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A scoping review of the impacts of forest dynamics on acari-borne diseases: beyond forest fragmentation

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Systematic Review

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Abstract

Background:

Forest cover has undergone significant changes, which have accelerated over recent decades. Acari vectors such as ticks and chigger mites are intricately linked to forest ecosystems because of the suitable hosts and microclimates they provide. However, the implications of forest cover change and dynamics on acari vectors and their pathogens remain poorly understood. This study aims to investigate the impacts of forest dynamics on the risk of acari-borne diseases worldwide through a comprehensive review of the literature.

Methods:

We conducted a scoping review following the PRISMA Method to retrieve citations related to forest dynamics and acari-borne diseases. Eligibility criteria were predefined and relevant data were extracted from selected articles. The analysis employed a descriptive approach and thematic narrative synthesis.

Results:

Our review reveals that the influence of forest dynamics on acari-borne diseases and related vectors was predominantly discussed within a Western context, particularly with regard to *Ixodes* ticks and Lyme disease. Four types of forest dynamics have been identified in the literature: deforestation, fragmentation, conversion and reforestation. However, there was no consensus on the impacts of those dynamics on the vectors and their associated pathogens. Studies have reported conflicting findings including: protective or risk effects, nonlinear relationships, dependent effects influenced by additional factors altering relationships or nonsignificant effects. Those outcomes had been reported across different forest dynamics and various locations. Although, there is limited empirical evidence on tropical contexts as well as for reforestation and conversion dynamics, making it difficult to draw conclusions regarding pathogen and vector trends. Differences in results trends emerge when comparing the entire article sample (n = 111) to empirical studies (n = 73), with literature reviews often overestimating the dilution effect observed in empirical research. Finally, our review identifies a notable absence of studies on scrub typhus disease in the context of forest dynamics.

Conclusions:

This scoping review offers a novel and comprehensive overview of global literature on the impacts of forest dynamics on acari vectors and the infectious agents they transmit. It highlights research gaps and the need for future research targeting specific forest dynamics, particularly chigger mite vectors in a tropical context.

Background

The subclass Acari with ticks and chigger mites play a crucial role in the transmission of several vector-borne diseases [1, 2]. The spread of tick-borne diseases, as Lyme disease, anaplasmosis or babesiosis, is a growing concern with significant implications for both humans and domestic animals [3, 4].

Concurrently, chigger mites, specifically of the genus *Leptotrombidium*, are causing a neglected tropical disease known as scrub typhus contaminating up to 77% of rural populations in Thailand [5].

Those vectors are ectoparasites. Ticks are recognized as some of the most common vectors of infectious diseases in temperate areas across North America, Europe, and Asia [6]. They are classified in two distinct families, the Ixodidae known as hard ticks and the Argasidae known as soft ticks. Ixodidae constitute a significant portion of these vectors, encompassing various species of medical and veterinary importance [2]. As Estrada Peña et al. [7] pointed out, the literature is much more developed on hard ticks. Thus, this scoping review concerns only the Ixodidae family. Among this family, *Ixodes* is the primary genus responsible for disease transmission in temperate forest, but other genera can be implicated worldwide such as *Dermacentor*, *Rhipicephalus*, *Amblyomma*, *Haemaphysalis*, *Hyalomma*, and *Rhipicentor*. As there is a wide variety of ticks, they can transmit numerous pathogens, including the most common: *Borrelia burgdorferi* sensu lato, the causative agent of Lyme disease, *Anaplasma* spp., *Babesia* spp., *Rickettsia* spp. etc. [2]. Chigger mites are globally distributed too but showed a higher diversity in tropical, subtropical and southern temperate zones [8]. They belong to the super-family Trombiculidea and species of the genus *Leptotrombidium* are the vectors of scrub typhus in Asia [9]. The causative agent of scrub typhus is known as *Orientia tsutsugamushi* belonging to the family Rickettsiaceae and formerly classified as *Rickettsia*. *Orientia tsutsugamushi* is endemic to the so-called Tsutsugamushi Triangle, which encompasses North Japan, Korea, Southeast Asia, Southwest Pacific, and East Russia. Although some human cases have also been reported in Chile and the vector in Africa [10]. While *Orientia tsutsugamushi* is the only agent confirmed to be transmitted by chigger bites [8], evidence of protist, viral and bacterial agents transmitted through tick bites had been referenced [11].

