predictors that threatened and codrivers that promoted system variables' resilience). Circles represent links between system variables (radii), resilience predictors or codrivers (concentric dotted circumferences in (a) and (b), respectively). Colors in (a) and (b) represent different modules, while circle sizes indicate the strength of each link (see Materials and Methods). Resilience predictors (a) and codrivers (b) are arranged based on increasing centrality values in terms of weighted degree (the sum of all links strength of a resilience predictor or codriver). The ones with the highest centrality are highlighted in bold. When dealing with categorical resilience predictors or codrivers, we considered the category that most frequently promoted system resilience as exhibiting a positive relationship. Accordingly, the name of the resilience predictor or codriver reflects the category with the highest promotion or threating effect, respectively. A detailed description of system variables, resilience predictors, and codrivers is provided in Tables S1–S3. Abbreviations: FD = functional diversity, TD = taxonomic diversity, prim. production = primary production.

mixed forests with high functional diversity proved to increase resilience across nine system variables (Figure S1a, Table S4).

Similarly, modules linking bundles of codrivers that tend to threaten the resilience (i.e., with prevalent negative relationships) of other sets of system variables were recognized (Figure 1b). Disturbance severity and climate (Figure 1b, Table S5), particularly drought conditions (Figure S1b, Table S5), were reported as the two main codrivers threatening forest resilience. Among them, disturbance severity emerged as particularly relevant, as it affected nearly all system variables, except soil enzymatic activity and non-plant functional diversity (Figure 1b).

For system variables, tree growth was the one most consistently threatened by codrivers, especially climate, with drought conditions exerting the most consistent negative impact (Figures 1b and S1b). However, tree growth was also positively related to many resilience predictors, notably active management and the preservation of gymnosperm-dominated forests (Figures 1a and S1a).

3.2 | Balance Between Positive and Negative Effects in Forest Resilience Networks

When examining the balance between positive (i.e., resilience promotion) and negative (i.e., resilience reduction) effects exerted by each broad category of resilience predictors (Figure 2), three main patterns emerged: exclusively positive effects, mixed but net positive effect, and mixed but net negative effect (see Table S7). This observation suggests resilience predictors with

