Spontaneous native–non-native tree mixtures worldwide: a systematic map of research patterns, with knowledge gaps and management implications

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Abstract

Purpose of Review Spontaneous mixtures of native and non-native tree species occur in forest landscapes affected by land-use change, species introductions and disturbances. However, research on these communities remains fragmented.

Recent Findings We identified 238 cases. Research was concentrated in high-income countries and studies included diverse combinations of native and non-native tree species. Land abandonment was the most frequently reported driver in tropical moist forests, whereas urbanization, forest management, land abandonment and nearby non-native tree plantings were more evenly represented in temperate forests. Research focused primarily on forest composition, structure, regeneration and dynamics, with comparatively limited attention to functional traits, soil properties, ecosystem functioning and associated biodiversity. Approximately two-thirds of cases relied on single-time assessments, while studies incorporating both native and fully non-native reference forests as reference conditions were uncommon.

Summary Spontaneous native–non-native tree mixtures involve diverse species combinations and develop under different ecological and land-use contexts. Our findings highlight the need for context-dependent forest management that considers species characteristics, potential ecological impacts, land-use history and landscape conditions, rather than biogeographical origin alone.

Keywords: Biodiversity; Ecosystem functioning; Forest management; Forest regeneration; Land-use change; Secondary succession

Introduction

Forest ecosystems are increasingly being reshaped by human-driven changes in land use, species introductions, disturbance regimes and climate. These interacting pressures can alter species composition and ecological processes, generating communities that differ from those that historically occurred in a given region [1-3]. Among these emerging communities, spontaneous mixtures of native and non-native tree species are increasingly reported across a wide range of ecosystems and regions [e.g., 4-6].

Spontaneous native–non-native tree mixtures can arise along contrasting trajectories of human influence, from land-use intensification to the relaxation or cessation of former land uses [7, 8]. For example, land abandonment can promote secondary succession and forest regeneration, allowing native and non-native tree species to colonize previously managed areas. Their coexistence may be maintained by differences in establishment strategies, growth rates and tolerance to environmental conditions, as well as by spatial and temporal heterogeneity during succession [e.g., 9, 10]. Similarly, hydrological alterations can modify river dynamics, flooding regimes and soil conditions, generating environmental heterogeneity that may favour the establishment and coexistence of native and non-native tree species with different tolerances to flooding and soil moisture [e.g., 11, 12]. Non-native tree plantations can also provide propagule sources to surrounding native forests [e.g., 13] and, when management is absent or of low intensity, they often provide opportunities for the establishment of native trees [e.g., 14]. Fire, whether of natural or anthropogenic origin, can also facilitate the development of these mixtures by reducing competition and creating opportunities for the establishment and regeneration of non-native trees [e.g., 15], as can natural disturbances such as hurricanes, floods, volcanic eruptions, and windthrow [e.g., 16, 17]. Thus, native–non-native tree mixtures are becoming an increasingly common feature of contemporary forest landscapes, and their prevalence is likely to increase as global change continues to alter forest ecosystem structure,

composition and dynamics [e.g., 18, 19]. Understanding the ecological consequences of these emerging tree mixtures is, therefore, an increasingly important challenge for forest management [20].

Native and non-native species often differ in their functional traits and life-history strategies [21, 22], potentially shaping patterns of coexistence and, in turn, forest composition and ecosystem functioning [23, 24]. Accordingly, their coexistence has been examined across a range of attributes, including plant diversity [e.g., 25, 26], tree regeneration [e.g., 15], soil properties [e.g., 27], carbon cycling [e.g., 28], and associated biodiversity [e.g., 29, 30]. However, the patterns and processes observed in these communities may vary markedly depending on tree species identities, functional characteristics, and species interactions [31].

Despite their ecological relevance, spontaneously assembled native–non-native tree mixtures have rarely been considered as a distinct forest system. Research on mixed forests has focused predominantly on native tree-species mixtures [e.g., 32-35] or deliberately established native–non-native mixed-species plantations [e.g., 36-38]. In contrast, research on spontaneous native–non-native mixtures is scattered across different fields, including invasion ecology [e.g., 39, 40], restoration ecology [e.g., 6, 41], urban ecology [e.g., 42, 43], and ecological succession [e.g., 44, 45]. As a result, these systems have been described and conceptualised differently depending on the research context, making it difficult to integrate findings across studies.

This fragmentation also limits our ability to obtain a comprehensive picture of the available evidence. It remains unclear where these mixtures have been studied, which native and non-native tree species are represented, under which anthropogenic drivers and natural disturbances they occur, how research has addressed them across spatial and temporal scales and study designs, and which ecological attributes have received the greatest attention. Mapping this evidence is, thus, a necessary first step towards a broader synthesis of current knowledge.

To provide this overview, we conducted a systematic map of the global evidence on spontaneously assembled native–non-native tree mixtures. Systematic maps are particularly well suited to synthesize broad and heterogeneous evidence bases because they use transparent and reproducible methods to identify, catalogue, and characterize how existing knowledge is distributed across multiple dimensions [46]. Specifically, we asked: (1) How is the available evidence on native–non-native tree mixtures geographically distributed?; (2) Which native and non-native tree species are more frequently represented?; (3) Under which anthropogenic drivers and natural disturbances have these mixtures been studied?; (4) How have they been studied across spatial and temporal scales and study designs?; and (5) Which ecological attributes have received attention? By providing the first global systematic map of these emerging forest systems, we seek to identify major research trends, evidence clusters, and knowledge gaps, thereby establishing a foundation for future research and for a broader evidence base to inform their management.

Methods

Conceptual framework

We adopted a Population-Outcome (PO) framework to define the scope of the review and categorise the available evidence:

- Population: Forest communities in which native and non-native tree species co-occur following spontaneous establishment, without intentional species mixing or plantation design. Intentionally established mixed-species plantations were therefore excluded.
- Outcome: Any reported ecological attribute of these forests including species composition and diversity (i.e., plant taxonomic groups), forest structure, natural regeneration, forest dynamics, functional traits, soil properties, ecosystem processes and functioning, and associated biodiversity (i.e., non-plant taxonomic groups).

Search strategy

Systematic maps and reviews require rigorous and transparent search strategies to ensure reproducibility and comprehensiveness and minimise selection bias [47, 48]. The primary search was conducted in the Web of Science Core Collection (all editions) between 2 and 3 March 2026. The search was applied to the field “Topic” (title, abstract, and keywords, those provided by the authors and those used for indexation purposes) using search terms that were intentionally broad to maximise sensitivity and no temporal restrictions. Following several rounds of exploratory testing and refinement, the final search string was:

("mixed forest*" OR "mixed-species forest*" OR "novel forest*" OR "novel ecosystem*" OR "tree species mixture*" OR ("native species" AND ("non-native species" OR exotic* OR alien* OR introduced* OR invasive*))) AND forest* NOT plantation*

Additional filters were applied within Web of Science to improve thematic relevance. Records were restricted to the document type Articles and to the following subject categories: Ecology, Forestry, Plant Sciences, Biodiversity Conservation, Soil Science, Zoology, Urban Studies, Geography Physical, and Environmental. Also, only studies published in the languages English, Spanish, and Portuguese were considered. After applying these filters, the search produced a total of 6,954 records (Fig. S1). To complement the database search, a backward citation search was conducted based on the reference lists of four relevant review studies identified within the initial search results [4, 6, 8, 19], which contributed 267 additional records (Fig. S1). Although the database search was filtered for "articles", all publication types retrieved during the search process (e.g., journal articles, books and book chapters) were considered for eligibility assessment when they met the predefined inclusion criteria. Following removal of duplicates, 7,179 unique records were retained for screening (Fig. S1).

Inclusion criteria

Studies were included in the systematic map if they met all of the following criteria:

- Study type: Peer-reviewed field studies or review articles had to address natural ecosystems; greenhouse and laboratory experiments were excluded;
- Population: Studies had to examine mixtures in which native and non-native tree species co-occurred following spontaneous establishment, without intentional design of the mixed system; intentionally planted mixed forests and commercial plantations were excluded, as well as studies focusing exclusively on single-species non-native invasion processes without explicit consideration of co-occurring native tree species;
- Outcome: Studies had to report at least one ecological attribute of the forest mixture (see section “Conceptual framework”).

Study selection procedure

Titles and abstracts of 7,179 records were screened by a single reviewer (RJ-O) to assess compliance with the predefined inclusion criteria, resulting in the exclusion of 6,619 records. Three additional records were inaccessible and were excluded. The full texts of 557 potentially eligible records were subsequently assessed by the same reviewer (RJ-O) for final inclusion (Fig. S1). Records excluded at the full-text stage (n = 322) either (i) examined intentionally designed mixed forests or plantations; (ii) focused on single-species non-native invasion processes without explicit consideration of co-occurring native tree species; or (iii) did not provide extractable information on any of the ecological attributes considered in the systematic map. In total, 235 studies met the inclusion criteria and were retained in the systematic map (Table S1). Three of these studies [16, 49, 50] each reported two independent cases that differed in study location, temporal scale, anthropogenic drivers, and/or ecological attributes. Accordingly, these cases were entered separately, yielding a final dataset of 238 data entries (Table S2). Hereafter, “study” refers to an individual publication included in the systematic map (n = 235), whereas “case” refers to the unit represented in the final dataset (n = 238).

Data extraction and systematic map dataset

Data extraction was conducted by five researchers. Before full extraction, a calibration exercise was performed to ensure consistency among researchers. Ten studies were randomly selected and independently extracted by all five researchers. The resulting data were compared across researchers, and any discrepancies were discussed to identify their source and reach a common interpretation of the extraction criteria. This calibration process led to clarification of variable definitions and refinement of the data-extraction matrix to reduce ambiguity and improve consistency. All resulting changes were communicated to the five researchers before proceeding with the full data extraction. Following calibration, the remaining studies were divided among the five researchers, with each study extracted by one researcher (Table S1).

Information was extracted at the study level, except when a study reported multiple independent cases [16, 49, 50], for which case-specific information was recorded separately. The following information was extracted from each case to construct the dataset:

i) Bibliographic information: Year of publication.

ii) General study characteristics: For each study, the study type (field study or review), the name of the study location, country, geographic realm, biome, whether the study was conducted on mainland or island systems, and the native and non-native tree species composing the mixture were extracted. Island systems were further classified as oceanic or continental according to their geological origin, except for New Zealand, which was classified as oceanic based on its ecological and biogeographical characteristics.

Each study was assigned to one country, considering sovereign states as the primary geographical unit; when a study included sites in more than one country, it was assigned to all countries represented. Each country was classified into income groups according to the World Bank Group Country Income Classification for fiscal year 2027 [51]. Each study location was also assigned to a biogeographic realm and terrestrial biome following the global ecoregion classification of [52]. When geographical coordinates were provided in the original publications, these were used to locate the

study sites; otherwise, locations were inferred from the reported location names. Studies including sites located in more than one biome were assigned to all corresponding biomes.

Dominant tree species were extracted using a standardized protocol. When studies reported quantitative measures of community composition, the three most dominant native tree species and the three most dominant non-native tree species were recorded according to the metric(s) reported by the authors. When quantitative dominance metrics were unavailable, all native and non-native tree species explicitly described as dominant, co-dominant, characteristic or major components of the forest community were recorded. In the few studies where authors reported the presence of one or more non-native tree species co-occurring with multiple native tree species, but did not identify the native species individually, this information was recorded as reported (e.g., “multiple native tree species”). Scientific names were standardized according to the Plants of the World Online taxonomic backbone [53]. When synonymous names were used in the original publications, they were updated to the currently accepted names following [53].

iii) Study design: For each study, the spatial scale of inference, the temporal scale, and comparison condition were extracted. The spatial scale of inference was classified according to the unit of inference addressed by each study rather than the spatial extent of sampling. Four categories were defined:

(a) Plot: the unit of inference was an individual sampling plot or localized experimental unit, and conclusions were restricted to the sampled plots.

(b) Forest: the unit of inference was a forest stand or forest patch. Studies could include one or several sampling plots, or even multiple stands within the same forest.

(c) Landscape: the unit of inference was the landscape, typically encompassing comparisons among multiple forest stands, fragments or patches within the same region.

(d) Regional: the unit of inference encompassed broad geographic regions including multiple landscapes, extensive environmental gradients or large geographic areas (e.g., islands, countries or broad climatic regions).

Temporal scale was characterized by classifying studies as based either on a single sampling occasion or on repeated measurements through time. Studies with repeated measurements were further classified according to monitoring duration as short-term (≤ 3 years), mid-term (> 3 to 10 years), or long-term (> 10 years).

For each study, comparisons of spontaneously established native–non-native tree mixtures with native reference forests, fully non-native forests, or both were recorded. Tree species-specific performance of native and non-native tree species was also recorded and defined as the assessment of growth, survival, physiology, reproduction, or functional traits at the individual species level.

iv) Drivers and disturbance context: For each study, the main anthropogenic driver most directly associated with the formation or development of the native–non-native tree mixtures was identified, and additional secondary anthropogenic drivers contributing to its dynamics were recorded. Drivers were classified as land abandonment (i.e., cessation of previous land use or management followed by spontaneous vegetation succession), land-use de-intensification (i.e., reduction, but not cessation, of land-use or management intensity), land-use intensification (i.e., increased intensity of land use or management), forest management (i.e., restoration or silvicultural practices such as logging, thinning, and clearing), nearby non-native tree plantations or ornamental plantings (i.e., when acting as propagule sources for colonization of adjacent forests), urbanization (i.e., replacement of previous land uses by urban development or infrastructures), hydrological alteration (e.g., channelization, dam construction, flow regulation or diversion, and flood suppression), human-mediated biotic interactions (e.g., introduced pathogens, altered herbivore pressure or introduced ecosystem engineers), and wildfire (i.e., when its human origin was supported by the study). Earlier land-use changes or disturbances that represented only historical context were not classified as main drivers.

When the available evidence was insufficient to identify the anthropogenic process associated with the mixture formation, the main driver was classified as “Not reported”. Natural disturbances affecting the study system (i.e., hurricanes, volcanic eruptions, windthrow, and flooding) were also recorded.

v) Ecological attributes assessed: Ecological attributes evaluated in each study were classified into eight non-mutually exclusive categories. Studies could therefore be assigned to more than one category when multiple ecological attributes were assessed:

(a) Forest composition and diversity: species identity of the communities, species richness and diversity indices.

(b) Forest structure: diameter at breast height (DBH), tree height, tree density, basal area, and vegetation stratification (i.e., understory and/or herbaceous cover).

(c) Natural regeneration: density of seedlings/saplings, and recruitment.

(d) Forest dynamics: growth, competition, and survival/mortality.

(e) Functional traits: stem, foliar, litter, root, and dispersal traits.

(f) Soil properties: chemical, physical, and microbiological properties.

(g) Ecosystem processes and functioning: primary productivity (e.g., biomass production or net primary productivity), decomposition (e.g., decomposition rates), nutrient cycling (e.g., nutrient mineralization or nutrient fluxes), carbon cycling (e.g., carbon sequestration or carbon fluxes), hydrological processes (e.g., water infiltration), and air regulation (e.g., pollutant removal).

(h) Associated biodiversity (i.e., non-plant taxonomic groups): amphibians, reptiles, mammals, birds, invertebrates, lichens, fungi, bacteria, and archaea.

Data visualization

Data were summarized at either the study level (n = 235) or the case level (n = 238), depending on the variable considered. Variables that could differ among independent cases within the same study were summarized at the case level. For non-mutually exclusive variables, a single case could contribute to more than one category;

accordingly, frequencies represent the number of cases assigned to each category, and summed frequencies may exceed the total number of data cases. Similarly, when a case encompassed more than one terrestrial biome, it was counted once in each corresponding biome, resulting in a total of 254 case-biome assignments. The unit of analysis used is indicated in the corresponding figure or table.

To assess whether the representation of terrestrial biomes in the evidence base was proportional to their global extent, we compared the percentage of case-biome assignments corresponding to each biome with the percentage of Earth's terrestrial area occupied by that biome, following [54]. Global biome extent was obtained from [52]. For each biome, relative representation was calculated as the difference, in percentage points, between its percentage of all case-biome assignments and its percentage of global terrestrial area. Positive values indicate greater representation in the evidence base relative to global biome extent, whereas negative values indicate lower representation.

Data processing was performed in R version 4.5.2 [55], and graphical visualizations were produced using the packages ggplot2 [56], ggh4x [57], ggalluvial [58], ggnewscale [59], igraph [60], and ggraph [61]. The global map showing the geographical distribution of the included studies was produced using QGIS version 3.40 [62].