Ectoparasites like ticks and chiggers do not live in isolation, but through cycles alternating stages in the environment and stages feeding on vertebrate hosts. Their abundance and activity are influenced by abiotic factors including climate, and biotic factors such as host community composition and the presence of predators and competitors [2, 5, 7]. Forest ecosystem favours the abundance of acari vectors because of favourable microclimate and potential vertebrate hosts. A meta-analysis of Bourdin et al. [12] has found that *Ixodes* ticks were on average more abundant and taxonomically more diverse in forests than in any other non-forested habitats. Chiggers are also often associated to forest or shrubland [13].

Forest is defined by FAO as “land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach these thresholds in situ. It does not include land that is predominantly under agricultural or urban land use.” [14]. What the FAO definition does not say is that forests are dynamic ecosystems undergoing constant changes, whether due to anthropogenic factors or natural processes, such as loss or expansion [15]. Changes in ecosystem structure and

function can modify habitat-host-vector-pathogen interactions. Forest characteristics can directly affect the microclimate conditions, which, in turn, may influence the presence and survival of acari vectors. Additionally, the abundance and composition of host communities, on which acari vectors feed and potentially transmit pathogens, are influenced by the resources and habitat provided by the forest.

Forest dynamics may lead to complex, often context dependant and non-predictable risks of acari-borne diseases for humans, domestic animals, and wildlife [16]. As a global emerging problem, those effects have been locally addressed in several parts of the world in the recent years. However, to our knowledge, all this information has never been gathered and summarized to produce a comprehensive overview of the links between forest dynamics, acari vectors and acari-borne diseases.

In this study we present the results of a scoping review, which aims to explore how studies have investigated the links between forest dynamics and the transmission of acari-borne diseases worldwide. More precisely the questions of this article are: (a) What data were used and how they were used to characterise the link between forest dynamics and acari-borne disease risk? (b) What are the major effects observed induced by forest factors? (c) What are the opportunities, challenges and key areas for further research?

To answer those questions, we described the type of pathogens, vectors, wildlife and geographic range under examination using the PRISMA-SCR method [17]. Then, we reported methodologies used to describe forest dynamics. We quantified the effects of forest dynamics on acari-borne disease risk to identify knowledge gaps for future studies.

Material and methods

Protocol and registration

Our protocol was drafted following the guidance of Arksey and O'Malley [18] and guided by the PRISMA extension for scoping reviews that provide a useful checklist of essential items in a scoping review.

Preliminary literature review

We started our scoping review by a preliminary literature examination to refine the research question and to properly design the search strategy. We combined broad key words like "forest", "infectious disease*", "vector-borne disease*", "ecosystem service*", "biodiversity", "dilution effect" and "ecohealth" to consider the links between forest and infectious disease. This work corresponded to the first stage: Identifying the research question formulated by Arksey and O'Malley [18]. At this stage, we were aware that "forest" could encompass various approaches regarding infectious diseases. We also recognised the need to determine what kind of infectious diseases to examine. Forest dynamics appeared to be important facets of the question. From this work, we made a list of forest dynamics encountered in the scientific articles: deforestation, fragmentation, conversion and reforestation. Once we had a general sense of the volume

and scope of this field, we decided to narrow the focus on acari-borne diseases that are relevant to the question and that represent a reasonable number of articles.

Eligibility criteria

All articles included in the scoping review were selected regardless of the study design, articles could be empirical studies, meta-analysis, book chapter or literature review. No restrictions were applied neither on the study geographical localisation nor the time span. Peer reviewed journal articles were included if they were written in English, dealing with forest or forested area in a context of land cover change and acari-borne zoonotic diseases. To ensure this selection criteria, a word research count was conducted on the entire article when the reading of the abstract was not sufficient. If the occurrence of forest or synonyms were above 10, then the article was selected, otherwise each forest word was considered. If it was a context element or a word from the bibliography, the article was discarded. Otherwise, if the forest was part of a study result, the article was retained. We also decided to include only the zoonotic diseases transmitted by acari vectors like ticks or chigger mites because those vectors are intimately associated with the forest ecosystem. Every article that dealt with non-acari vectors like mosquitoes, were excluded. Table 1 showed a summary table of the eligibility criteria.