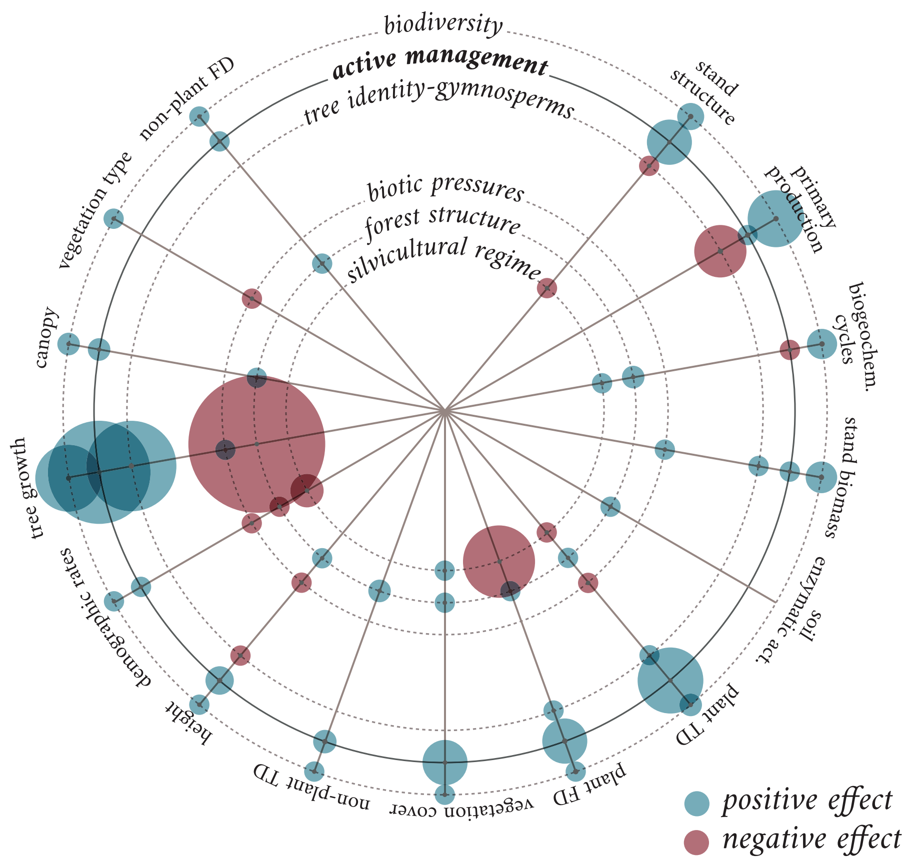

FIGURE 2 | Network illustrating broad categories of resilience predictors that have either exclusively positive effects or both positive and negative effects on different system variables resilience. Circle size represents the strength of the effect (positive in blue and negative in red) of each resilience predictor (circumferences) on each system variable (radii). Resilience predictors are ordered according to the balance between positive and negative effects, from bottom to top: Net negative effect, net positive effect, and exclusively positive effect. The resilience predictor exerting the highest promotion on ecosystem resilience is highlighted in bold (see Table S7). Abbreviations: FD = functional diversity, TD = taxonomic diversity.

exclusively positive effects are the most reliable ones for enhancing resilience while preventing detrimental cascading effects. Among broad categories, biodiversity was the only resilience predictor with this exclusively positive effect. Within the detailed categorization, only three out of 22 resilience predictors exhibited such effects exclusively promoting the resilience of more than one system variable. These predictors, tightly connected with biodiversity, encompass plant functional diversity, forest type (mixed forests), and land use (natural non-planted forests) (Figure S3, Table S7). Beyond this set of predictors with exclusively positive effects, only a few resilience predictors had negative impacts while still maintaining a net positive effect on system variable resilience (see Table S7). Here, active management and tree identity emerged as key resilience predictors, with only detrimental effects on specific system variables: forest biogeochemical cycles for active management and stand structure, primary production, and tree height for tree identity (Figure 2). From the perspective of system variables, the resilience of demographic rates and plant functional diversity was the most consistently threatened by the interplay between negative and positive effects of resilience predictors.

Modularity analysis also revealed cascading effects through the entire ecosystem, as certain detailed categories of resilience predictors affected the resilience of distinct system variables, which in turn act as predictors for the resilience of other variables, amplifying both positive and negative effects across the system (Figure 3 and Figure S3). For instance, plant functional diversity was reported as a system variable whose resilience may be enhanced (e.g., by implementing management practices such as fuel reduction and harvesting) and, in turn, it has been found to be a resilience predictor of stand primary production.

Furthermore, the cascading effects resulting from the dual role of taxonomic and functional diversity, and forest vegetation type acting as both system variables and resilience predictors (Tables S1 and S2), revealed a net positive effect on forest resilience considering the whole set of system variables (Figure 3, Table S7). In turn, stand structure, landscape vegetation cover, and canopy characteristics have a potential detrimental effect on overall forest resilience (see Table S7).

3.3 | Spatiotemporal Coupling of Resilience Predictors and Codrivers

The system variables-resilience predictors network identified a set of resilience predictors capable of fostering forest resilience across all spatial extents (Figure 4a). Active management focused on prioritizing non-planted, mixed forests with high taxonomic and functional diversity proved to promote forest resilience from site to global extents, especially at the