Results

Geographical distribution of the evidence

The 238 cases were reported from 43 countries, with the USA accounting for the largest number (n = 87; 37%), followed by Brazil (n = 18; 8%), Poland (n = 16; 7%), Argentina (n = 15; 6%), and Chile (n = 9; 4%) (Fig. 1). Most cases were in mainland systems (n = 155; 65%), while 83 cases (35%) occurred on islands (Table S2). Of the island cases, 66 (80%) were located on oceanic islands and 17 (20%) on continental islands (Table S2). Evidence was also strongly skewed towards high-income countries (178; 75%), followed by upper-middle-income (n = 48; 20%), lower-middle-income (n = 8; 3%), and low-

income countries (n = 4; 2%) (Table S2). At the biogeographic-realm level, the 238 cases were distributed across all seven realms, with the highest representation in the Neotropical (33%), Palearctic (23%), and Nearctic (19%) realms, while fewer cases occurred in the Oceanian (9%), Afrotropical (8%), Australasian (5%), and Indo-Malayan (4%) realms (Fig. 1). Evidence was found across 12 of the 14 terrestrial biomes, although it was strongly concentrated in two: “Tropical and Subtropical Moist Broadleaf Forests” (39% of cases) and “Temperate Broadleaf and Mixed Forests” (37% of cases), while all other biomes contained 15 or fewer cases (≤6% each) (Fig. 1). Relative to their global terrestrial extent, the two dominant biomes were also the most strongly overrepresented (+21.8 and +25.7 percentage points, respectively), whereas several biomes were underrepresented (Table S3).

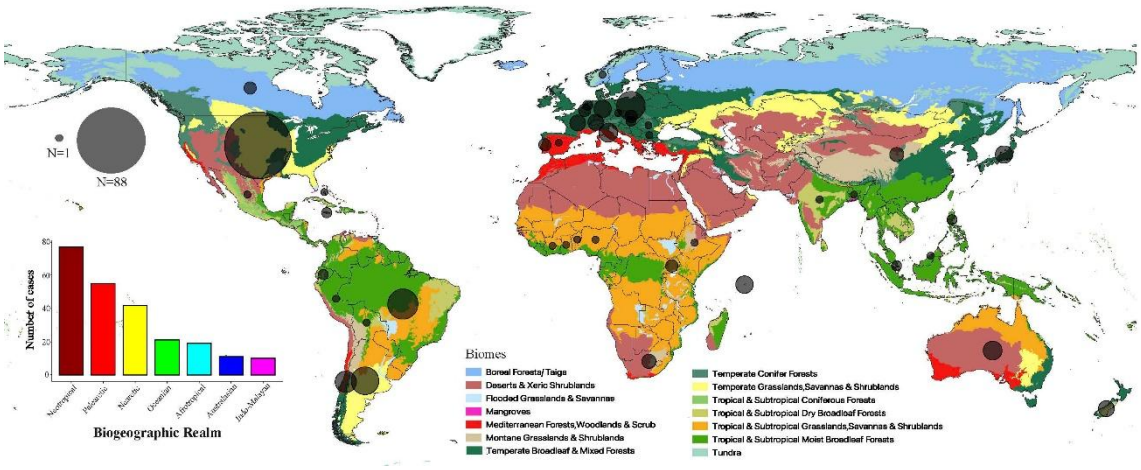


Figure 1. Global distribution of evidence included in the systematic map. Dark-grey circles indicate the geographical distribution of cases, with circle size proportional to the number of cases reported in each country; reference circles indicate the minimum and maximum numbers of cases per country. Background colours represent terrestrial biomes (*sensu* Dinerstein et al., 2017). The inset bar plot shows the number of cases in each biogeographic realm. Cases spanning more than one country were counted once in each corresponding country.

Native and non-native tree species represented in the evidence

The most frequently represented native and non-native tree species differed markedly among terrestrial biomes (Fig. 2). In “Tropical and Subtropical Moist Broadleaf Forests”,

356 the most frequently represented native species were *Metrosideros polymorpha* (16% of
357 cases within the biome), *Guarea guidonia* (14%), and *Cecropia schreberiana* (9%),
358 whereas the most frequently represented non-native species were *Psidium cattleyanum*
359 and *Spathodea campanulata* (17% each), followed by *Leucaena leucocephala* (14%). In
360 “Temperate Broadleaf and Mixed Forests”, the most frequently represented native
361 species were *Quercus robur* (24% of cases), *Pinus sylvestris* (15%), and *Acer rubrum*
362 (14%), whereas the most frequently represented non-native species were *Robinia*
363 *pseudoacacia* (26%), *Prunus serotina* (18%), and *Acer platanoides* (16%). Despite being
364 the most frequently represented species, none occurred in more than 26% of cases
365 within either biome.

366 Nevertheless, some non-native species recurred among the most frequently
367 represented species across different biomes (Fig. 2). *Psidium cattleyanum* and
368 *Leucaena leucocephala* were among the most frequently represented non-native
369 species in “Tropical and Subtropical Moist Broadleaf Forests”, “Tropical and Subtropical
370 Dry Broadleaf Forests”, and “Tropical and Subtropical Grasslands, Savannas and
371 Shrublands”. *Schinus terebinthifolia* was similarly among the most frequently
372 represented non-native species in “Tropical and Subtropical Grasslands, Savannas and
373 Shrublands”, “Flooded Grasslands and Savannas”, and “Mangroves”. These cross-
374 biome patterns should, however, be interpreted cautiously for poorly represented
375 biomes, as five biomes were represented by three or fewer cases.



376 **Figure 2.** Most frequently reported native and non-native tree species in each biome. For each
377 biome, the figure displays up to three native and three non-native tree species with the highest
378 frequencies across cases, selected from all species recorded during data extraction. Values next
379 to the bars indicate the number of cases within each biome reporting each species. Numbers in
380 parentheses in biome headers indicate the total number of cases assigned to that biome. Cases
381 spanning more than one biome were counted once in each corresponding biome.
382

Biome-specific bipartite networks further showed substantial variation in the number of dominant tree taxa represented in the evidence (Fig. S2). Across biomes, the number of native taxa reported as dominant ranged from 1 to 181 and the number of non-native taxa from 2 to 91. “Tropical and Subtropical Moist Broadleaf Forests”, the biome with the largest number of cases, also contained the largest number of represented taxa (181 native and 91 non-native taxa). In general, biomes represented by fewer cases tended to include fewer dominant tree taxa. However, this pattern was not consistent across all biomes, as some biomes with relatively few cases included a comparatively large number of taxa. For example, “Tropical and Subtropical Grasslands, Savannas and Shrublands” included 37 native and 25 non-native taxa across only seven cases.

Anthropogenic drivers and natural disturbances represented in the evidence

Land abandonment was the most frequently identified main anthropogenic driver associated with the development of native–non-native tree mixtures (n = 60; 25% of cases), followed by urbanization (n = 42; 18%), forest management (n = 37; 16%), and nearby non-native tree plantations or ornamental plantings (n = 33; 14%). Together, these four drivers accounted for 73% of all cases included in the systematic map. Hydrological alteration (n = 17; 7%) and human-mediated biotic interactions (n = 15; 6%) were less frequently identified, whereas land-use de-intensification, wildfire, and land-use intensification were each associated with fewer than 10 cases. The main anthropogenic driver was not reported for 16 cases (7%).

Within the two most represented biomes, the distribution of main anthropogenic drivers differed markedly (Fig. 3). In “Tropical and Subtropical Moist Broadleaf Forests”, land abandonment was the most frequently represented driver (n = 41; 45% of cases within the biome), whereas in “Temperate Broadleaf and Mixed Forests” the main driver was more evenly distributed among urbanization (n = 23; 26%), forest management (n = 20; 23%), land abandonment (n = 12; 14%), and nearby non-native tree plantations or

ornamental plantings (n = 11; 12%). Some drivers were also particularly frequent in specific biomes with smaller evidence bases (Fig. 3). In particular, land abandonment accounted for 11 of the 15 cases in “Tropical and Subtropical Dry Broadleaf Forests”, nearby non-native tree plantations or ornamental plantings for 7 of the 15 cases in “Mediterranean Forests, Woodlands and Scrub”, and hydrological alteration for 5 of the 12 cases in “Deserts and Xeric Shrublands”.

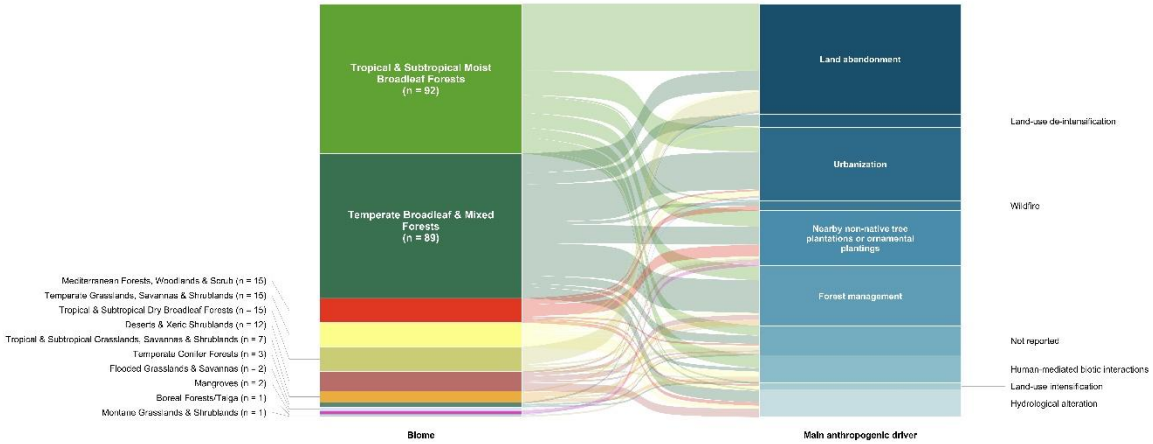


Figure 3. Alluvial plot illustrating the distribution of main anthropogenic drivers associated with the formation or development of spontaneously assembled native–non-native tree mixtures across biomes. Flow widths are proportional to the number of cases associated with each biome-driver combination. Numbers in parentheses in biome headers indicate the total number of cases assigned to each biome. Cases spanning more than one biome were counted once in each corresponding biome and therefore contribute to multiple flows.

Secondary anthropogenic drivers were frequently reported alongside the main drivers (Fig. S3), particularly nearby non-native tree plantations or ornamental plantings (n = 34) and forest management (n = 30). The most frequent main–secondary driver combinations involved land abandonment with forest management (n = 13), urbanization with nearby non-native tree plantations or ornamental plantings (n = 11), and land abandonment with nearby non-native tree plantations or ornamental plantings (n = 8). Natural disturbances were less frequently represented, with flooding (n = 11) and hurricanes (n = 9) being the most frequently reported. Flooding co-occurred most

frequently with hydrological alteration (n = 5), whereas hurricanes were most often reported in cases associated with land abandonment (n = 7).

Spatial and temporal scales and study design

The available evidence was predominantly generated at the forest (43% of all cases) or landscape scales (32%), while plot- (17%) and regional-scale cases (8%) were less frequent (Fig. 4a). Regarding the temporal dimension, two-thirds of the cases (67%) were based on a single sampling occasion and only one-third (33%) included repeated measurements through time (Fig. 4b). Among the latter, half were short-term (≤3 years; 50%), followed by long-term (>10 years; 35%), and mid-term (>3–10 years; 15%) cases (Fig. 4c).

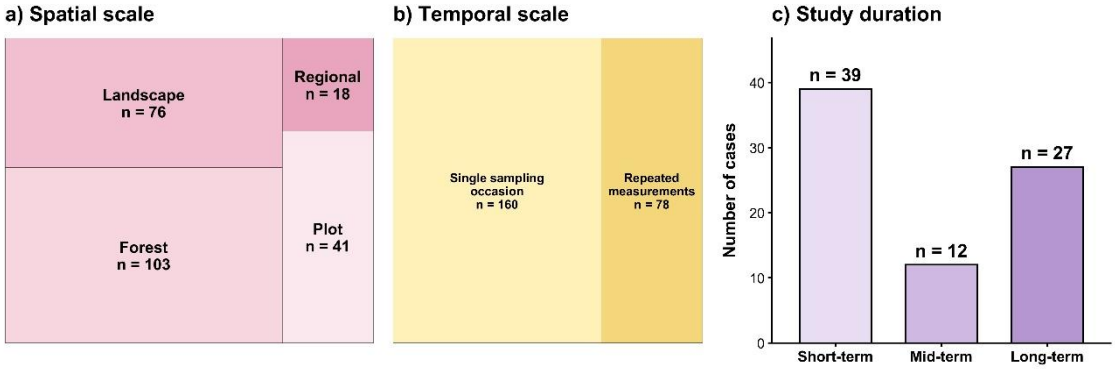


Figure 4. Spatial and temporal characteristics of the cases included in the systematic map (n = 238). (a) Spatial scale of the cases, distinguishing between landscape, forest, regional, and plot scales. (b) Temporal scale, distinguishing between single sampling occasions and repeated measurements. (c) Study duration for cases with repeated measurements, classified as short-term (≤ 3 years), mid-term (> 3–10 years), or long-term (> 10 years). Values indicate the number of cases in each category.

Comparative study designs were also unevenly represented (Table S2). Native reference forests were included as comparators in 76 cases (32% of all cases), whereas fully non-native forests were used much less frequently (n = 21; 9%), and only 15 cases (6%) included comparisons with both native reference and fully non-native forests (Table

S2). In addition, the species-specific performance of the native and non-native tree species comprising the mixtures was evaluated in 80 cases (34%) (Table S2).

Ecological attributes assessed in the evidence

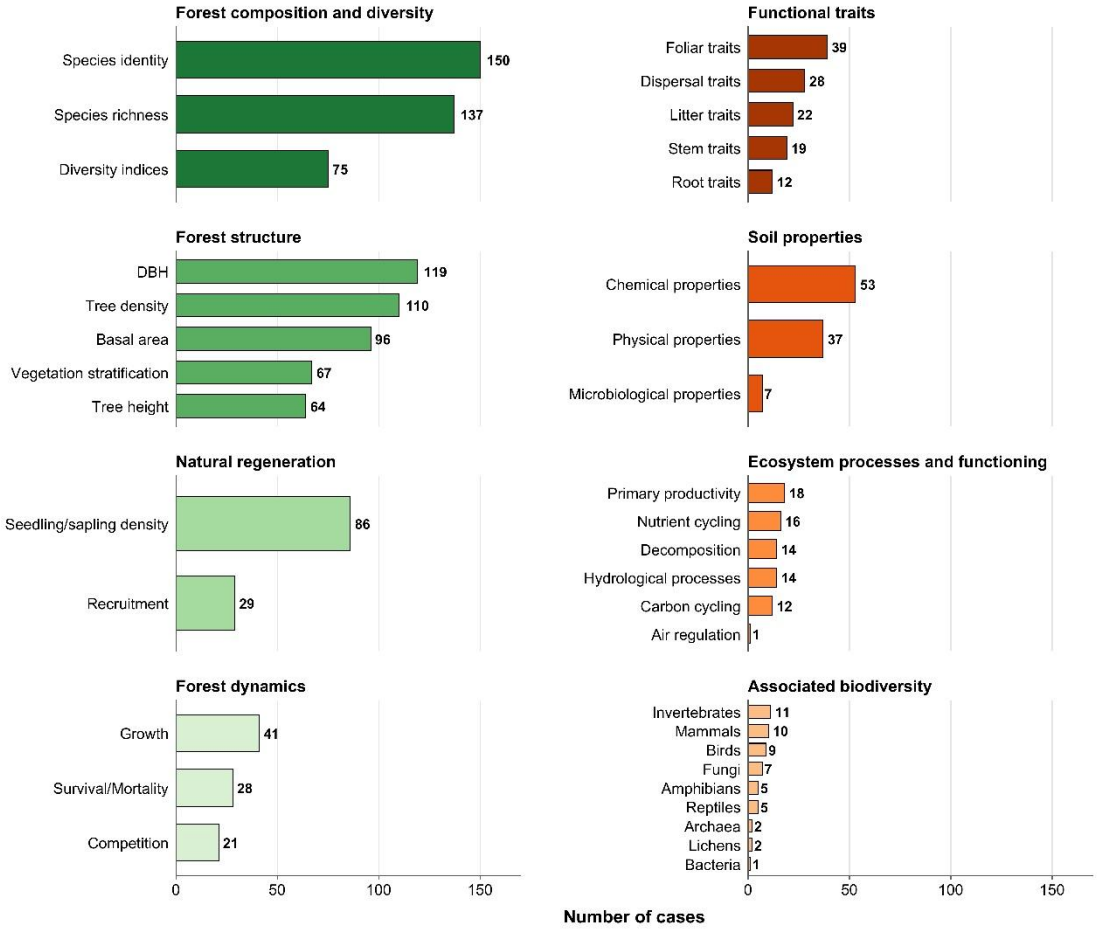


Figure 5. Distribution of the ecological attributes evaluated in the cases included in the systematic map (n = 238). Horizontal bars show the frequency of individual variables recorded within each of the eight ecological-attribute categories. Numbers next to the bars indicate the number of cases in which each variable was evaluated. Categories and variables were non-mutually exclusive and, therefore, individual cases could contribute to multiple categories and variables.