Table 1
Summary of the eligibility criteria used for the scoping review

Criteria	Decision
Any study design or methodology	Inclusion
Any geographical area	Inclusion
Any publication date	Inclusion
Forest or woodland specifically addressing land cover changes or spatiotemporal evolution.	Inclusion
Acari-borne zoonotic diseases	Inclusion
Not addressing forest dynamics as the main subject or as a factor	Exclusion
Not addressing vector-borne zoonotic diseases	Exclusion
Vector-borne diseases but not transmitted by acari vectors	Exclusion
Not written in English	Exclusion

Table 1: Summary of the eligibility criteria used for the scoping review.

Information sources

To retrieve all relevant articles, three main databases were searched without time limits: PubMed, Scopus, Web of Science. The search strategies had been tested and approved by all co-authors. After collecting all

references from the three databases, a complementary and simplified search on google scholar was performed.

Search

Three parts composed the final search strategy. The first one is based on all the synonyms and thesaurus for forest. The second part qualified the vectors and diseases. The third part described all the forest dynamics based on the preliminary literature review. The final request is:

(forest OR "forest ecosystem" OR "forest cover" OR "wooded area" OR woodland OR jungle OR wilderness) AND

("vector-borne disease" OR "tick-borne disease" OR "lyme disease" OR "scrub typhus" OR "disease risk" OR "enzootic hazard" OR "mite-borne disease" OR "arthropod-borne disease") AND

(deforestation OR fragmentation OR reforestation OR afforestation OR "woodland expansion" OR "woodland encroachment" OR "woodland modification" OR "woodland degradation" OR "tree plantation" OR conversion)

This search strategy had been performed at the title and abstract levels on the 15th of May 2023.

After going through the retrieved documents, a second complementary search was done in google scholar to assess that all the relevant materials specially concerning non-tick vector-borne diseases have been retrieved. The complementary request was written as followed:

(forest OR "forest ecosystem" OR "forest cover" OR "wooded area" OR woodland OR jungle OR wilderness) AND ("scrub typhus" OR "mite-borne disease" OR "acari-borne disease" OR "orientia tsutsugamushi") AND (deforestation OR fragmentation OR reforestation OR afforestation OR "woodland expansion" OR "woodland encroachment" OR "woodland modification" OR "woodland degradation" OR "tree plantation" OR conversion)

This search had been performed in all fields on the 7th of September 2023.

Selection of sources of evidence

Before selecting articles, the four reviewers amended and validate the search request, criteria selection, and the data extraction methodology. One reviewer was responsible for all the steps of articles screening, going from the selection based on the evaluation of titles, the evaluation of abstracts and the final full text evaluation. In the meantime, she performed the data extraction. To check validity of the selection and data extraction, one additional reviewer made random screening of a smaller sample of articles and independently charted the data. Any possible disagreements on article selection or data extraction were resolved by consensus.

Data extraction

The data-charting form was developed based on the preliminary literature review and validated by all four reviewers. This form is accessible in the additional file 1: Text S1. We used Zotero [19] and spreadsheet to retrieve items of importance. Some of them were saved as explanatory texts, others were directly translated into qualitative or quantitative variables to further perform descriptive statistical analysis. A variable dictionary is available in the additional file 2: Dataset S3. Concerning the data items, as mentioned by Arksey and O'Malley [18], we retrieved data on the article characteristics (such as the authors, year of publication, location studied etc.), the objects of study (information of disease, vector, hosts, humans, forest dynamics), the objectives (research question, lacks, variables to be explained), the methodology (type of study, methodology, forest parameters, statistical analysis, spatial and temporal scales, indicators used, methods to describe the dynamics) and the results (important results, synthesized effects of the forest, limits described by the authors). Some classifications were created ad hoc while screening the articles as the forest parameters or the methods to describe the forest temporal dynamics.