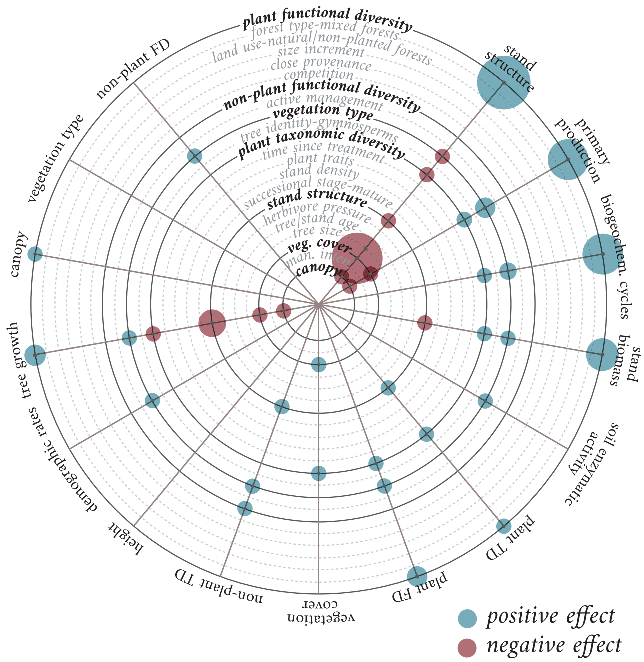

FIGURE 3 | Dual role of some resilience predictors as both system variables and resilience predictors (detailed categories). Circle size represents the strength of the effect (positive in blue and negative in red) of each resilience predictor (circumferences) on each system variable (radii). The seven resilience predictors that act both as system variables and resilience predictors are emphasized in bold. Abbreviations: Biogeochem. = biogeochemical, FD = functional diversity, man. inten. = management intensity, TD = taxonomic diversity, veg. cover = landscape vegetation cover.

landscape scale, and spanning from days to centuries, especially at the yearly scale. This is particularly important since the codrivers with a higher reported ability for threatening forest resilience (i.e., higher centrality, see Table S5) were also the ones that operate across a wider range of spatiotemporal scales. As such, disturbance severity and climate (specifically drought) stand out as consistent challenges to forest resilience across all spatiotemporal scales studied, contrasting with the more spatially and temporally restricted effects of other codrivers (Figure 4b). Active management, biodiversity (specifically plant traits), tree identity-gymnosperms, and forest structure (specifically tree/stand age) proved to enhance forest resilience at those scales where many codrivers have a more consistent detrimental effect.

3.4 | Dissecting the Effect of Active Management on Forest Resilience

Active management appeared as the most consistent resilience predictor promoting resilience in temperate and Mediterranean forests, whereas biodiversity was particularly effective in enhancing resilience in boreal and tropical/subtropical forests (Figure S4, Table S8). Both active management and biodiversity (especially plant functional diversity) proved to be key for promoting the resilience of the system variables more threatened by codrivers (i.e., tree growth in boreal, temperate, and Mediterranean forests, and stand biomass in tropical/subtropical forests). Specifically, forests facing higher levels of disturbance severity exhibited reduced resilience, with drought emerging as the main codriver threatening boreal and Mediterranean forests (Figure S4).

A consistent pattern highlights the integral role of management in promoting forest resilience by maintaining taxonomically and functionally diverse forests with high levels of tree growth and vegetation cover within large and continuous forest stands. Specifically, silvicultural practices such as cutting and prescribed burning exhibited the highest centrality, thus consistently enhancing the resilience of an ample number of system variables. These practices contributed to more resilient forests in terms of tree growth, plant taxonomic and functional diversity, landscape vegetation cover, and stand structure, but negatively affected the resilience of stand biomass and biogeochemical cycles. Conversely, the control of pests and herbivores may diminish the resilience of plant taxonomic diversity, while having a less reported effect on the other variables of the module (Figure 5). In turn, the implementation of restoration projects over decades ($n = 55$ relationships) did not increase the resilience in terms of stand structure.

4 | Discussion

By combining an operational approach for assessing resilience (Lloret et al. 2024) with network analysis, this study identified key patterns in forest resilience through the examination of bundles of resilience predictors and codrivers across biomes. Specifically, this approach allowed (i) identify measurable forest characteristics (i.e., systems variables) that are at risk under climate change; (ii) pinpoint specific codrivers linked to climate change that constrain forest resilience (e.g., disturbance severity); and (iii) identify bundles of actions (i.e., predictors) to enhance resilience under the contexts (i.e., determined by codrivers) where they are more likely to be more effective. As a result, recognizing the factors that promote or threaten current forest resilience can assist in refining ongoing management strategies towards those actions that are most effective in enhancing forest resilience (i.e., to guide future decision-making).