Ecological attributes related to forest composition and diversity, forest structure, natural regeneration, and forest dynamics were assessed more frequently than functional traits, soil properties, ecosystem processes and functioning, and associated biodiversity (Fig.

5). Among individual variables, species identity (63% of cases), species richness (58%), DBH (50%), tree density (46%), basal area (40%), and natural regeneration evaluated through seedling and sapling density (36%) were the most frequently assessed (Fig. 5). In contrast, variables related to ecosystem processes and functioning and associated biodiversity were generally less frequently assessed, with no individual variable occurring in more than 8% and 5% of cases, respectively (Fig. 5).

Furthermore, these differences in research emphasis persisted throughout the development of the evidence base (Fig. 6). Although the cumulative number of studies increased across all ecological attributes, forest composition and diversity and forest structure consistently dominated the literature, with their representation increasing particularly rapidly from the late 2000s onwards (Fig. 6).

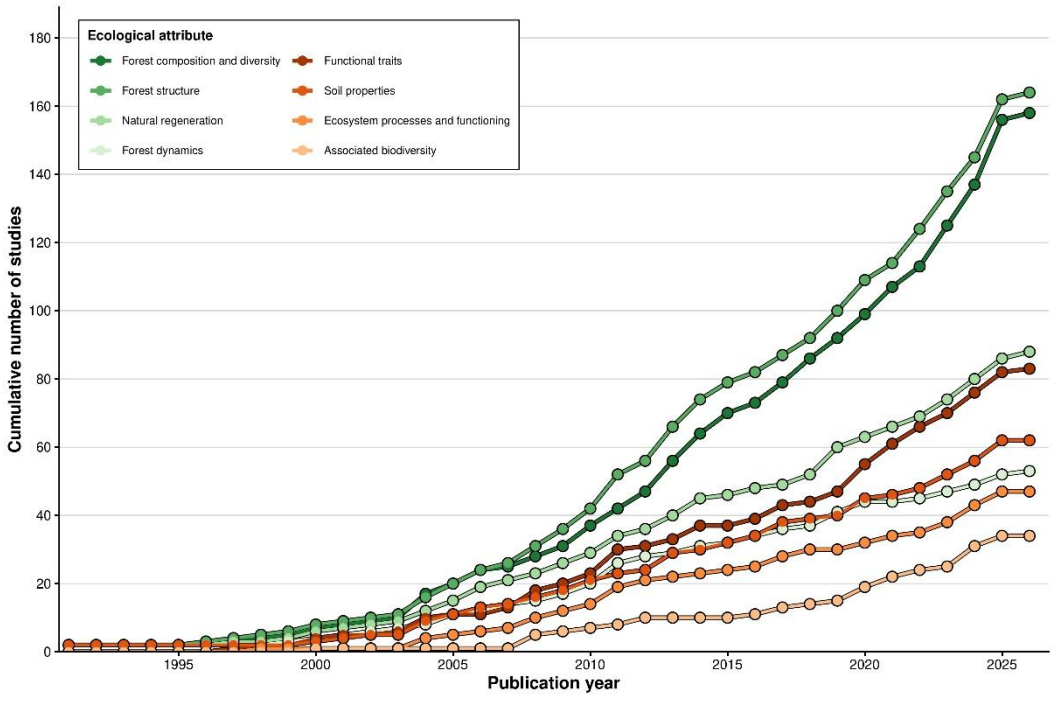


Figure 6. Accumulation curves of studies evaluating different ecological attributes in native–non-native tree mixtures over time (n = 235). Dots represent the cumulative number of studies evaluating each ecological-attribute category by year of publication. Note that data for 2026 are incomplete because the literature search was conducted before the end of the year.

Discussion

Uneven geography of the evidence

The available evidence on spontaneous native–non-native tree mixtures was geographically and socioeconomically uneven. Most cases were concentrated in high-income countries, particularly in the USA and several European countries. Nevertheless, the geographical coverage extended beyond these regions, with a relatively high number of cases in South America, particularly Brazil, Argentina, and Chile, as well as evidence from several African countries. The representation of several African countries is noteworthy, as previous global evidence syntheses on forest management, disturbance, and biodiversity have shown a strong concentration of research in Europe and North America, with considerably less evidence from other regions [63-65]. The predominance of high-income countries is also consistent with broader geographical biases in ecological and biodiversity research, where research effort has been associated with economic capacity [66], potentially reflecting global disparities in research funding and infrastructure [67]. Similar geographical imbalances have been documented in invasion ecology, where research effort remains unevenly distributed across regions [68].

Beyond these geographical imbalances, countries differed in the distribution and focus of their research. Although both USA and Poland were among the countries with the largest number of cases, the underlying research patterns differed considerably. In Poland, much of the evidence was concentrated among a relatively small number of recurring authors, whose research primarily focused on the invasion and spread of non-native trees in temperate forests [e.g., 39, 40, 69, 70]. In contrast, studies from the continental USA involved a broader range of authors and research contexts [e.g., 28, 43, 71-73]. Puerto Rico, an unincorporated territory of the USA, showed yet another pattern, with much of the evidence arising from long-term ecological research and forest monitoring, particularly studies in the Luquillo Experimental Forest [e.g., 74, 75], as well as from analyses of national forest inventory datasets [e.g., 76, 77].

514 Evidence was also unevenly distributed across biomes, with most cases
515 concentrated in “Tropical & Subtropical Moist Broadleaf Forests” and “Temperate
516 Broadleaf & Mixed Forests”. Both biomes were strongly overrepresented relative to their
517 global extent, so their prominence cannot be explained by biome area alone. This pattern
518 may partly reflect the geographical concentration of research effort, particularly in high-
519 income countries with greater research capacity (e.g., USA, several European
520 countries). Conversely, the limited representation of non-forest biomes (e.g., deserts,
521 tundra or grasslands) is expected, given the more restricted occurrence of trees in these
522 environments.

523 The two most represented biomes showed contrasting geographical patterns.
524 Evidence from “Tropical & Subtropical Moist Broadleaf Forests” was strongly associated
525 with islands, particularly those located in the Caribbean such as Puerto Rico, Virgin
526 Islands, Bahamas and Jamaica [e.g., 4, 16, 76], Hawaii [e.g., 78, 79], and the Seychelles
527 [e.g., 80, 81]. In contrast, evidence from “Temperate Broadleaf & Mixed Forests” was
528 predominantly associated with mainland areas, particularly in continental USA [e.g., 73,
529 82] and Europe [e.g., 69, 70, 83]. The high representation of temperate forests is
530 consistent with their well-documented predominance in ecological and evolutionary
531 research, likely driven by their overlap with high-income countries [84]. In contrast, the
532 pronounced insular component of the tropical evidence may partly reflect the long history
533 and high rates of non-native species introductions to islands [85], which have contributed
534 to the emergence of novel native–non-native communities in human-modified
535 landscapes [5]. Despite the broad biogeographical coverage of the systematic map,
536 evidence from the remaining biomes was much more limited, even in predominantly
537 forested biomes such as “Temperate Conifer Forests”, “Mangroves” and “Boreal
538 Forests/Taiga”. This limited representation may reflect both a genuine deficit of studies
539 and differences among biomes in the opportunities for non-native trees to establish and
540 persist. Environmental constraints, biotic resistance, or limited availability of suitable
541 microsites may restrict establishment, and the relative importance of these factors is

likely to vary substantially among biomes [86-88]. As a result, the patterns observed in the best-represented biomes may not be generalizable to less-represented biomes and regions.

High tree compositional diversity

The available evidence on spontaneous native–non-native tree mixtures encompassed a high diversity of tree species and species combinations. Patterns of species representation, however, differed between native and non-native trees. While the most frequently reported native species varied among biomes, reflecting differences in their natural species pools, certain non-native species recurred across different biomes. This was particularly evident for *P. cattleyanum* and *L. leucocephala*, which were among the most frequently reported non-native species in several tropical biomes. Their recurrence may partly reflect their long histories of human use and introduction outside their native ranges. *Psidium cattleyanum*, native to Brazil, was introduced into many tropical and subtropical regions for its edible fruits and ornamental use, including on oceanic islands [89]. Similarly, *L. leucocephala*, native to Central America, has been widely introduced throughout the tropics as a multipurpose tree for agroforestry, fodder, and wood production [90]. *Schinus terebinthifolia*, another South American species widely introduced as an ornamental tree [91, 92], was among the most frequently represented non-native species in “Tropical & Subtropical Grasslands, Savannas & Shrublands”, “Flooded Grasslands & Savannas”, and “Mangroves”. However, its prominence in the latter two biomes should be interpreted cautiously, as each was represented by only two cases. All three species have been documented as invasive in different regions [93], which may have contributed to the scientific attention they have received and their representation in the available literature.

Despite the recurrence of some species, no single native or non-native tree dominated the evidence even within the most represented biomes, where the most frequently reported species occurred in approximately one quarter of cases. Rather, the

evidence encompassed a wide variety of native–non-native species combinations, suggesting that non-native trees may establish and coexist across a broad range of native species pools and ecological contexts. This diversity of species combinations is consistent with the formation of novel communities, in which human-mediated species introductions and environmental change can generate diverse assemblages that differ from those occurring under historical conditions [18]. Importantly, the same non-native species may coexist with different native species pools across biomes, potentially resulting in species combinations with different functional characteristics. The degree of functional similarity or dissimilarity between native and non-native trees may therefore vary depending on the traits of the species involved [94]. Thus, biogeographical origin alone may provide limited information about the ecological consequences of native–non-native tree coexistence [95].

Context-dependency of anthropogenic drivers and natural disturbances

The anthropogenic drivers associated with the development of spontaneous native–non-native tree mixtures varied across ecological and geographical contexts. Differences in the relative representation of main drivers were particularly evident in the two best-represented biomes, which points to contrasting pathways to native–non-native tree coexistence.

In the “Tropical & Subtropical Moist Broadleaf Forests” biome, land abandonment was particularly frequent as the main driver on Caribbean islands (i.e., Puerto Rico, Virgin Islands, Bahamas and Jamaica), where agricultural abandonment was followed by secondary forest recovery and the development of new combinations of native and non-native tree species [e.g., 4, 76, 96]. This successional context was also recurrently affected by hurricanes, illustrating how natural disturbances can occur alongside anthropogenic drivers and influence the conditions under which native–non-native mixtures develop [e.g., 16, 97]. More broadly across the Neotropics, the occurrence of non-native species during secondary forest succession appears to be widespread: [98]

found non-native woody species in 81% of more than 50 secondary-forest chronosequences across ten countries, with a particularly high contribution during early succession.

In contrast, four anthropogenic drivers predominated in the studies of the "Temperate Broadleaf & Mixed Forests" biome. Land abandonment showed a broader geographical distribution than in tropical moist forests, being documented across widely separated regions in Europe [e.g., 83, 99, 100], North America [e.g., 28, 101], and Australasia [e.g., 27, 102]. Nearby non-native tree plantations or ornamental plantings were also a widely represented driver. For example, studies from Japan [17], Chile [103], and Poland [104] illustrate how planted non-native trees can spread into surrounding forests and become part of native–non-native mixtures, with this process depending on species-specific capacities for dispersal, establishment, and regeneration. Forest management was also a frequent main driver, mainly through management-induced canopy openings that promoted the regeneration of non-native trees [e.g., 105, 106]. Finally, urbanization was associated with shifts in the proportion of native and non-native trees along urban-rural and forest-edge gradients [e.g., 73, 107]. This is consistent with the strong focus of research on plant responses to urbanization in temperate Europe and North America [108]. Importantly, these drivers were not mutually exclusive, and several cases involved different combinations of land abandonment, forest management, nearby non-native plantations or ornamental plantings, and urbanization (Fig. S3a). Consequently, their co-occurrence may reflect the long history of human modification of temperate forest landscapes, where successive and overlapping land-use changes have left persistent impacts [109].

Other anthropogenic drivers were more prominent in some of the less-represented biomes. In the "Mediterranean Forests, Woodlands & Scrub" biome, nearby non-native tree plantations or ornamental plantings represented the most frequently identified main driver, and often co-occurred with forest management and anthropogenic fire, although their classification as main or secondary drivers varied among cases [e.g.,

13, 15, 110]. In the “Deserts & Xeric Shrublands” biome, hydrological alteration was particularly represented, and much of the evidence involved non-native *Tamarix* coexisting with native *Populus* and *Salix* species in riparian forests [e.g., 50, 71, 111]. Although the limited number of cases in these biomes prevents broader generalization, they provide additional examples of context-specific pathways to spontaneous mixture development.

Overall, natural disturbances were less frequently represented than anthropogenic drivers (Fig. S3b), but the recurrent occurrence of hurricanes in tropical forests shows that they can also influence the development of native–non-native tree mixtures and should not be overlooked. The predominance and frequent combination of anthropogenic drivers, operating in contexts that can also be influenced by natural disturbances, exemplify the interaction of forces typically linked to the emergence of novel ecosystems [18, 112]. Nevertheless, this does not necessarily imply that all spontaneous native–non-native tree mixtures identified in the systematic map qualify as novel ecosystems.

Knowledge gaps for understanding the ecological consequences of spontaneous native–non-native tree mixtures

The available evidence focused predominantly on forest composition, structure, regeneration and dynamics, whereas other ecological attributes (e.g., biodiversity, soil properties or ecosystem functioning) received considerably less attention. Despite the increasing number of studies over time, research has remained largely focused on these four ecological attributes (i.e., composition, structure, regeneration and dynamics; Fig. 6). As a result, we have a detailed picture of how spontaneous native–non-native tree communities are assembled and structured, but a less complete understanding of their ecological consequences. Addressing this knowledge gap will require moving beyond their description towards greater attention to the functional relationships between native

and non-native trees, their consequences for ecosystem functioning, and their effects on associated biodiversity.

Species identity alone provides limited information on how native and non-native trees interact when growing together. One key step is therefore to better understand the functional characteristics of the species that coexist in these forests. Functional traits and species-specific performance were considered in some studies, but they represented only a small fraction of the available evidence. Investigating differences in resource acquisition and use, tolerance to abiotic conditions or responses to disturbance could help determine whether coexisting species exhibit functional similarity or dissimilarity, and whether this results in complementarity or competition [113-115]. Linking functional traits with species-specific performance would therefore help move beyond describing which species coexist towards understanding the mechanisms underlying their coexistence and how species perform when growing together.

Importantly, this functional perspective should also extend beyond individual species to the ecosystem level. Soil properties were relatively underrepresented in our systematic map (Fig. 5), despite considerable evidence that non-native trees and woody plant invasions can modify soil physical, chemical, and biological properties relative to native or uninvaded vegetation [116, 117].Similarly, ecosystem processes and functioning were among the least studied ecological attributes in spontaneous native–non-native tree mixtures (Fig. 5). This contrasts with the extensive evidence comparing ecosystem properties and processes between forests dominated by native trees and those dominated by non-native trees [118-120].

Individual ecosystem functions do not necessarily respond in the same direction: a given species combination may enhance some functions, while reducing or having little effect on others, potentially resulting in trade-offs and synergies among ecosystem functions [121-123]. Considering several functions simultaneously, and relating their responses to the functional characteristics of coexisting tree species, would therefore

provide a more complete picture of what the emergence of these new tree combinations means for forest functioning.

Beyond ecosystem functioning, associated biodiversity also received little attention in our systematic map, and consequently little is known about how native–non-native tree mixtures affect other above- and belowground organisms. This is particularly relevant because ecological novelty can involve different dimensions of community organization [124], and changes in tree communities can influence multiple groups of associated organisms through changes in habitat conditions and resource availability [125-127]. These responses may involve species gains, losses, and turnover, resulting in changes in community composition that are not necessarily reflected in species richness [128, 129]. Extending research beyond tree communities is, thus, necessary to understand whether the development of spontaneous native–non-native tree mixtures is accompanied by a broader reorganization of forest biota. Once again, assessing ecosystem processes and functioning, as well as associated biodiversity, is essential to allow forecasting effects of native–non-native tree mixtures on ecosystem services provision, as the latter depends on the former.

Understanding spontaneous native–non-native tree mixtures also requires moving from snapshots towards their long-term trajectories. The available evidence covered a wider range of spatial than temporal scales, despite the inherently dynamic nature of these tree mixtures. Many develop in contexts of land abandonment, spread from plantations, forest management or urbanization, and their composition and species dominance may continue to change over decades. Longitudinal studies are needed to determine whether these mixtures represent relatively persistent communities or transitional stages, whether native and non-native trees continue to coexist or one group becomes increasingly dominant, and how their composition, structure, and functioning change through time. Understanding these trajectories also requires comparing tree mixtures with surrounding forest types. However, only a subset of studies compared tree mixtures with native forests, even fewer included forests dominated by non-native trees,

and relatively few considered both. Such comparisons are essential to determine whether mixtures retain characteristics of native forests, resemble forests dominated by non-native trees, or develop distinct characteristics. Together, long-term monitoring and comparative approaches would provide a better understanding of how these emerging forests develop and change.