Synthesis of the results

We synthesized the findings through a narrative approach. First, we categorized articles based on their exploration of forest dynamics and acari-borne diseases. Then, we delineated the various pathogen types, vectors, hosts and humans investigated. This was followed by a detailed account of forest characteristics. In evaluating the impact of forest dynamics, we organized studies according to the specific dynamics under investigation, such as fragmentation, deforestation, conversion, or reforestation.

Results

Most studies investigating North American and European forest dynamics

The search strategy identified 413 articles from the three databases. After removing the duplicates, 337 abstracts and titles were screened and 188 of them were selected for a full-text reviewing. Seven articles from the complementary search were added. A total of 111 relevant articles were selected for the scoping review (see Fig. 1). The complete list of those articles in the analysis grid is available in the additional file 2: Dataset S2. Among the 111 articles analysed in this review, 70% are empirical studies, while literature reviews make up 15% of the total. The remaining articles cover a smaller proportion of meta-analyses, modelling papers, science popularization pieces, and expert opinion contributions. The Fig. 2 reveals an increasing interest in tick-borne diseases since the 1970s. It was not until the early 2000s that most authors started addressing forest dynamics and acari-borne diseases together.

The preliminary literature examination described in the methodology categorized forest dynamics into four distinct types. Firstly, "deforestation" entails the loss of forest cover whether of anthropogenic origin or not [14]. Secondly, "fragmentation" refers to the conversion of formerly continuous forest into patches of forest separated by non-forest lands [20]. Thirdly, we considered a category not explicitly defined by FAO but recognized in scientific discourse as "conversion". We define "conversion" as the transition from spontaneous forests to commercially oriented woody plantations. Finally, we broadened the scope of "reforestation" to encompass the establishment of forests through planting, deliberated seedling or

natural regeneration on land previously classified as forest or not. This expanded definition deviates from the one originally provided by FAO [14], which combines reforestation, afforestation, and natural regeneration. We have adopted this approach to address the scarcity of information available regarding the forests examined in the literature.

Most of the research exploring the relationship between acari-borne diseases and forest dynamics concerned tick models and tick-borne diseases, focusing mostly on *Ixodes* and Lyme disease in North America (53 articles) or in Europe (27 articles). Only 12 articles focus on Asia and even fewer on the rest of the world (see Table 2).

As seen in Table 3, *Borrelia* spp. responsible for Lyme disease and *Anaplasma* spp. responsible for anaplasmosis were the main pathogens studied (resp. 60,5% and 11,3% of all studied infectious agents). Out of the 11 identified pathogens in the reviews, eight are bacteria. The number of pathogens studied varied according to the type of forest. In temperate forest, 72.5% of the examined pathogens are *Borrelia* spp., followed by *Anaplasma* spp. (11.8%). In tropical forests, the scientific community equally prioritized Kyasanur Forest Disease Virus, *Orientia tsustugamushi* and *Rickettsia* spp. (resp. 22.7%, 22.7% and 18.2%).

Table 2
 Number and percentage of articles
 sorted by relevant categories

	Overall (N = 111)
Nature	
Empirical studies	78 (70.3%)
Expert opinion	2 (1.8%)
Literature Review	17 (15.3%)
Meta-analyse	3 (2.7%)
Modeling	8 (7.2%)
Science popularization	3 (2.7%)
Continent	
Africa	1 (0.9%)
Asia	12 (10.8%)
Europe	27 (24.3%)
North America	53 (47.7%)
Oceania	1 (0.9%)
South America	4 (3.6%)
Worldwide	13 (11.7%)
Forest	
Temperate	86 (77.5%)
Tropical	17 (15.3%)
Both	8 (7.2%)
Vector	
Tick	97 (87.4%)
Chigger mite	5 (4.5%)
Both	2 (1.8%)
Missing	7 (6.3%)

Table 3
Distribution of examined pathogens in the dataset.