4.1 | The Modular Structure of Resilience Drivers

The network analyses benefited from an operational procedure that enables the identification of predictors and codrivers influencing the resilience of distinct system variables in response to diverse disturbances and stressors (Lloret et al. 2024). Our findings, based on an extensive literature search encompassing different biomes, reveal the existence of modular structures corresponding to bundles of factors that predict the resilience of sets of variables defining forest ecosystems' properties. This modular structure extends to unmanageable codrivers, with disturbance severity—and to a lesser extent, disturbance regime—driving major resilience threats. These threats affect not only individual variables, such as tree growth, but also bundles of structural, functional, biodiversity, and ecosystem service-related variables. Despite the context-dependent nature of the modular structures

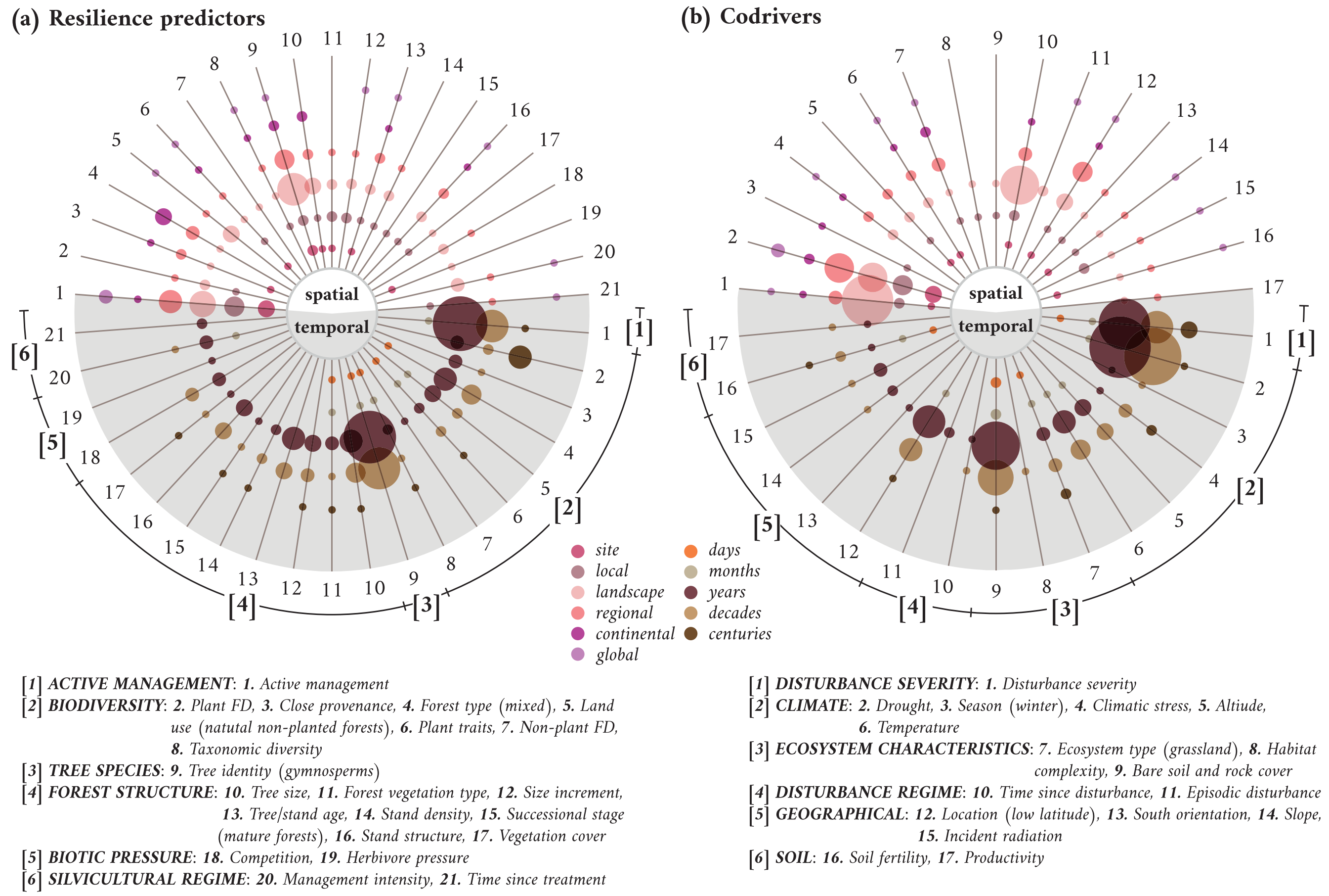

FIGURE 4 | Effect of resilience predictors (a) and codrivers (b) on forest resilience across diverse spatiotemporal scales, ranging from site to global and over timeframes spanning from days to centuries. Circle size represents the number of studies that have reported a significant promoting effect for each resilience predictor (a) or a significant detrimental effect for each codriver (b) on forest resilience at a certain spatiotemporal scale (see Materials and Methods).