Methodological limitations of the systematic map

Several methodological limitations should be considered when interpreting the patterns identified in this systematic map. First, as with systematic maps more generally, the frequency with which a particular variable or topic is represented in the evidence base should not be interpreted as an indication of its relative extent or importance [130]. In our case, the frequency with which species, drivers or ecological attributes were recorded reflects research effort, rather than their ecological importance in spontaneous native–non-native tree mixtures.

Our data extraction also involved some limitations in the characterization of these tree mixtures. We recorded up to three dominant native and non-native tree species reported in each case rather than the complete species composition of each mixture. This approach was adopted because the level of detail in species composition varied considerably among studies, with dominant species being more consistently reported than complete species lists. This allowed us to identify the most frequently represented species, but not to systematically compare species combinations among cases or determine how frequently particular native–non-native assemblages occurred. Similarly, although we identified the main anthropogenic drivers associated with the development of these mixtures, we did not reconstruct the complete history of each mixture. Therefore, we could not systematically assess how legacies of previous land use, forest management or disturbances influenced them as they appear in each individual study.

Finally, our search was restricted to studies published in English, Spanish and Portuguese, and did not include grey literature. Although English is the predominant

language of international scientific publishing, relevant research is not always published in English, and language restrictions can affect the geographical coverage of evidence syntheses [131]. The inclusion of Spanish and Portuguese broadened the scope of our review by allowing the inclusion of 12 additional studies, but relevant evidence published in other languages may still have been missed. Future global evidence syntheses would benefit from a broader range of languages, particularly those relevant to currently underrepresented regions [132]. The exclusion of grey literature may also have limited the representation of evidence generated outside academic publishing, including technical and management-oriented information [133].

Implications for forest management

The emergence of spontaneous native–non-native tree mixtures raises important questions for forest management. These forests are part of a broader increase in ecological novelty associated with species introductions, land-use change, and other human-driven environmental changes [134, 135]. Our systematic map shows that these tree mixtures encompass diverse species combinations arising under different ecological and anthropogenic contexts and coexist within landscape mosaics that include native forests, non-native tree plantations, and other forest types. Their management should therefore consider both the characteristics of individual stands and their broader landscape context. This heterogeneity also suggests that management implications cannot be inferred from species biogeographical origin alone (i.e., from the native *vs.* non-native status of tree species). Rather, they should consider the ecological roles and functional characteristics of coexisting species, as well as the processes and historical conditions that have shaped these communities, consistent with recent perspectives on managing ecological novelty [135, 136]. Spontaneous native–non-native tree mixtures should, therefore, not necessarily be treated as a single management category.

A context-dependent approach also requires defining clear management objectives. The presence of non-native trees within a mixed forest does not, by itself,

764 determine whether restoration, control or other interventions are required. Instead,
765 management decisions should consider the ecological characteristics and potential
766 impacts of the species involved, including their functional similarity or dissimilarity to
767 native species, the processes that led to the development of the mixture, and its
768 surrounding landscape. They should also account for the mixture's capacity to persist
769 and maintain ecosystem structure and functioning without continued management, its
770 effects on biodiversity, ecosystem functioning and ecosystem services, and site-specific
771 management priorities, such as conservation, production or ecosystem service provision
772 [137]. For example, preventing the further spread of a non-native species may be a
773 priority where mixed stands occur adjacent to native forests of high conservation value,
774 particularly when the species involved pose a risk to native biodiversity or ecosystem
775 functioning. Conversely, in highly modified landscapes where the mixture may persist
776 without continued intervention and its effects on biodiversity, ecosystem functioning or
777 ecosystem services are limited or acceptable in relation to management objectives,
778 monitoring or allowing forest dynamics to proceed may be more appropriate than active
779 control [138].
780
781 **Conclusions**
782 This systematic map provides the first global overview of research on spontaneous
783 native–non-native tree mixtures. The available evidence covers a wide range of tree
784 species, geographical regions and ecological contexts, showing that these forests can
785 develop under different combinations of anthropogenic drivers and natural disturbances.
786 However, research is unevenly distributed across countries and biomes, which limits our
787 ability to generalize the patterns observed.
788 Although the number of studies has increased over time, research has mainly
789 focused on forest composition, structure, regeneration and dynamics. In contrast,
790 functional traits, soil properties, ecosystem functioning and associated biodiversity have
791 received much less attention. Furthermore, most studies were based on a single

sampling occasion, and comparisons with native and fully non-native forests remain limited. Consequently, important questions remain about how these mixtures function, how they affect biodiversity and how they change over time. Future research should therefore combine the assessment of tree functional characteristics, ecosystem processes and associated biodiversity with long-term monitoring and comparisons among different forest types.

Overall, our findings highlight the need to better understand the ecological consequences of spontaneous native–non-native tree mixtures. These forests include different species combinations and develop under different environmental conditions and land-use histories, suggesting that their management cannot be based on the biogeographical origin of tree species alone. Instead, management decisions should consider the characteristics of the species involved, their effects on biodiversity and ecosystem functioning, and the specific objectives and conditions of each forest.

Supplementary Material

Online Resource 1. Supplementary tables (Excel file) containing Table S1 (list of publications included in the systematic map), Table S2 (systematic map data-extraction matrix), and Table S3 (representation of terrestrial biomes in the evidence base relative to their global terrestrial extent).

Online Resource 2. Supplementary figures (PDF file) containing Fig. S1 (study selection flow diagram), Fig. S2 (biome-specific bipartite networks of native and non-native tree taxa), and Fig. S3 (main and secondary anthropogenic drivers and natural disturbances associated with spontaneous native–non-native tree mixtures).

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Author Contributions

Writing - original draft preparation and visualization: RJ-O. Conceptualization: RJ-O, MC-C; Data extraction: RJ-O, ES-V, NC, GV-A, MC-C. Writing - review and editing: ES-V, NC, GV-A, MC-C, VF. Funding acquisition: RJ-O, GV-A, MC-C. Supervision: VF, MC-C. All authors have read and agreed to the published version of the manuscript.

Data Availability

The dataset with all extracted information is made available in the Supplementary Material (Table S2).

Declarations Human and Animal Rights and Informed Consent

This article does not contain any studies with human or animal subjects performed by any of the authors.

Competing interests

The authors declare no competing interests.

Key References

- Blumenthal DM, Diez J, Pearse I, Sofaer HR, Sorte CJ, Barnett D, et al. Why are non-native plants successful? Consistently fast economic traits and novel origin

jointly explain abundance across US ecoregions. New Phytol 2025;248:1192-204. https://doi.org/10.1111/nph.70307
- Demonstrates how functional traits and biogeographical origin jointly explain the abundance of non-native plants, highlighting the context dependency of these relationships across ecoregions.

- Divíšek J, Pyšek P, Richardson DM, Gotelli NJ, Beckage B, Molofsky J, et al. Naturalized and invasive species integrate differently in the trait space of local plant communities. Ecol Lett 2025;28:e70235. https://doi.org/10.1111/ele.70235
- Shows how naturalized and invasive plants differ in their functional integration into local communities, highlighting the importance of species traits and community context.

- Kerr MR, Ordonez A, Riede F, Atkinson J, Pearce EA, Sykut M, et al. Widespread ecological novelty across the terrestrial biosphere. Nat Ecol Evol 2025;9:589-98. https://doi.org/10.1038/s41559-025-02662-2
- Demonstrates the widespread occurrence of ecological novelty across terrestrial ecosystems, providing a global context for understanding the emergence of new ecological communities.

- McGeoch MA, Clarke DA, Mungi NA, Ordonez A. A nature-positive future with biological invasions: theory, decision support and research needs. Philos Trans R Soc Lond B Biol Sci 2024;379:20230014. https://doi.org/10.1098/rstb.2023.0014
- Provides a conceptual framework for integrating biological invasions into nature-positive conservation and management strategies, highlighting key research needs and decision-making challenges.

References

[1] Ellis EC. Ecology in an anthropogenic biosphere. Ecol Monogr 2015;85:287-331. https://doi.org/10.1890/14-2274.1

[2] Ellis EC, Gauthier N, Klein Goldewijk K, Bliege Bird R, Boivin N, Díaz S, et al. People have shaped most of terrestrial nature for at least 12,000 years. Proc Natl Acad Sci USA 2021;118:e2023483118. https://doi.org/10.1073/pnas.2023483118

[3] Enquist BJ, Erwin D, Savage V, Marquet PA. Scaling approaches and macroecology provide a foundation for assessing ecological resilience in the Anthropocene. Philos Trans R Soc Lond B Biol Sci 2024;379:20230010. https://doi.org/10.1098/rstb.2023.0010

[4] Lugo AE. Novel tropical forests: Nature's response to global change. Trop Conserv Sci 2013;6:325-37.

[5] Kueffer C, Kaiser-Bunbury CN. Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. Front Ecol Environ 2014;12:131-137. https://doi.org/10.1890/120201

[6] Catterall CP. Values of weedy regrowth for rainforest restoration. Ecol Manag Restor 2020;21:9-13. https://doi.org/10.1111/emr.12397

[7] Martinuzzi S, Gavier-Pizarro GI, Lugo AE, Radeloff VC. Future land-use changes and the potential for novelty in ecosystems of the United States. Ecosystems 2015;18:1332-42. https://doi.org/10.1007/s10021-015-9901-x

[8] Radeloff VC, Williams JW, Bateman BL, Burke KD, Carter SK, Childress ES, et al. The rise of novelty in ecosystems. Ecol Appl 2015;25:2051-68. https://doi.org/10.1890/14-1781.1

[9] Abelleira-Martínez OJ, Rodríguez MA, Rosario I, Soto N, López A, Lugo AE. Structure and species composition of novel forests dominated by an introduced species in northcentral Puerto Rico. New For 2010;39:1-18. https://doi.org/10.1007/s11056-009-9154-7

902 [10] Malizia A, Blundo C, Osinaga Acosta O, Carilla J, Ceballos SJ, Fernández RD, et al.
903 Three decades of above-ground biomass dynamics in subtropical Andean forests. Plant
904 Ecol Divers 2025;18:1-9. https://doi.org/10.1080/17550874.2025.2519230
905 [11] Petrášová M, Jarolímek I, Medvecká J. Neophytes in Pannonian hardwood
906 floodplain forests–History, present situation and trends. For Ecol Manage 2013;308:31-
907 39. https://doi.org/10.1016/j.foreco.2013.07.041
908 [12] Granda E, Antunes C, Máguas C, Castro-Díez P. Water use partitioning of native
909 and non-native tree species in riparian ecosystems under contrasting climatic conditions.
910 Funct Ecol 2022;36:2480-92. https://doi.org/10.1111/1365-2435.14149
911 [13] Badalamenti E, Cusimano D, La Mantia T, Pasta S, Romano S, Troia A, Ilardi V. The
912 ongoing naturalisation of *Eucalyptus* spp. in the Mediterranean Basin: new threats to
913 native species and habitats. Aust For 2018;81:239-49.
914 https://doi.org/10.1080/00049158.2018.1533512
915 [14] Teo A, Evans TA, Chisholm RA. Elevated litterfall phosphorus reduces litter and soil
916 organic matter pools in exotic-dominated novel forests in Singapore. J Trop Ecol
917 2024;40:e4. https://doi.org/10.1017/S0266467424000026
918 [15] Gómez P, Espinoza S, Garrido P, Martín JS, Ormazábal Y. Post-fire tree
919 regeneration from seed of the endangered *Nothofagus alessandrii* Espinosa in the Maule
920 region of central Chile. South For 2022;84:75-82.
921 https://doi.org/10.2989/20702620.2022.2039044
922 [16] Bellingham PJ, Tanner EV, Healey JR. Hurricane disturbance accelerates invasion
923 by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. J Veg Sci
924 2005;16:675-84. https://doi.org/10.1111/j.1654-1103.2005.tb02410.x
925 [17] Akasaka M, Tsuyuzaki S. Comparisons of recruitment, survival, and growth in
926 invasive and native saplings on a volcano. Plant Ecol 2009;202:235-45.
927 https://doi.org/10.1007/s11258-008-9464-4

928 [18] Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, et al. Novel
929 ecosystems: theoretical and management aspects of the new ecological world order.
930 Glob Ecol Biogeogr 2006;15:1-7. https://doi.org/10.1111/j.1466-822X.2006.00212.x
931 [19] Morse NB, Pellissier PA, Cianciola EN, Brereton RL, Sullivan MM, Shonka NK, et al.
932 Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for
933 pragmatic applications. Ecol Soc 2014;19. https://doi.org/10.5751/ES-06192-190212
934 [20] Ordonez A, Riede F, Normand S, Svenning JC. Towards a novel biosphere in 2300:
935 rapid and extensive global and biome-wide climatic novelty in the Anthropocene. Philos
936 Trans R Soc Lond B Biol Sci 2024;379:20230022.
937 [21] Ordonez A, Wright IJ, Olff H. Functional differences between native and alien
938 species: a global-scale comparison. Funct Ecol 2010;24:1353-61.
939 https://doi.org/10.1098/rstb.2023.0022
940 [22] van Kleunen M, Weber E, Fischer M. A meta-analysis of trait differences between
941 invasive and non-invasive plant species. Ecol Lett 2010;13:235-45.
942 https://doi.org/10.1111/j.1461-0248.2009.01418.x
943 [23] Truitt AM, Granek EF, Duveneck MJ, Goldsmith KA, Jordan MP, Yazzie KC. What is
944 novel about novel ecosystems: managing change in an ever-changing world. Environ
945 Manage 2015;55:1217-26. https://doi.org/10.1007/s00267-015-0465-5
946 [24] Miller JR, Bestelmeyer BT. What's wrong with novel ecosystems, really? Restoration
947 Ecology 2016;24:577-582. https://doi.org/10.1111/rec.12378
948 [25] Aide TM, Zimmerman JK, Rosario M, Marcano H. Forest recovery in abandoned
949 cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica
950 1996;537-548.
951 [26] Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H. Forest
952 regeneration in a chronosequence of tropical abandoned pastures: implications for
953 restoration ecology. Restor Ecol 2000;8:328-38. https://doi.org/10.1046/j.1526-
954 100x.2000.80048.x

[27] Paul M, Catterall CP, Pollard PC, Kanowski J. Recovery of soil properties and functions in different rainforest restoration pathways. For Ecol Manage 2010;259:2083-92. https://doi.org/10.1016/j.foreco.2010.02.019

[28] Mejía GA, Su C, Allen D, Chaudhary VB, Ong TW. Land-use legacies affect the composition and distribution of tree species and their belowground functions in a succession from old-field to mature temperate forest. For Ecosyst 2024;11:100249. https://doi.org/10.1016/j.fecs.2024.100249

[29] Abelleira-Martínez OJ. Observations on the fauna that visit African tulip tree (*Spathodea campanulata* Beauv.) forests in Puerto Rico. Acta Científica 2008;19:37-43.