	Temperate (N = 102)	Tropical (N = 20)	Overall¹ (N = 122)
Pathogen			
<i>Borrelia</i> (bacteria)	74 (72.5%)	1 (4.5%)	75 (60.5%)
<i>Anaplasma</i> (bacteria)	12 (11.8%)	2 (9.1%)	14 (11.3%)
<i>Rickettsia</i> (bacteria)	4 (3.9%)	4 (18.2%)	8 (6.5%)
<i>Babesia</i> (protist)	6 (5.9%)	0 (0%)	6 (4.8%)
<i>Ehrlichia</i> (bacteria)	5 (4.9%)	1 (4.5%)	6 (4.8%)
<i>Orientia</i> (bacteria)	0 (0%)	5 (22.7%)	5 (4.0%)
KFDV ² (virus)	0 (0%)	5 (22.7%)	5 (4.0%)
<i>Bartonella</i> (bacteria)	0 (0%)	2 (9.1%)	2 (1.6%)
<i>Coxiella</i> (bacteria)	0 (0%)	1 (4.5%)	1 (0.8%)
<i>Francisella</i> (bacteria)	0 (0%)	1 (4.5%)	1 (0.8%)
LIV ³ (virus)	1 (1.0%)	0 (0%)	1 (0.8%)
¹ As on article can deal with several type of pathogen, the overall amounts to 122.			
² KFDV = Kyasanur Forest Disease Virus			
³ LIV = Looping Ill Virus			

Table 2: Number and percentage of articles sorted by relevant categories.

Table 3: Distribution of examined pathogens in the dataset.

Vectors, hosts and humans: characterisation of the pathogen presence or the hazard thanks to ecological-epidemiological data

The methodologies addressing the connection between forests and acari-borne diseases appeared heterogeneous and mainly focusing on the pathogen. Seventeen-point one percent of the studies investigated pathogens and humans. Sixteen-point two percent looked at pathogens, humans, vectors and wildlife. Fourteen-point four percent considered only pathogens, vectors and wildlife. Nine-point nine percent looked the vectors and the wildlife without the pathogens, and only 17.1% of the studies did not consider pathogen presence focusing on vectors as a proxy for estimating the hazard of disease

transmission (see the Venn diagram in the additional file 3: Figure S4 for the whole repartition). Ticks were investigated in 97 articles, while chiggers were the subject of only five articles, and two articles considered both (see Table 2).

Regarding the studied wildlife, we identified the presence of deer, rodents, mammal carnivores, domestic animals (dogs, cats, cattle, etc.), birds, other mammals (excluding rodents, domestic animals and predators) and reptiles across all articles (see Fig. 3). The primary emphasis concerned rodents, deer, and other mammals. Specifically, 12 studies only focused on deer followed by those exclusively examining rodents ($n = 10$), which are respectively the most important hosts for *Ixodes* ticks and the main reservoirs for *Borrelia burgdorferi*. Forty-five articles also assessed the wildlife that may not directly serve as hosts or reservoirs using camera trapping, capture, mark-recapture or mark-resight, the collaborating with veterinarians or hunters or the use of biodiversity data bases.

Humans have a particular place in the system because they are hosts for the pathogens, and they also have an important impact on forest dynamics as users or through their governance. Among the 111 articles, 50.5% include humans in the system either as host being infecting with the pathogen or vector, as user of the forest or as management and political interventions related to governance. Most articles (48.2%, $n = 27$) investigated pathogen prevalence in humans, viewing them as a potentially vulnerable population. This perspective had implications for public health. Twenty articles (35.7%) consider humans as users meaning they considered their activities or behaviour in forests and their impacts. Eleven articles (19.6%) dealt with governance, meaning policies, conservation practices or institutions regulating forests and forest resources.

Forest: characterisation of factors modifying the hazard

Articles either focused on one specific forest dynamic or studied two or several together. Fragmentation is the first studied dynamic regarding its impact on acari-borne disease transmission. Out of 111 articles, 25% of them focused on deforestation, 75% on fragmentation, 14% on forest conversion and 18% on reforestation. The Fig. 4 illustrates the diversity of studied forest dynamics according to the continent under examination. The effect of deforestation was mostly investigated in tropical areas, constituting 64% of tropical forest studies compared to 22% concerning temperate forests studies. Conversion was overrepresented in tropical areas as well, with 40% of tropical forests studies, whereas temperate area accounted for 8% of temperate forests studies. Conversely, fragmentation was predominantly investigated in temperate forest studies, comprising 82%, in contrast to 48% in tropical areas. Reforestation was underrepresented in both context with 18% of the studies located in temperate areas and 32% in tropical area.