observed in the networks, there is a notable congruence in the key resilience predictors and codrivers influencing forest resilience worldwide. We found a hierarchy of such predictors and codrivers affecting the resilience of interrelated system properties, thereby enabling a comprehensive appraisal of the entire system. This knowledge supports the identification of targeted management actions (Hood et al. 2016; Peterson St-Laurent et al. 2021; Stoddard et al. 2021) affecting a short list of key predictors, potentially maximizing the promotion of forest resilience to global change challenges.

When addressing the resilience of the most consistently threatened system variables, we found that these targeted actions should consider multiple predictors likely belonging to different modules, thus reflecting the complex network of relationships determining forest resilience (Selwyn et al. 2025). For instance, tree growth—followed by stand structure, biomass, and biogeochemical cycles—is among the system variables whose resilience is most consistently negatively affected by codrivers (Figure S1b, Table S6). In this case, enhancing the resilience of these variables would require implementing management strategies focused on increasing plant functional diversity and manipulating tree species composition (Silva Pedro et al. 2015; Spasojevic et al. 2016; Schmitt et al. 2020), which are resilience predictors included in different modules (i.e., modules 2, 1, and 3, respectively; Figure S1a).

4.2 | Biodiversity and Active Management as Key Tools for Enhancing Resilience

Biodiversity emerges as a fundamental element of the forest resilience network across biomes. Moreover, biodiversity-related predictors consistently contribute to the resilience of specific system variables without negatively impacting any system variable. For example, highly diverse old-growth forests with tall canopies appear as the most consistently resilient in terms of primary production. Moreover, biodiversity also proved to enhance the resilience of several bundles of system variables, including structural (i.e., stand biomass, canopy cover) and functional (e.g., primary production, biogeochemical cycles) forest attributes. This positive effect of biodiversity-related predictors on forest resilience can be explained by multiple ecological mechanisms including resource partitioning and facilitation among species (Messier et al. 2019), species selection (Grossiord 2020), averaging effects of species multifunctionality (Van der Plas et al. 2016), compensatory processes in biotic interactions (Connell and Ghedini 2015), and the diversity of responses to environmental change among functionally equivalent species (Elmqvist et al. 2003). These mechanisms operate at multiple levels, reinforcing the influence of biodiversity-related predictors on forest resilience across spatiotemporal scales, as detected by our network analysis. Among these predictors, functional diversity has a