[30] Rapaccini G, Porro Z, Passatore L, Trentanovi G, Zoderer BM, Pirelli P, et al. Interdisciplinary Approach to Regenerate Contaminated Urban Sites with Novel Ecosystems: The Multi-Layer Analysis of La Goccia Forest, a Case Study in Milan. Forests 2025;16:1410. https://doi.org/10.3390/f16091410

[31] Kawaletz H, Mölder I, Zerbe S, Annighöfer P, Terwei A, Ammer C. Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. J Plant Ecol 2013;6:305-15. https://doi.org/10.1093/jpe/rts044

[32] del Río M, Pretzsch H, Alberdi I, Bielak K, Bravo F, Brunner A, et al. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. Eur J For Res 2016;135:23-49. https://doi.org/10.1007/s10342-015-0927-6

[33] del Río M, Löf M, Bravo-Oviedo A, Jactel H. Understanding the complexity of mixed forest functioning and management: Advances and perspectives. For Ecol Manage 2021;489:119138. https://doi.org/10.1016/j.foreco.2021.119138

[34] del Río M, Pretzsch H, Ruiz-Peinado R, Jactel H, Coll L, Löf M, et al. Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect. J Appl Ecol 2022;59:2730-41. https://doi.org/10.1111/1365-2664.14267

981 [35] Pretzsch H. Facilitation and competition reduction in tree species mixtures in Central
982 Europe: Consequences for growth modeling and forest management. Ecol Model
983 2022;464:109812. https://doi.org/10.1016/j.ecolmodel.2021.109812
984 [36] Piotto D. A meta-analysis comparing tree growth in monocultures and mixed
985 plantations. For Ecol Manage 2008;255:781-786.
986 https://doi.org/10.1016/j.foreco.2007.09.065
987 [37] Gómez-González S, Paniw M, Blanco-Pastor JL, García-Cervigón AI, Godoy O,
988 Herrera JM, et al. Moving towards the ecological intensification of tree plantations.
989 Trends Plant Sci 2022;27:637-45. https://doi.org/10.1016/j.tplants.2021.12.009
990 [38] Warner E, Cook-Patton SC, Lewis OT, Brown N, Koricheva J, Eisenhauer N, et al.
991 Young mixed planted forests store more carbon than monocultures—a meta-analysis.
992 Front For Glob Change 2023;6:1226514. https://doi.org/10.3389/ffgc.2023.1226514
993 [39] Bury S, Dyderski MK. No effect of invasive tree species on aboveground biomass
994 increments of oaks and pines in temperate forests. For Ecosyst 2024;11:100201.
995 https://doi.org/10.1016/j.fecs.2024.100201
996 [40] Bury S, Dyderski MK. Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does
997 temperate forest natural regeneration respond to their quantity? NeoBiota 2025;97:179-
998 213. https://doi.org/10.3897/neobiota.97.135421
999 [41] Rivas-Torres G, Wilson C, Loiselle B, Luke Flory S. Experimental removal of an
1000 invasive tree in Galápagos promotes native and endemic species but also secondary
1001 invaders. Restor Ecol 2025;33:e14356. https://doi.org/10.1111/rec.14356
1002 [42] Trammell TL, D'Amico III V, Avolio ML, Mitchell JC, Moore E. Temperate deciduous
1003 forests embedded across developed landscapes: Younger forests harbour invasive
1004 plants and urban forests maintain native plants. J Ecol 2020;108:2366-75.
1005 https://doi.org/10.1111/1365-2745.13400
1006 [43] Lagrosa IV JJ, Andreu MG, Friedman MH, Zipperer WC, Northrop RJ. Effect of
1007 legacy on hydric forest structure in a subtropical urban watershed. Urban Ecosyst
1008 2021;24:49-58. https://doi.org/10.1007/s11252-020-01009-y

[44] Guariguata MR, Ostertag R. Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manage 2001;148:185-206. https://doi.org/10.1016/S0378-1127(00)00535-1

[45] Zimmerman N, Flint Hughes R, Cordell S, Hart P, Chang HK, Perez D, et al. Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai ‘i. Biotropica 2008;40:277-84. https://doi.org/10.1111/j.1744-7429.2007.00371.x

[46] James KL, Randall NP, Haddaway NR. A methodology for systematic mapping in environmental sciences. Environ Evid 2016;5:7. https://doi.org/10.1186/s13750-016-0059-6

[47] Pullin AS, Stewart GB. Guidelines for systematic review in conservation and environmental management. Conserv Biol 2006;20:1647-56. https://doi.org/10.1111/j.1523-1739.2006.00485.x

[48] O'Dea RE, Lagisz M, Jennions MD, Koricheva J, Noble DWA, Parker TH, et al. Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: A PRISMA extension. Biol Rev 2021;96:1695-722. https://doi.org/10.1111/brv.12721

[49] Smith SD, Devitt DA, Sala A, Cleverly JR, Busch DE. Water relations of riparian plants from warm desert regions. Wetlands 1998;18:687-96. https://doi.org/10.1007/BF03161683

[50] Sher AA, Marshall DL, Taylor JP. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecol Appl 2002;12:760-72. https://doi.org/10.1890/1051-0761(2002)012[0760:EPONPA]2.0.CO;2

[51] World Bank. World Bank Group country classifications by income level for FY27 (July 2026–June 2027). Washington, DC, World Bank. https://www.worldbank.org/ [Last access: 18th September 2026] 2026.

[52] Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, et al. An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 2017;67:534-45. https://doi.org/10.1093/biosci/bix014

[53] POWO (2026). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. https://powo.science.kew.org/ [Last access: 31st July 2026]

[54] Christie AP, Amano T, Martin PA, Petrovan SO, Shackelford GE, Simmons BI, et al. The challenge of biased evidence in conservation. Conserv Biol 2021;35:249-62. https://doi.org/10.1111/cobi.13577

[55] R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria 2025.

[56] Wickham H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York. 2016.

[57] van den Brand T. ggh4x: Hacks for ‘ggplot2’. R package version 0.3.1. 2025.

[58] Brunson JC, Read QD. ggalluvial: Alluvial Plots in 'ggplot2'. R package version 0.12.6. 2026.

[59] Campitelli E. ggnewscale: Multiple Fill and Colour Scales in ‘ggplot2’. R package version 0.5.2. 2025.

[60] Csárdi G, Nepusz T. The igraph software package for complex network research. InterJournal, Complex Systems 2006;1695.

[61] Pedersen TL. ggraph: An Implementation of Grammar of Graphics for Graphs and Networks. R package version 2.2.2. 2025.

[62] QGIS Development Team. QGIS Geographic Information System. QGIS Association 2024.

[63] Leverkus AB, Rey Benayas JM, Castro J, Boucher D, Brewer S, Collins BM, et al. Salvage logging effects on regulating and supporting ecosystem services—A systematic map. Can J For Res 2018;48:983-1000. https://doi.org/10.1139/cjfr-2018-0114

[64] Martin PA, Pérez-Izquierdo L, Biryol C, Brasseur S, Li Q, Aviles IL, et al. A systematic map of forest disturbance impacts on soil and litter fauna: Knowledge gaps and a roadmap for future research. EcoEvoRxiv [Preprint]. https://doi.org/10.32942/X2R929. 2025.

[65] Biryol C, Baldy V, Prevosto B, Trap J, Forey E, Perez-Izquierdo L, et al. Influence of forest thinning on the soil fauna: a systematic review of current knowledge and research gaps. Ann For Sci 2026;83:6. https://doi.org/10.1186/s13595-025-01320-8

[66] Tydecks L, Jeschke JM, Wolf M, Singer G, Tockner K. Spatial and topical imbalances in biodiversity research. PLoS One 2018;13:e0199327. https://doi.org/10.1371/journal.pone.0199327

[67] Pettorelli N, Graham NA, Seddon N, Bustamante M, Lowton MJ, Sutherland WJ, et al. Time to integrate global climate change and biodiversity science-policy agendas. J Appl Ecol 2021;58:2384-93. https://doi.org/10.1111/1365-2664.13985

[68] Seebens H, Meyerson LA, Richardson DM, Lenzner B, Tricarico E, Courchamp F, et al. Biological invasions: a global assessment of geographic distributions, long-term trends, and data gaps. Biol Rev 2025;100:2542-83. https://doi.org/10.1111/brv.70058

[69] Woziwoda B, Dyderski MK, Kobus S, Parzych A, Jagodziński AM. Natural regeneration and recruitment of native *Quercus robur* and introduced *Q. rubra* in European oak-pine mixed forests. For Ecol Manage 2019;449:117473. https://doi.org/10.1016/j.foreco.2019.117473

[70] Woziwoda B, Dyderski MK, Jagodziński AM. Forest land use discontinuity and northern red oak *Quercus rubra* introduction change biomass allocation and life strategy of lingonberry *Vaccinium vitis-idaea*. For Ecosyst 2021;8:9. https://doi.org/10.1186/s40663-021-00287-y

[71] Bateman HL, Chung-MacCoubrey A, Snell HL. Impact of non-native plant removal on lizards in riparian habitats in the southwestern United States. Restor Ecol 2008;16:180-90. https://doi.org/10.1111/j.1526-100X.2007.00361.x

[72] Mejía GA, Groffman PM, Avolio ML, Bratt AR, Cavender-Bares J, Grijseels NH, et al. Woody Plant–Soil Relationships in Interstitial Spaces Have Implications for Future Forests Within and Beyond Urban Areas. Ecosystems 2024;27:185-206. https://doi.org/10.1007/s10021-023-00881-x

[73] Baker M, Yesilonis I, Templeton L, Shobe B, Bos J, Sonti NF, Lautar K. Distributed urban forest patch sampling detects edge effects and woodland condition for monitoring and management. Ecosphere 2025;16:e70236. https://doi.org/10.1002/ecs2.70236

[74] Álvarez-Ruiz MÁ, Lugo AE. Landscape effects on structure and species composition of tabonuco forests in Puerto Rico: implications for conservation. For Ecol Manage 2012;266:138-47. https://doi.org/10.1016/j.foreco.2011.10.044

[75] Nytch CJ, Rojas-Sandoval J, Oliveras AE, Garcia RJS, Meléndez-Ackerman EJ. Effects of historical land use and recovery pathways on composition, structure, ecological function, and ecosystem services in a Caribbean secondary forest. For Ecol Manage 2023;546:121311. https://doi.org/10.1016/j.foreco.2023.121311

[76] Franklin J, Ripplinger J, Freid EH, Marcano-Vega H, Steadman DW. Regional variation in Caribbean dry forest tree species composition. Plant Ecol 2015;216:873-86. https://doi.org/10.1007/s11258-015-0474-8

[77] Presley SJ, Rojas-Sandoval J, Willig MR. Long-term stability of tropical forest metacommunities in Puerto Rico: Native and non-native species. Biotropica 2025;57:e13419. https://doi.org/10.1111/btp.13419

[78] Allison SD, Vitousek PM. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 2004;141:612-619. https://doi.org/10.1007/s00442-004-1679-z

[79] Tuttle NC, Beard KH, Pitt WC. Invasive litter, not an invasive insectivore, determines invertebrate communities in Hawaiian forests. Biol Invasions 2009;11:845-55. https://doi.org/10.1007/s10530-008-9298-y

[80] Dietz H, Wirth LR, Buschmann H. Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. Biol Invasions 2004;6:511-21. https://doi.org/10.1023/B:BINV.0000041566.23330.60

[81] Baguette F, Harryba S, Baboorun T, Adam PA, Senterre B. Characterization and evolution of the lowland tropical rain forest of the smallest oceanic Gondwana fragments, with implications for restoration and invasion ecology. For Ecol Manage 2022;504:119837. https://doi.org/10.1016/j.foreco.2021.119837

[82] Pennington DN, Hansel JR, Gorchov DL. Urbanization and riparian forest woody communities: diversity, composition, and structure within a metropolitan landscape. Biol Conserv 2010;143:182-94. https://doi.org/10.1016/j.biocon.2009.10.002

[83] Conedera M, Wohlgemuth T, Tanadini M, Pezzatti GB. Drivers of broadleaved evergreen species spread into deciduous forests in the southern Swiss Alps. Reg Environ Change 2018;18:425-36. https://doi.org/10.1007/s10113-017-1212-7

[84] Culumber ZW, Anaya-Rojas JM, Booker WW, Hooks AP, Lange EC, Pluer B, et al. Widespread biases in ecological and evolutionary studies. Bioscience 2019;69:631-40. https://doi.org/10.1093/biosci/biz063

[85] Russell JC, Kueffer C. Island biodiversity in the Anthropocene. Annu Rev Environ Resour 2019;44:31-60. https://doi.org/10.1146/annurev-environ-101718-033245

[86] Lonsdale WM. Global patterns of plant invasions and the concept of invasibility. Ecology 1999;80:1522-36. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

[87] Lugo AE. Mangrove forests: a tough system to invade but an easy one to rehabilitate. Mar Pollut Bull 1999;37:427-30. https://doi.org/10.1016/S0025-326X(98)00120-9

[88] Delavaux CS, Crowther TW, Zohner CM, Robmann NM, Lauber T, van den Hoogen J, et al. Native diversity buffers against severity of non-native tree invasions. Nature 2023;621:773-81. https://doi.org/10.1038/s41586-023-06440-7

[89] Proença CEB, Tuler AC, Lucas EJ, Vasconcelos TNDC, de Faria JEQ, Staggemeier VG, et al. Diversity, phylogeny and evolution of the rapidly evolving genus *Psidium* L. (Myrtaceae, Myrteae). Ann Bot 2022;129:367-88. https://doi.org/10.1093/aob/mcac005

[90] Bageel A, Honda MD, Carrillo JT, Borthakur D. Giant leucaena (*Leucaena leucocephala* subsp. *glabrata*): a versatile tree-legume for sustainable agroforestry. Agrofor Syst 2020;94:251-68. https://doi.org/10.1007/s10457-019-00392-6

[91] Mukherjee A, Williams DA, Wheeler GS, Cuda JP, Pal S, Overholt WA. Brazilian peppertree (*Schinus terebinthifolius*) in Florida and South America: evidence of a

1146 possible niche shift driven by hybridization. Biol Invasions 2012;14:1415-30.
1147 https://doi.org/10.1007/s10530-011-0168-7
1148 [92] Wheeler GS, Kay FM, Vitorino MD, Manrique V, Diaz R, Overholt WA. Biological
1149 control of the invasive weed *Schinus terebinthifolia* (Brazilian Peppertree), a review of
1150 the project with an update on the proposed agents. South East Nat 2016;15:15-34.
1151 https://doi.org/10.1656/058.015.sp802
1152 [93] Global Invasive Species Database (GISD). Global Invasive Species Database.
1153 IUCN Species Survival Commission, Invasive Species Specialist Group.
1154 https://www.iucngisd.org/gisd/ [Last access: 12th October 2026] 2026.
1155 [94] Blumenthal DM, Diez J, Pearse I, Sofaer HR, Sorte CJ, Barnett D, et al. Why are
1156 non-native plants successful? Consistently fast economic traits and novel origin jointly
1157 explain abundance across US ecoregions. New Phytol 2025;248:1192-204.
1158 https://doi.org/10.1111/nph.70307
1159 [95] Buckley YM, Catford J. Does the biogeographic origin of species matter? Ecological
1160 effects of native and non-native species and the use of origin to guide management. J
1161 Ecol 2016;104:4-17. https://doi.org/10.1111/1365-2745.12501
1162 [96] Lugo AE, Brandeis TJ. New mix of alien and native species coexists in Puerto Rico's
1163 landscapes. In: Burslem DFRP, Pinard MA, Hartley SE, editors. Biotic interactions in the
1164 tropics: their role in the maintenance of species diversity. Cambridge: Cambridge
1165 University Press; 2005. p. 484-509.
1166 [97] Brandeis TJ, Helmer EH, Marcano-Vega H, Lugo AE. Climate shapes the novel plant
1167 communities that form after deforestation in Puerto Rico and the US Virgin Islands. For
1168 Ecol Manage 2009;258:1704-18. https://doi.org/10.1016/j.foreco.2009.07.030
1169 [98] Resende AF, Poorter L, Matos FA, Bongers F, César R, Heringer G, et al. Non-native
1170 and invasive tree species are abundant in neotropical secondary forest but decline over
1171 time. Nat Plants 2026;1-13. https://doi.org/10.1038/s41477-026-02327-3

[99] Knüsel S, Conedera M, Bugmann H, Wunder J. Low litter cover, high light availability and rock cover favour the establishment of *Ailanthus altissima* in forests in southern Switzerland. NeoBiota 2019;46:91-116. https://doi.org/10.3897/neobiota.46.35722

[100] Knüsel S, Conedera M, Zweifel R, Bugmann H, Etzold S, Wunder J. High growth potential of *Ailanthus altissima* in warm and dry weather conditions in novel forests of southern Switzerland. Trees 2019;33:395-409. https://doi.org/10.1007/s00468-018-1785-x

[101] Miller AC, Woeste KE, Anagnostakis SL, Jacobs DF. Exploration of a rare population of Chinese chestnut in North America: stand dynamics, health and genetic relationships. AoB Plants 2014;6:plu065. https://doi.org/10.1093/aobpla/plu065

[102] Lee WG, Wilson JB, Meurk CD, Kennedy PC. Invasion of the subantarctic Auckland Islands, New Zealand, by the asterad tree *Olearia lyallii* and its interaction with a resident myrtaceous tree *Metrosideros umbellata*. J Biogeogr 1991;493-508.

[103] Urrutia J, Pauchard A, Garcia RA. Differences in plant composition in an *Araucaria araucana* (Molina) K. Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. Gayana Bot 2013;70:92-100.