A diverse array of variables is employed to describe forest dynamics. The Table 4 retrieves all the forest variables used according to their spatial and temporal scales. Common factors included surface area and forest type (deciduous, coniferous, or mixed). Additional indices encompassed configuration elements such as the number, surface, connectivity, aggregation, density, shape, and length of patches, as well as edge characteristics and neighbourhood features. Some authors analysed composition parameters,

including species composition, diversity of vegetal species, litter and soil composition. Forest structure parameters, such as stand story, tree age, biomass, height, diameter at breast height, canopy cover, and dead wood percentage were also considered. Functionality indicators, such as food resource availability for hosts or habitat provisions, are examined in two studies. Finally, some articles mentioned the type of forest management as a parameter. The number of parameters varied widely across articles, ranging from 0 to 14 (median = 3) and an important variability (with an inter-quartile distance of 3.5). Studies on fragmentation dynamics employed the highest number of variables (median = 4) compared to deforestation, conversion and reforestation that all accounted for a median of 2. Certain groups of indicators were better suited for different spatial scales, ranging from patch to landscape and to country to global. As seen in the Table 4, the patch scale was well adapted to local species or litter composition. Metrics of forest structure felt also more adapted because it could be measured directly on the sample plot. At the landscape scale, the authors rather chose forest configuration indices that were directly estimated from a landcover map. Then, the choice of forest variables was determined by the data availability, the research question and the related spatial scale.

Table 4

Classification of forest variables used according to spatial and temporal scale in the collected articles.

	Plot/Patch	Landscape	Region	Country +
0–5	Composition: Species Soil Invasive species Wildlife Diversity Litter	Composition: Species (rather categorical) Soil Diversity	Composition: Species (rather categorical) Soil Diversity Wildlife	Composition: Species (rather categorical) Wildlife
	Structure: Density Canopy Stories Mortality (coarse- woody debris) Height and DBH Age Biomass	Structure: Density	Structure:	Structure:
	Configuration: Area Edge/perimeter Neighbour Shape	Configuration: Area Edge/perimeter Number of patches Neighbour Connectivity Aggregation Shape	Configuration: Area Edge/perimeter Number of patches Neighbour Connectivity Aggregation Shape	Configuration: Area Edge/perimeter
	Functionality: Food resources Habitat resources	Functionality:	Functionality:	Functionality:
<p>The variables are classified by types (composition, configuration, structure, functionality, human factors) for each dimension. In columns the temporal scale is indicated in years. Those classifications had been done post hoc the data extraction.</p>				

	Plot/Patch	Landscape	Region	Country +
	Human factor: Management	Human factor:	Human factor:	Human factor:
6–10	Composition: Species (rather categorical)	Composition: Species (rather categorical)	Composition: Species (rather categorical)	Composition: Species (rather categorical)
	Configuration: Edge/perimeter Area Neighbour	Configuration: Edge/perimeter Area Number of patches	Configuration: Edge/perimeter Area Number of patches	Configuration: Edge/perimeter Area
11–99	Composition: Species (rather categorical) Diversity	Composition: Species (rather categorical) Diversity	Composition: Species (rather categorical) Wildlife Diversity	Composition: Species (rather categorical) Wildlife Diversity
	Structure: Canopy Stories Age	Structure:	Structure:	Structure:
	Configuration: Area Neighbour Edge/perimeter	Configuration: Area Neighbour Number of patches Edge/perimeter	Configuration: Area Edge/perimeter Neighbour Number of patches	Configuration: Area Edge/perimeter
100+	Composition: Species (rather categorical) Invasive species	Composition: Species (rather categorical) Wildlife Invasive species	Composition: Species (rather categorical) Wildlife	Composition: Species (rather categorical) Wildlife

The variables are classified by types (composition, configuration, structure, functionality, human factors) for each dimension. In columns the temporal scale is indicated in years. Those classifications had been done post hoc the data extraction.

Plot/Patch	Landscape	Region	Country +
Structure: Canopy Stories	Structure:	Structure:	Structure:
Configuration: Area	Configuration: Area	Configuration: Area	Configuration: Area
The variables are classified by types (composition, configuration, structure, functionality, human factors) for each dimension. In columns the temporal scale is indicated in years. Those classifications had been done post hoc the data extraction.			