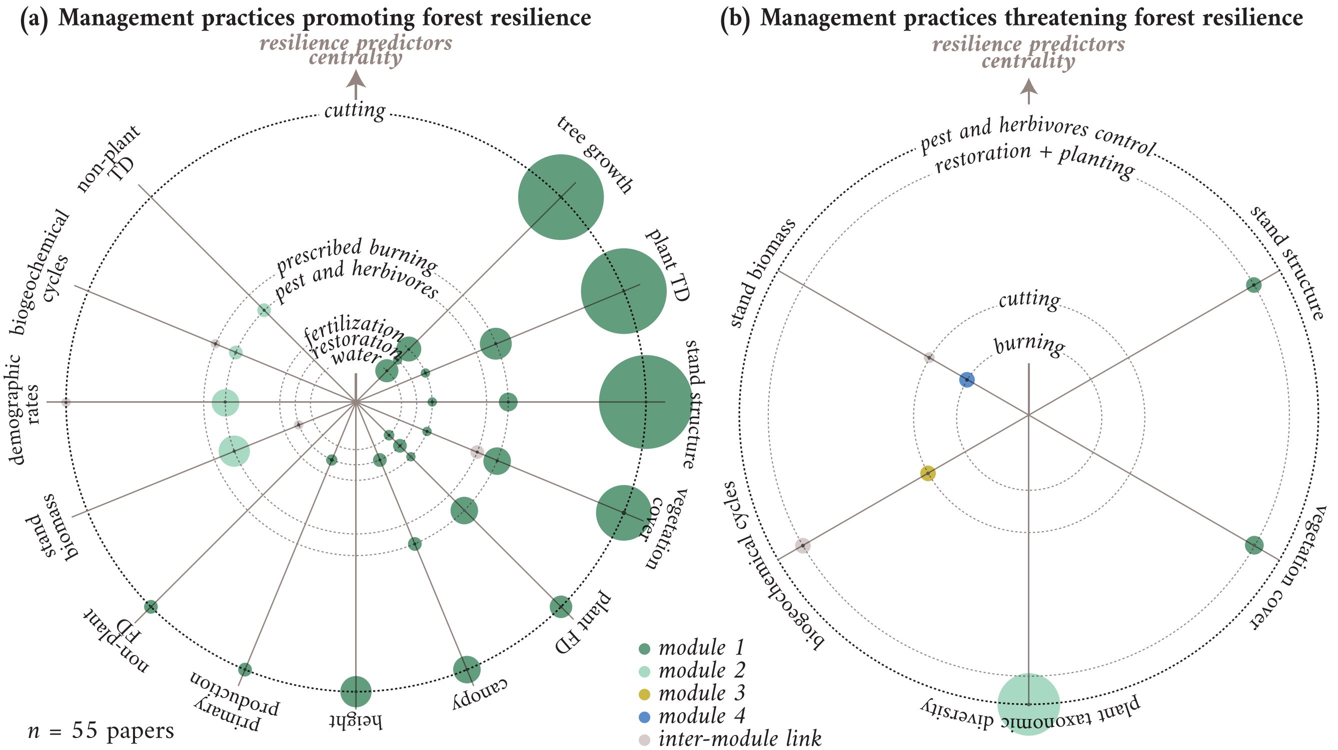

FIGURE 5 | Promotion (a) or threat (b) to the resilience of specific groups of forest system variables by certain silvicultural practices. The circles represent the relationships between system variables (radii) and forest management practices (concentric circumferences). Colors represent different modules, while circle sizes indicate the strength of each particular relationship. In (a) and (b), management practices are arranged based on increasing centrality values in terms of weighted degree (the sum of all links strength of each management category).

more consistent reported influence on forest resilience than taxonomic diversity (Figure 3), since the former better reflects physiological mechanisms critical for resilience (for instance in response to stressors like drought; Choat et al. 2018), while also interacting with phylogenetic, climatic and soil variability, as well as biotic interactions (O'Brien et al. 2017; Anderegg et al. 2018). Furthermore, the pivotal role of biodiversity is reinforced by its dual role not only as a predictor of the resilience of a bundle of structural and functional forest attributes, but also because its resilience is determined by other predictors related to active management. This interplay between biodiversity and management reflects the intricate network of relationships underlying forest resilience. Therefore, the analysis of the modular structure of networks reveals the importance of explicitly considering biodiversity-related attributes when planning and implementing effective resilience management strategies (Cantarello et al. 2024; Selwyn et al. 2025).

Active management stands out as the resilience predictor with the highest centrality, emerging as a key driver of forest resilience operating across spatiotemporal scales. The integral role of management in promoting forest resilience is supported by its contribution to maintaining taxonomically and functionally diverse forests with high levels of tree growth and vegetation cover within large and continuous forest stands. The effects of management-related predictors spread across multiple system variables within the networks. Specifically, management actions focused on prioritizing non-planted and mixed forests with high functional diversity emerge as a sound approach to balance the promotion and detrimental effects on the resilience of different system variables (see Table S7) (Bongers et al. 2021). These actions exemplify close-to-nature forestry strategies, particularly those promoting forest resilience in terms of tree growth, stand biomass, and primary production, landscape vegetation cover, and taxonomic and functional diversity. However, this resilience enhancement of some forest attributes by management practices is often not exempt from cascading effects (Pires et al. 2020) that could also lead to negative impacts on the resilience of other system variables, as is the case of silvicultural practices, the control of pests and herbivores, or the execution of restoration projects (Figure 5). Therefore, decisions regarding the implementation of management actions should consider the context-dependency of the relevant responses.