[104] Wilgan R, Kujawska MB, Leski T. Impact of invasive alien tree species on symbiotic soil fungal communities in pine-dominated forest ecosystems in central Europe. Geoderma 2024;452:117111. https://doi.org/10.1016/j.geoderma.2024.117111

[105] Chabrerie O, Verheyen K, Saguez R, Decocq G. Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 2008;14:204-12. https://doi.org/10.1111/j.1472-4642.2007.00453.x

[106] Chmura D. The spread and role of the invasive alien tree *Quercus rubra* (L.) in novel forest ecosystems in central Europe. Forests 2020;11:586. https://doi.org/10.3390/f11050586

[107] Schmit JP, Johnson LR, Baker M, Darling L, Fahey R, Locke DH, et al. The influence of urban and agricultural landscape contexts on forest diversity and structure across ecoregions. Ecosphere 2025;16:e70188. https://doi.org/10.1002/ecs2.70188

[108] de Barros Ruas R, Costa LMS, Bered F. Urbanization driving changes in plant species and communities–A global view. Glob Ecol Conserv 2022;38:e02243. https://doi.org/10.1016/j.gecco.2022.e02243

[109] Gilliam FS. Forest ecosystems of temperate climatic regions: from ancient use to climate change. New Phytol 2016;212:871-87. https://doi.org/10.1111/nph.14255

[110] Fuentes-Ramírez A, Pauchard A, Cavieres LA, García RA. Survival and growth of *Acacia dealbata* vs. native trees across an invasion front in south-central Chile. For Ecol Manage 2011;261:1003-1009. https://doi.org/10.1016/j.foreco.2010.12.018

[111] Bateman HL, Merritt DM. Complex riparian habitats predict reptile and amphibian diversity. Glob Ecol Conserv 2020;22:e00957. https://doi.org/10.1016/j.gecco.2020.e00957

[112] Jackson ST. Perspective: Ecological novelty is not new. In: Hobbs RJ, Higgs ES, Hall CM, editors. Novel ecosystems: intervening in the new ecological world order. John Wiley & Sons; 2013. p. 61-65.

[113] de Bello F, Price JN, Münkemüller T, Liira J, Zobel M, Thuiller W, et al. Functional species pool framework to test for biotic effects on community assembly. Ecology 2012;93:2263-73. https://doi.org/10.1890/11-1394.1

[114] Loiola PP, de Bello F, Chytrý M, Götzenberger L, Carmona CP, Pyšek P, Lososová Z. Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. J Ecol 2018;106:2230-41. https://doi.org/10.1111/1365-2745.12986

[115] Divíšek J, Pyšek P, Richardson DM, Gotelli NJ, Beckage B, Molofsky J, et al. Naturalized and invasive species integrate differently in the trait space of local plant communities. Ecol Lett 2025;28:e70235. https://doi.org/10.1111/ele.70235

[116] Wohlgemuth T, Gossner MM, Campagnaro T, Marchante H, Van Loo M, Vacchiano G, et al. Impact of non-native tree species in Europe on soil properties and biodiversity: a review. NeoBiota 2022;78:45-69. https://doi.org/10.3897/neobiota.78.87022

[117] Pu J, Cai L, Mak-Mensah E. Ecological impacts of woody plant invasions on soil biochemical properties: A meta-analysis. Biol Invasions 2026;28:154. https://doi.org/10.1007/s10530-026-03875-7

[118] Castro-Díez P, Vaz AS, Silva JS, Van Loo M, Alonso Á, Aponte C, et al. Global effects of non-native tree species on multiple ecosystem services. Biol Rev 2019;94:1477-501. https://doi.org/10.1111/brv.12511

[119] Castro-Díez P, Alonso A, Saldana-Lopez A, Granda E. Effects of widespread non-native trees on regulating ecosystem services. Sci Total Environ 2021;778:146141. https://doi.org/10.1016/j.scitotenv.2021.146141

[120] Lázaro-Lobo A, Fernandez RD, Alonso A, Cruces P, Cruz-Alonso V, Ervin GN, et al. Worldwide comparison of carbon stocks and fluxes between native and non-native forests. Biol Rev 2025;100:1105-26. https://doi.org/10.1111/brv.13176

[121] Felipe-Lucia MR, Soliveres S, Penone C, Manning P, van der Plas F, Boch S, et al. Multiple forest attributes underpin the supply of multiple ecosystem services. Nat Commun 2018;9:4839. https://doi.org/10.1038/s41467-018-07082-4

[122] Van der Plas F, Ratcliffe S, Ruiz-Benito P, Scherer-Lorenzen M, Verheyen K, Wirth C, et al. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. Ecol Lett 2018;21:31-42. https://doi.org/10.1111/ele.12868

[123] Van Der Plas F. Biodiversity and ecosystem functioning in naturally assembled communities. Biol Rev 2019;94:1220-45. https://doi.org/10.1111/brv.12499

[124] Schittko C, Bernard-Verdier M, Heger T, Buchholz S, Kowarik I, von der Lippe M, et al. A multidimensional framework for measuring biotic novelty: How novel is a community? Glob Change Biol 2020;26:4401-4417. https://doi.org/10.1111/gcb.15140

[125] Ampoorter E, Barbaro L, Jactel H, Baeten L, Boberg J, Carnol M, et al. Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. Oikos 2020;129:133-46. https://doi.org/10.1111/oik.06290

[126] Schuldt A, Huke P, Glatthorn J, Hagge J, Wildermuth B, Matevski D. Tree mixtures mediate negative effects of introduced tree species on bird taxonomic and functional diversity. J Appl Ecol 2022;59:3049-60. https://doi.org/10.1111/1365-2664.14300

[127] Wildermuth B, Seifert CL, Husemann M, Schuldt A. Metabarcoding reveals that mixed forests mitigate negative effects of non-native trees on canopy arthropod diversity. Ecol Appl 2023;33:e2921. https://doi.org/10.1002/eap.2921

[128] Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH. Terrestrial ecosystem responses to species gains and losses. Science 2011;332:1273-1277. https://doi.org/10.1126/science.1197479

[129] Kortz AR, Magurran AE. Complex community responses underpin biodiversity change following invasion. Biol Invasions 2021;23:3063-76. https://doi.org/10.1007/s10530-021-02559-8

[130] Martin PA, Amirmohammedi F, Barreto C, Berger I, Bissessur P, Christie AP, et al. Factors influencing the use of scientific evidence in conservation practice and policy: Insights from a systematic map. J Appl Ecol 2026;63:e70565. https://doi.org/10.1111/1365-2664.70565

[131] Nuñez MA, Amano T. Monolingual searches can limit and bias results in global literature reviews. Nat Ecol Evol 2021;5:264. https://doi.org/10.1038/s41559-020-01369-w

[132] Hannah K, Haddaway NR, Fuller RA, Amano T. Language inclusion in ecological systematic reviews and maps: Barriers and perspectives. Res Synth Methods 2024;15:466-82. https://doi.org/10.1002/jrsm.1699

[133] Haddaway NR, Collins AM, Coughlin D, Kirk S. The role of Google Scholar in evidence reviews and its applicability to grey literature searching. PLoS One 2015;10:e0138237. https://doi.org/10.1371/journal.pone.0138237

[134] Kerr MR, Ordonez A, Riede F, Atkinson J, Pearce EA, Sykut M, et al. Widespread ecological novelty across the terrestrial biosphere. Nat Ecol Evol 2025;9:589-98. https://doi.org/10.1038/s41559-025-02662-2

[135] Kerr MR, Svenning JC, Riede F, Buitenwerf R, Abraham AJ, Marjakangas EL, et al. The making of novel ecosystems: A process-based framework for measurement, analysis and application. Methods Ecol Evol 2026;17:683-704. https://doi.org/10.1111/2041-210x.70255

[136] Groner E, Peeters A, Shachak M. Ecological Integrity of Hybrid Ecosystems in the Anthropocene: The Impact of Self-Organization on Function and Sustainability. Ecol Evol 2026;16:e73403. https://doi.org/10.1002/ece3.73403

[137] Hobbs RJ, Higgs E, Harris JA. Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol 2009;24:599-605. https://doi.org/10.1016/j.tree.2009.05.012

[138] McGeoch MA, Clarke DA, Mungi NA, Ordonez A. A nature-positive future with biological invasions: theory, decision support and research needs. Philos Trans R Soc Lond B Biol Sci 2024;379:20230014. https://doi.org/10.1098/rstb.2023.0014

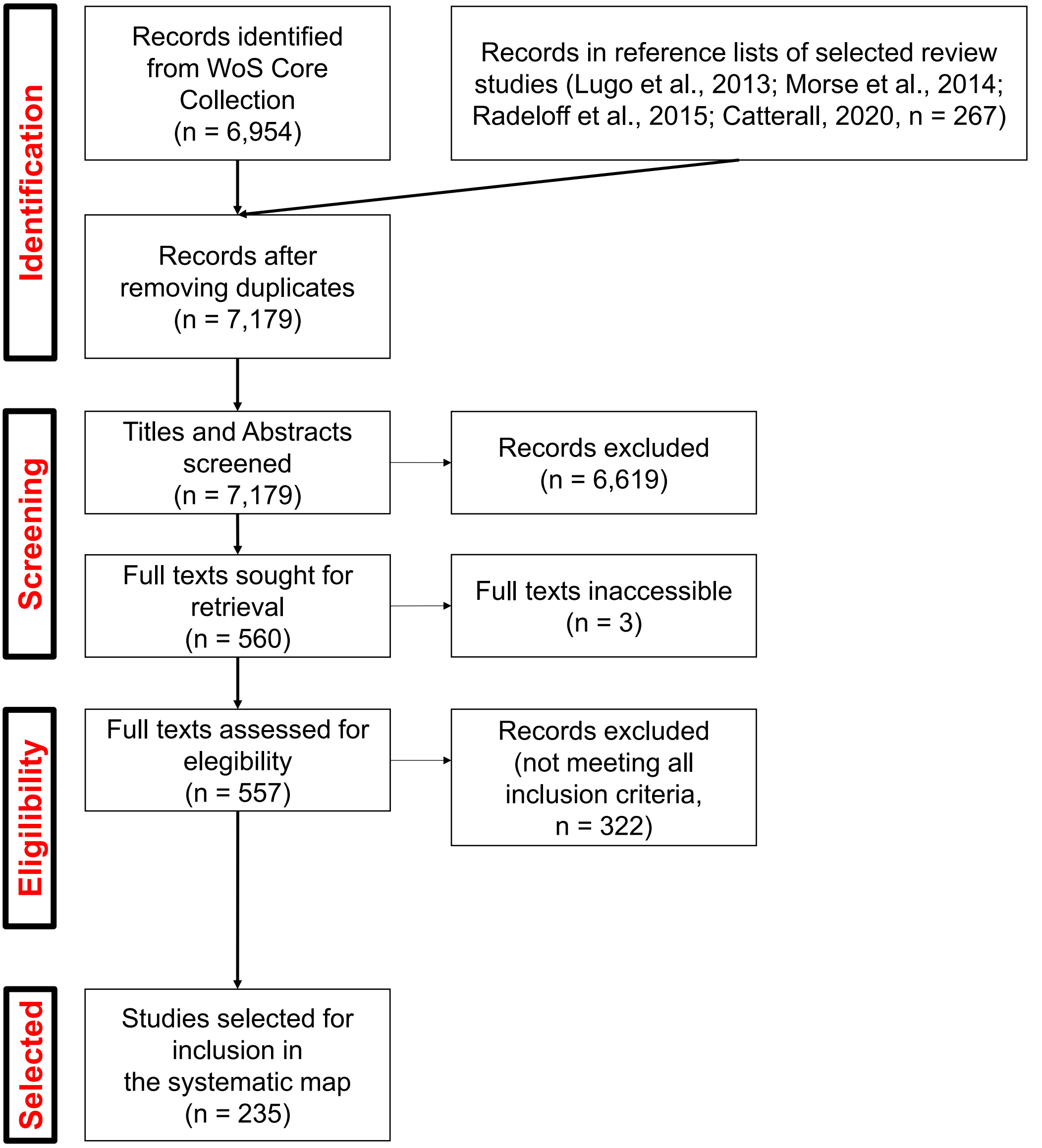


Fig. S1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram of the literature search and selection process. The diagram illustrates the number of records identified, screened, excluded, and retained at each stage. The search was conducted in Web of Science (WoS).

Tropical & Subtropical Moist Broadleaf Forests (n = 92)

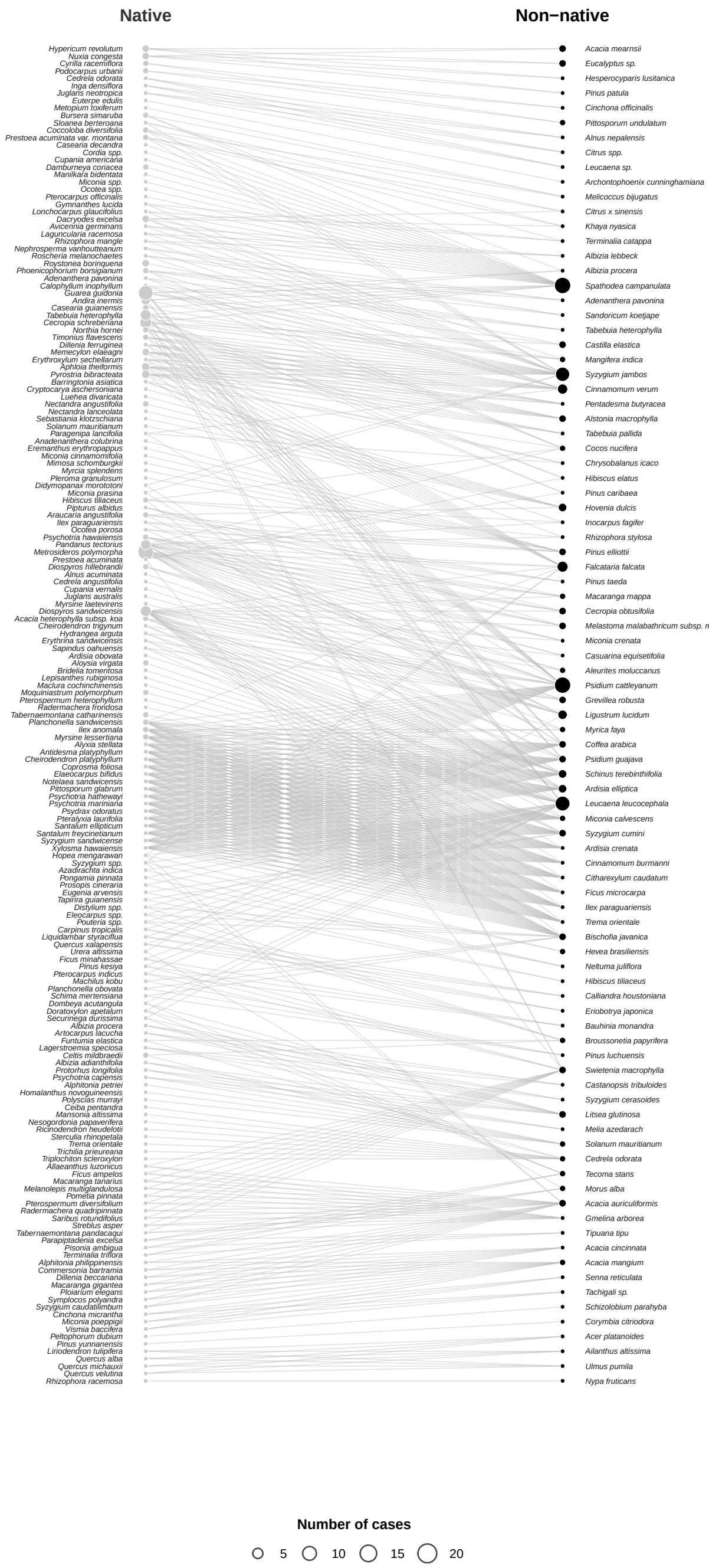


Fig. S2. Bipartite networks showing the dominant native and non-native tree taxa represented in the evidence for each terrestrial biome. Nodes represent tree taxa, with native taxa (grey colour) shown on the left and non-native taxa (black colour) on the right. Node size is proportional to the number of cases within the corresponding biome in which each taxon was recorded. Links are unweighted and indicate co-occurrence of native and non-native taxa within the same case, irrespective of its frequency; other native and/or non-native tree taxa could occur within the same case. The networks include only the dominant tree taxa extracted for each case and should therefore not be interpreted as complete inventories of the tree-community composition. Numbers in parentheses in biome headers indicate the total number of cases assigned to each biome. Cases spanning more than one biome were counted once in each corresponding biome.

Temperate Broadleaf & Mixed Forests (n = 89)

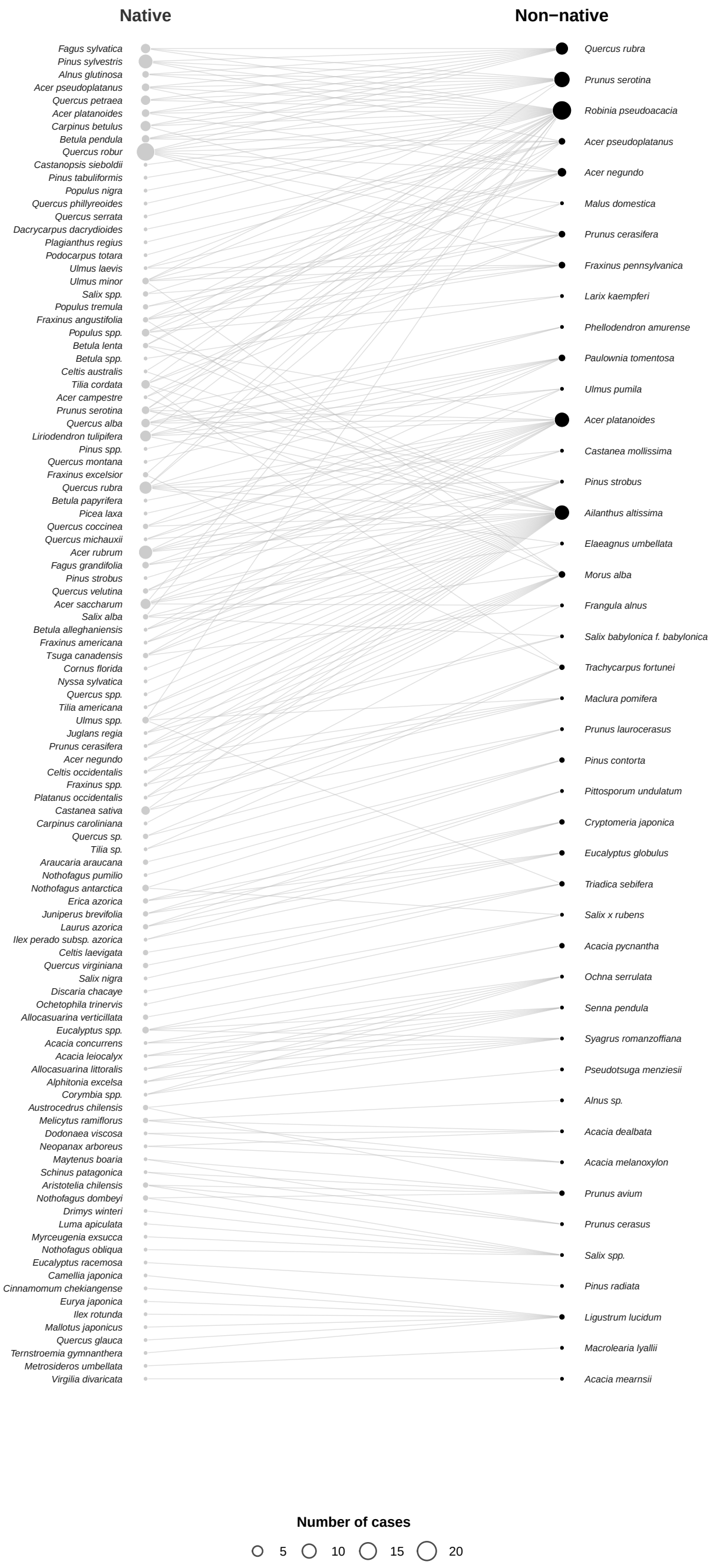


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

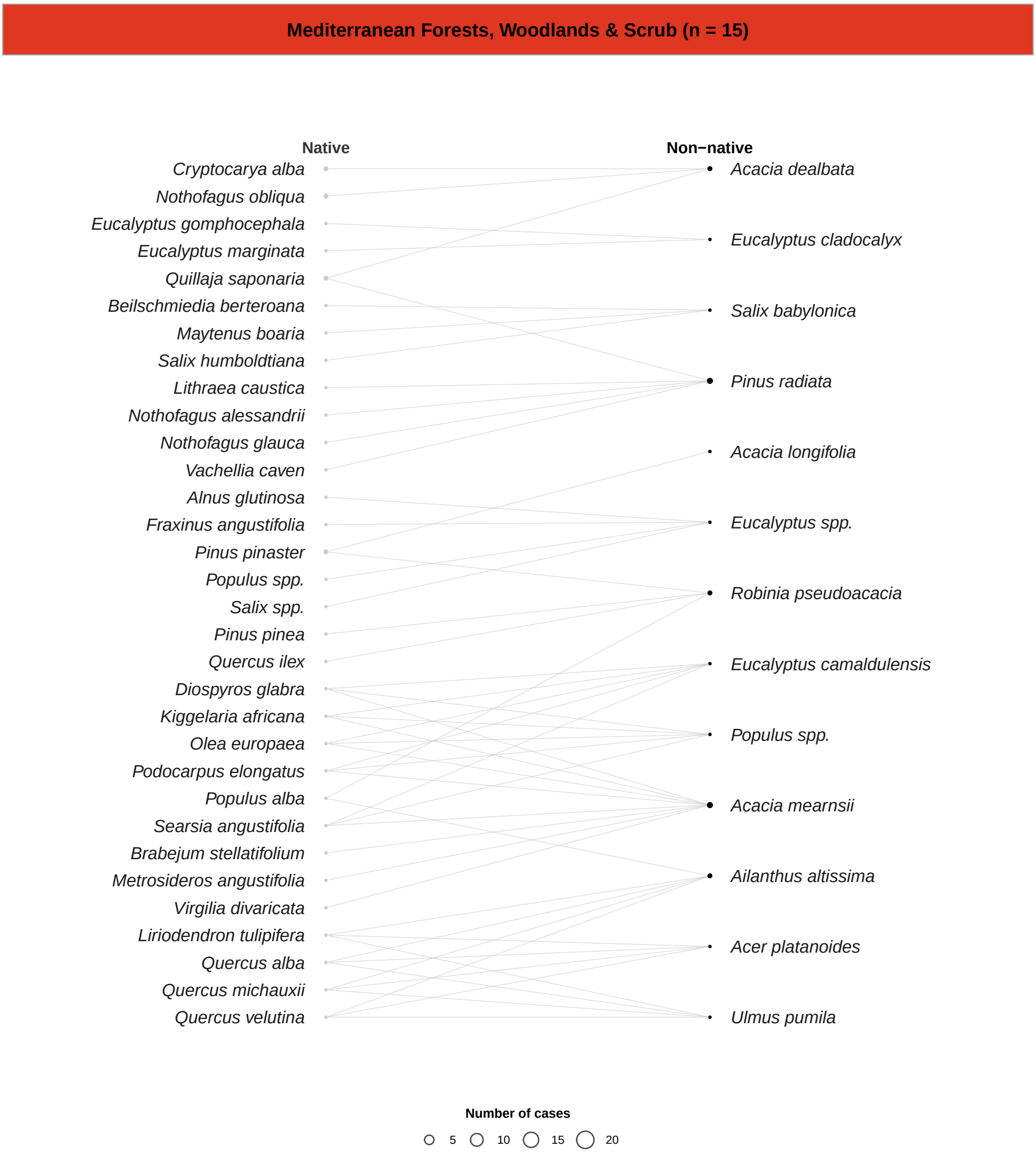


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

Temperate Grasslands, Savannas & Shrublands (n = 15)

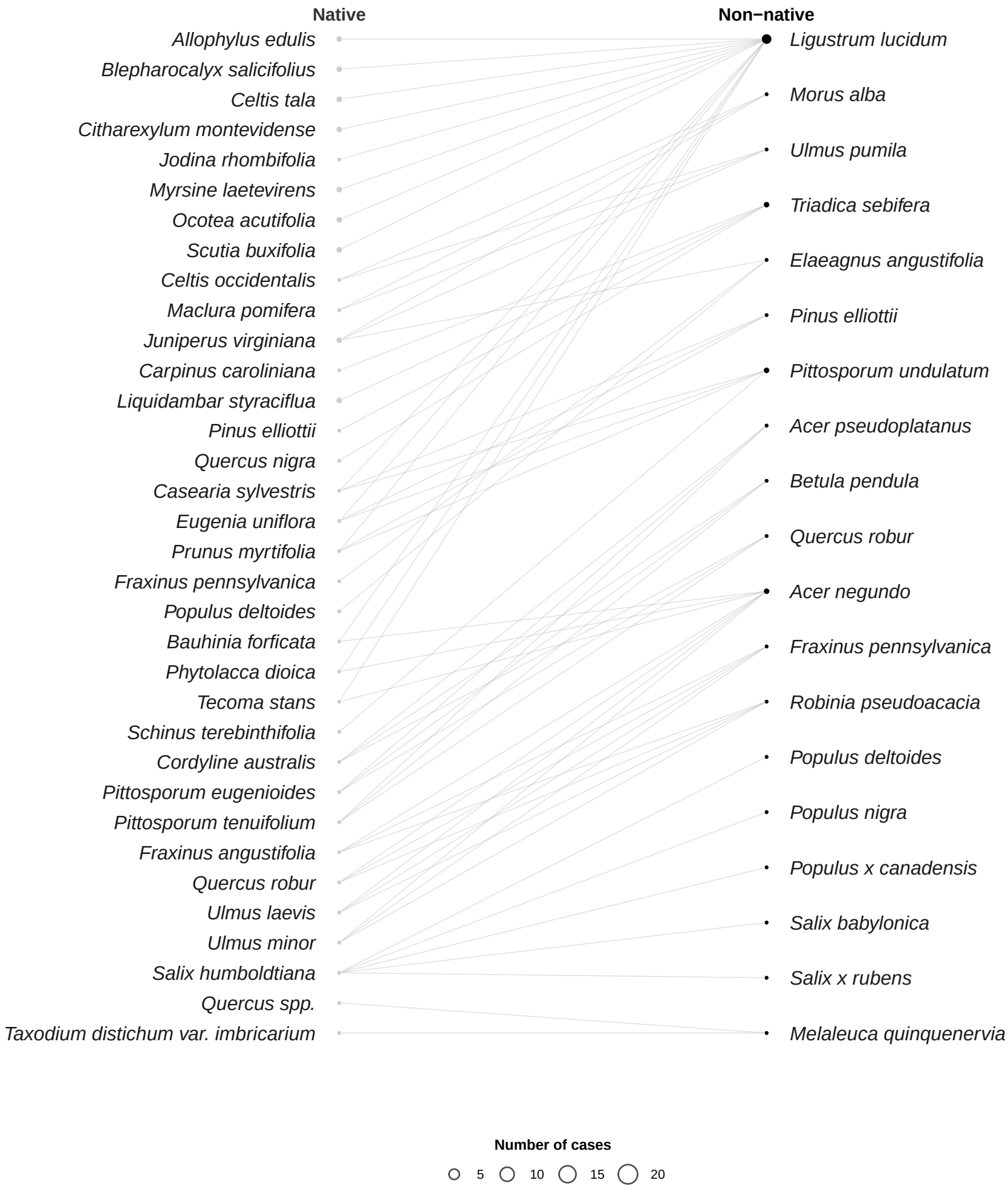


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

Tropical & Subtropical Dry Broadleaf Forests (n = 15)

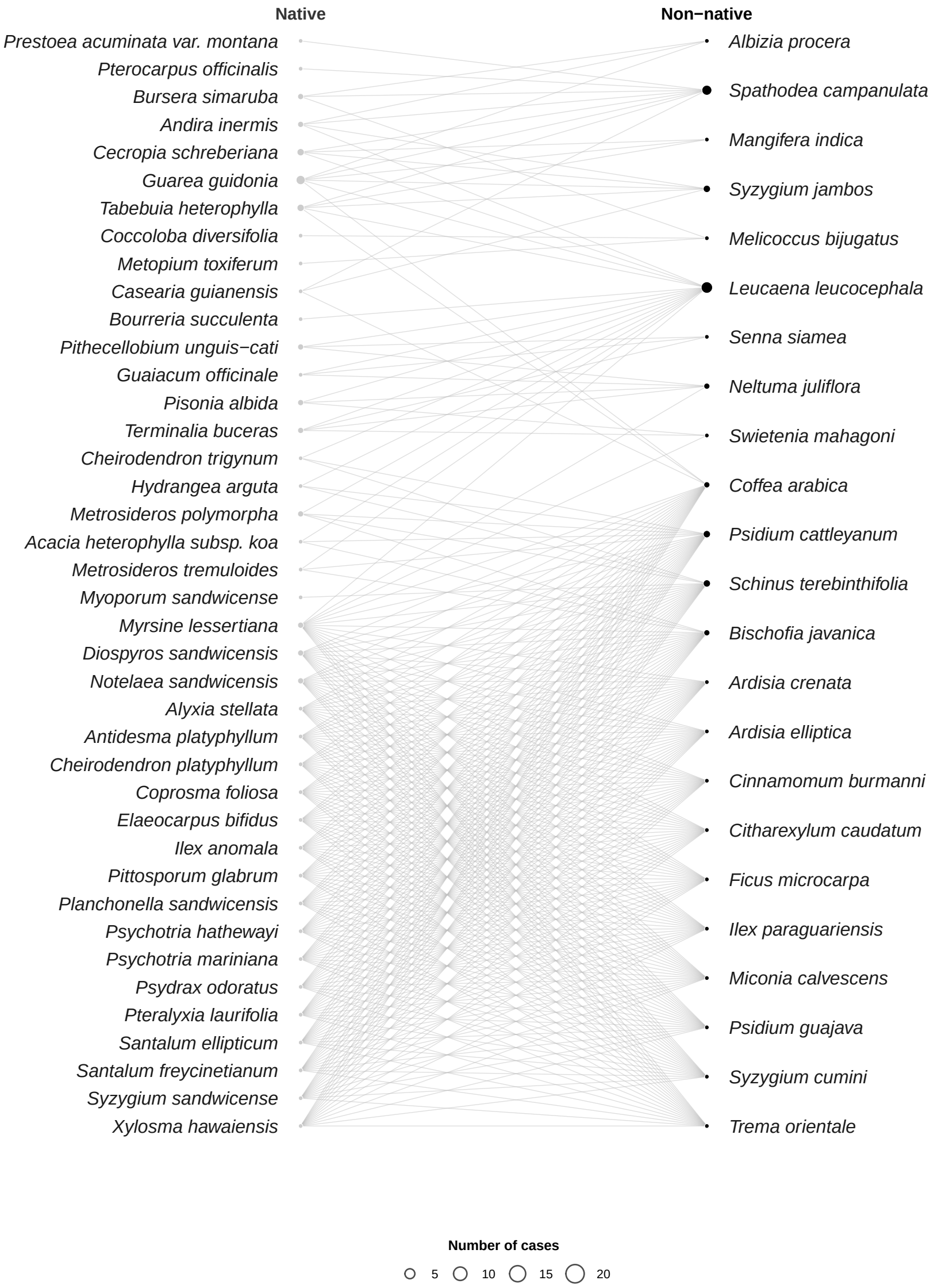


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

Deserts & Xeric Shrublands (n = 12)

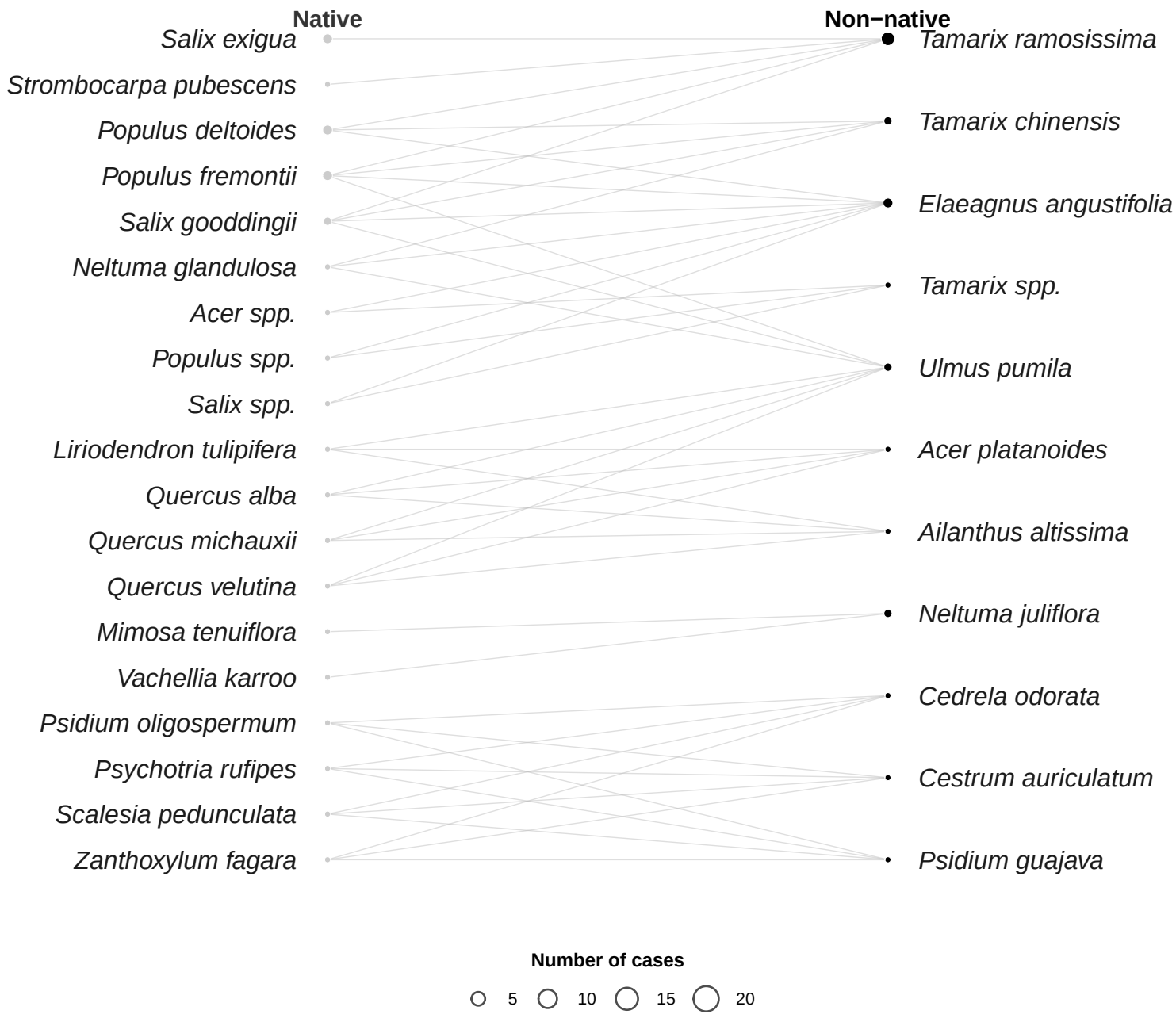


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

Tropical & Subtropical Grasslands, Savannas & Shrublands (n = 7)