4.3 | Spatiotemporal Coupling of Resilience Predictors and Codrivers

The intricate interplay between resilience predictors and codrivers that shapes forest resilience unfolds across a broad spatiotemporal spectrum. Both resilience predictors and codrivers have been reported to operate at a broad spatial range, but they tend to have more constrained temporal effects (Figure 4). Although assessing long-term impacts is challenging due to the scarcity of historical data, available studies indicate that the spatiotemporal scale at which codrivers threaten the resilience of system variables aligns with the scale at which resilience predictors proved to effectively promote forest resilience. Our analysis emphasizes the role of landscape and years as pivotal levels of the spatiotemporal scale. The landscape scale has been recognized as one of the most appropriate spatial units for managing forest resilience, as it integrates forest multifunctionality (Messier et al. 2019; Simion et al. 2023) and many of the social-ecological processes shaping forests (Fischer 2018). Overall, active management has been shown to enhance forest resilience across spatial (from site to global) and temporal (from months to centuries) scales, with years being the main timeframe in which the positive impact on resilience has been demonstrated. This is because managing forests for resilience requires actions that unfold over the years to allow time for tree growth, stand development, recovery from disturbances, and adaptation to climate, while also maintaining the flexibility to adjust silvicultural practices (Lindner et al. 2010; D'Amato et al. 2011).

4.4 | Caveats in Resilience Assessment

Although our analysis reveals sound patterns of resilience predictors and codrivers across forest biomes, the results are inherently influenced by the employed sources. The methodology used in the different studies varies according to the resilience approach (e.g., focus on resistance or recovery, see Zheng et al. 2021), the specific disturbances or stressors determining resilience, the spatiotemporal scale considered, the number and attributes of the selected system variables, and the features of the reference state to which resilience is assessed (Lloret et al. 2024). These methodological choices, along with the specific features of the system considered, the assessment goals, and the available information, can introduce potential biases that require further investigation. For instance, the differences observed among biomes may reflect disparities in the distribution of variables of interest and the approaches used across studies. Similarly, the identification of key resilience predictors and cascading effects is sensitive to the idiosyncrasy and context of individual studies (Garmestani et al. 2009). Hence, the consideration of these nuances should guide the future operationalization of resilience predictors, ensuring a balanced approach that weighs their potential benefits and associated risks when designing and implementing management actions (Fischer et al. 2009; Sellberg et al. 2018; Nikinmaa et al. 2023). This rationale particularly applies to active management as a key driver of forest resilience. For instance, special caution should be taken when modifying stand structure, landscape vegetation cover, and canopy characteristics, due to their net effect on forest resilience (Table S7). Overall, our findings provide a general overview of the most promising resilience predictors and contextual factors to guide decision-making for promoting forest resilience, while also acknowledging the importance of considering potential caveats and cascading effects of modifying these predictors.

5 | Conclusions

Our network analysis contributes to unveiling the complex, modular structure of interconnected factors underlying forest resilience and provides key insights for operational strategies to ameliorate the response of forest ecosystems to increasing disturbances and stressors. The existence of bundles of factors that remarkably affect bundles of forest attributes suggests that a somewhat holistic approach to enhance forest resilience is needed (Selwyn et al. 2025). Biodiversity, expressed as functional diversity, mixed forests, and non-planted forests, constitute the core of the main bundle of resilience predictors that have proved to drive the resilience of multiple forest attributes and spread positive cascading effects promoting resilience throughout the whole network. Thus, it becomes a key target for maintaining overall forest functionality, in line with approaches based on nature-based solutions to cope with climate change effects (Dymond et al. 2014; Oliver et al. 2015; Mori et al. 2021; Messier et al. 2022). Active management also constitutes a key bundle for promoting resilience across a wide range of spatial and temporal scales. However, in contrast with the universally positive effects of biodiversity, the implementation of effective management strategies to foster resilience requires a nuanced understanding of specific context-dependent patterns and potential negative cascading effects, emphasizing the importance of designing tailored practices. Ultimately, our findings highlight the critical need to conserve forest biodiversity, with forest management having a key role particularly when biodiversity is eroded.

Author Contributions

Pilar Hurtado: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **Josep Maria Espelta:** investigation, writing – review and editing. **Luciana Jaime:** investigation, writing – review and editing. **Jordi Martínez-Vilalta:** investigation, writing – review and editing. **Manto Samou Kokolaki:** data curation, writing – review and editing. **Marcus Lindner:** funding acquisition, investigation, writing – review and editing. **Francisco Lloret:** conceptualization, funding acquisition, investigation, methodology, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.28738217.

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Supporting Information

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