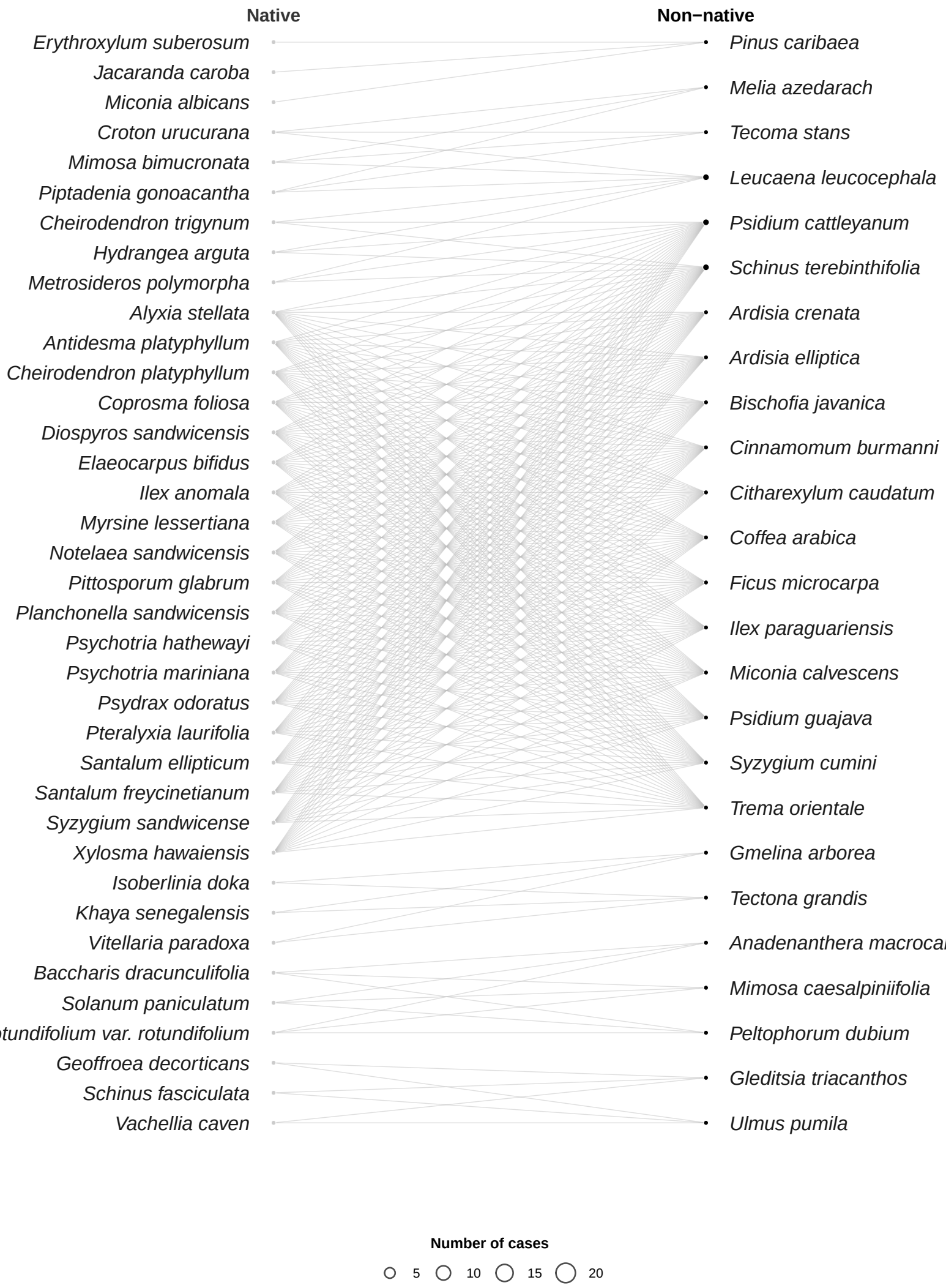


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

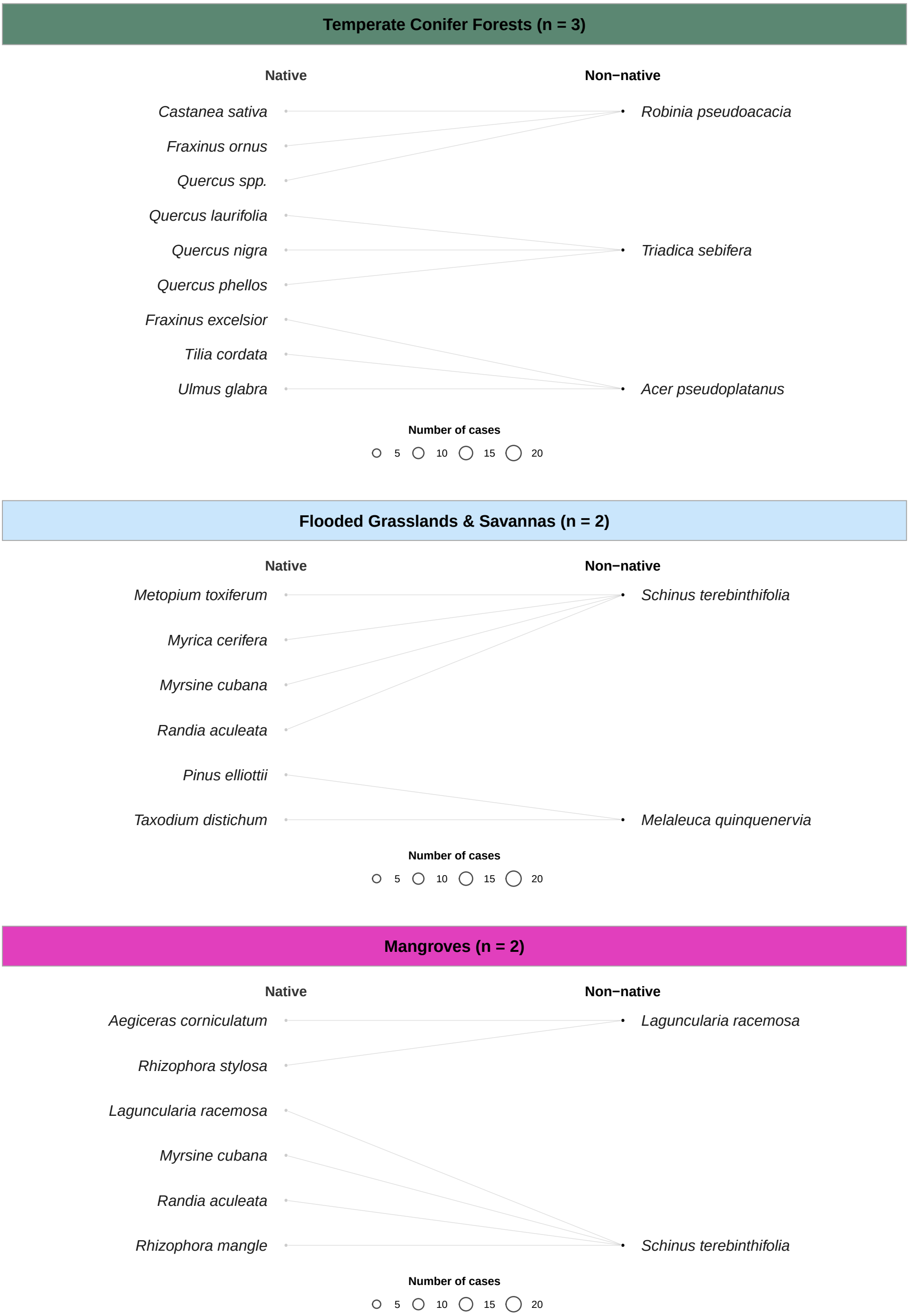


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

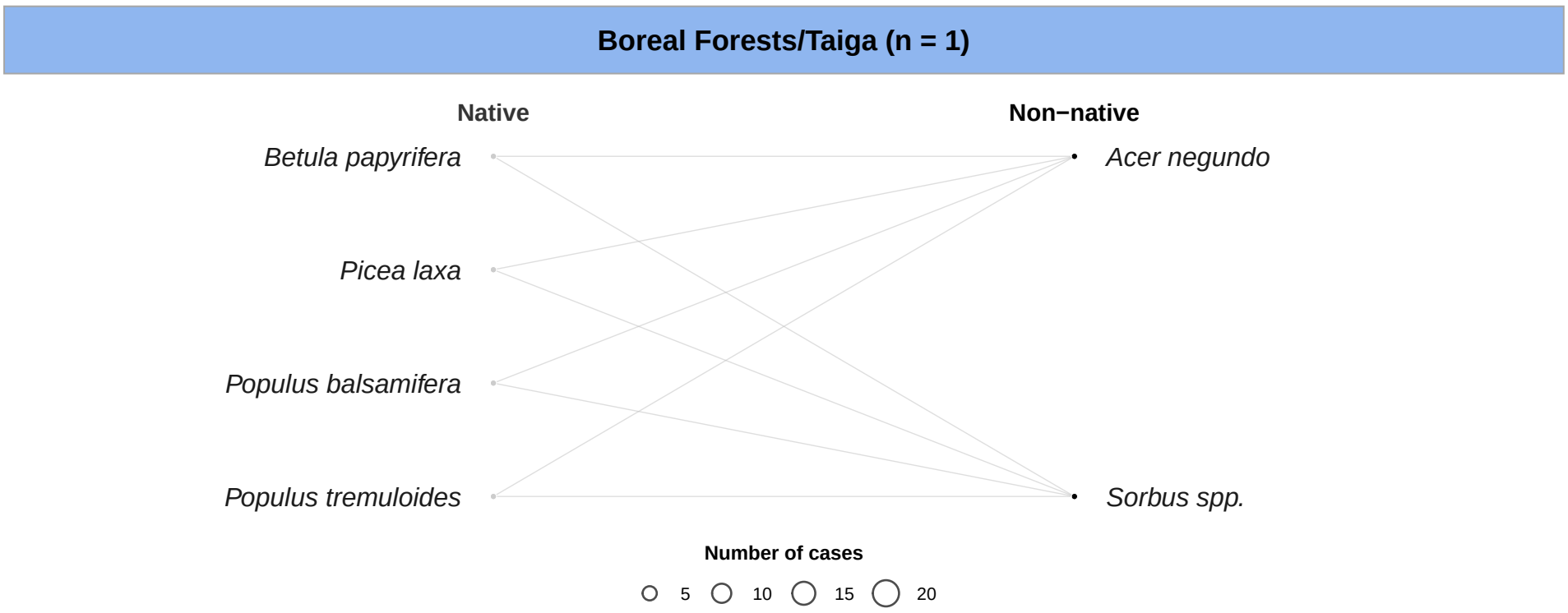


Fig. S2 (continued). Bipartite networks of native and non-native tree taxa across terrestrial biomes.

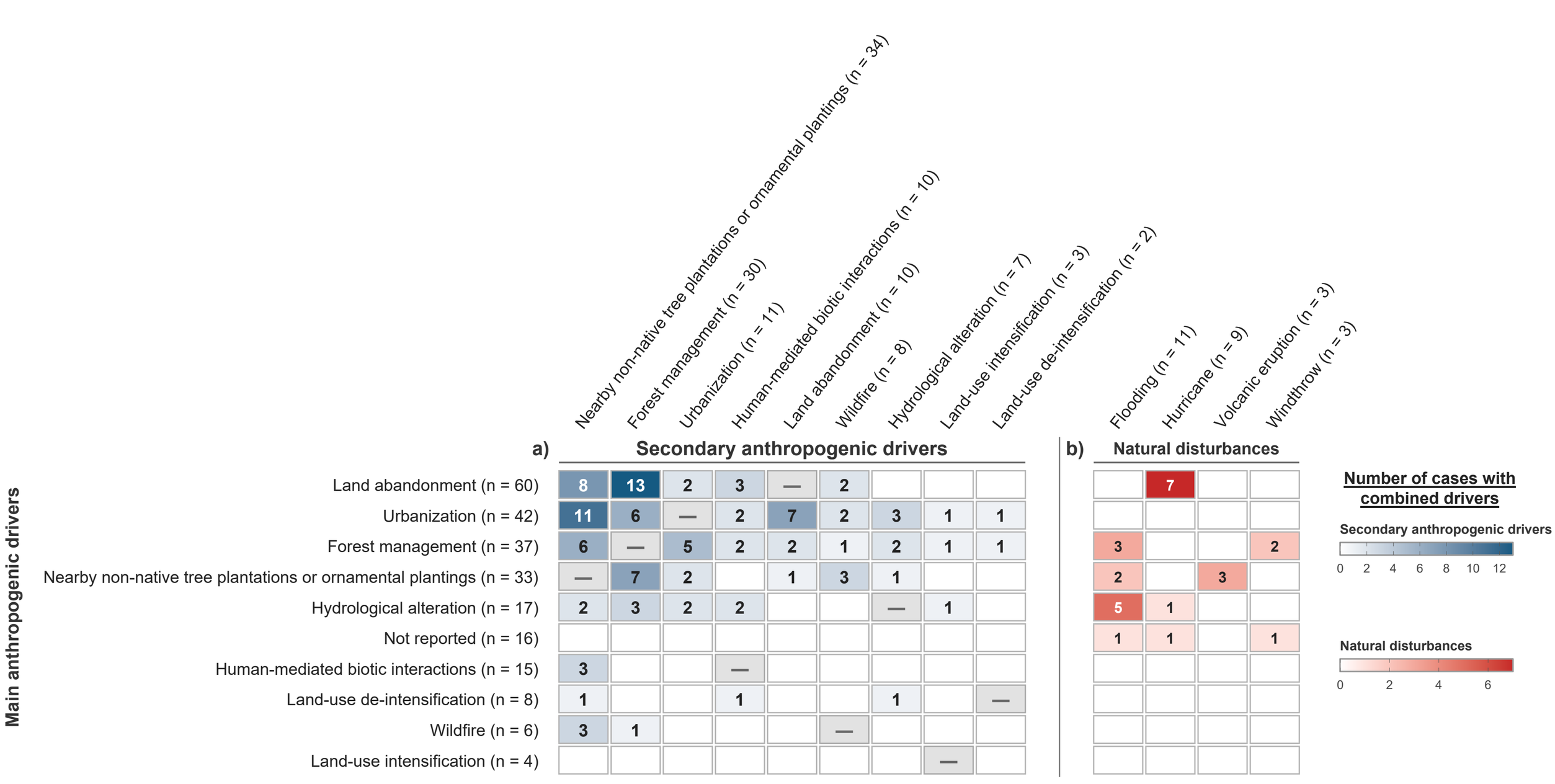


Fig. S3. Heatmap showing associations between main anthropogenic drivers and (a) secondary anthropogenic drivers, and (b) natural disturbances. Numbers within cells indicate the number of cases reporting each combination. Values in parentheses indicate the total number of cases assigned to each main anthropogenic driver category (rows), and to each secondary anthropogenic driver category or natural disturbance (columns). Grey cells indicate combinations that are not applicable (i.e., the same driver recorded as both main and secondary anthropogenic driver), and empty cells indicate that no cases reported the corresponding combination. When multiple secondary anthropogenic drivers were reported for a single case, each driver was counted separately; therefore, a case could contribute to several cells within the same row, but only once to each unique main-secondary driver combination.