Table 4: Classification of forest variables used according to spatial and temporal scale in the collected articles.

Studies predominantly investigated forests on a large dimension, covering several tens to hundreds of kilometres or more (54%), examining regions, countries, or continents. A smaller proportion of studies focused on a small dimension (35%), encompassing several kilometres corresponding to villages or isolated sample plots. Additionally, 11% of studies considered both small and large dimensions, transitioning between the two. This distribution tendency remains for all forest dynamics considered individually.

The temporal scale poses a real challenge, as forest ecological process may not align with the scientific temporality. Hence the authors have developed various methodologies to adapt temporal scale and data availability for characterising forest dynamics. We listed five of them. First, in 13 studies, the authors used two different maps with a determined time difference to compute rate of changes (deforestation, reforestation). Second, in three studies, the authors reconstructed a chrono sequence on the field to determine the amount of time between the oldest and the newest forests composing the chrono sequence. Third, in 69 articles, a proxy was computed using a map (edge, perimeter, perforation, aggregation etc...) or on the field. This method was largely used for fragmentation to estimate and compare forest fragmentation level. Fourth, when the perturbation was short term and adapted to small spatial dimension spatial scale, the authors could measure forest parameters directly on the field during the ecological sampling (vectors or hosts). It was the case for two articles, that both had a 3-year sampling period. Fifth, in one article, the authors developed a predictive model of the forest occupancy based on climatic data.

Despite concerted efforts, reconciling eco-epidemiology and forest temporal scales remained challenging. Three scenarios emerged (see Fig. 5). Some authors (n = 61) used ecological or epidemiological data covering from 0 to numerous years and viewed the forest as a snapshot, particularly evident in studies investigating fragmentation. This case was represented in the Fig. 5 by the scenario 1. A few authors (n = 5) captured extensive periods of forest change using temporal maps but lacking ancient ecological data

(scenario 3). Lastly, 12 articles managed to match their eco-epidemiological data with the temporal changes in the forest parameters (scenario 2).

Heterogenous forest effects

A comprehensive analysis revealed a lack of consensus on the outcomes of reforestation, deforestation, forests fragmentation or conversion on pathogens and vectors dynamics. Five types of effects have been identified in the literature. An increase in forest surface could increase or decrease the pathogen or vector presence. The relationship between the two can be non-linear or non-significant. And lastly, the authors can identify dependant effects that altered the relationship.

For all confounded forest dynamics, the most observed effect was that forest has a protective effect on the pathogen (prevalence, incidence, etc), decreasing the presence of pathogen when increasing surface area for 27% of all articles. But this percentage remained quite low and close to the other types of effects (see Table 5). The same pattern is observed regarding the effect of forest on the vector presence (see Table 6)

Table 5

Distribution of articles by effects on pathogens presence, forest dynamics, spatial and temporal dimensions.

Type of effects	Number of articles	Nb. of articles by forest dynamics	Nb. of articles by spatial dimensions	Median and interquartile of forest temporal scale variables
All articles	111			
<i>Forest surface increases pathogens</i>	21 (19%)	Deforestation: 4 Fragmentation:15 Conversion:2 Reforestation:4	Large:10 Small:11 Both:0.	Median: 0 Interquartile:0
<i>Forest surface decreases pathogens</i>	30 (27%)	Deforestation:13 Fragmentation:23 Conversion:4 Reforestation:4	Large:20 Small:6 Both:4	Median: 0 Interquartile: 11
<i>Non-linear relationship</i>	6 (5%)	Deforestation:2 Fragmentation:5 Conversion:1 Reforestation:2	Large:3 Small:0 Both:3	Median: 0 Interquartile: 5
<i>Non-significant relationship</i>	9 (8%)	Deforestation:0 Fragmentation:8 Conversion:1 Reforestation:2	Large:5 Small:4 Both:0	Median: 0 Interquartile: 0
<i>Dependant effects</i>	20 (18%)	Deforestation:3 Fragmentation:17 Conversion:2 Reforestation:3	Large:13 Small:4 Both:3	Median: 0 Interquartile: 10
<i>Non-studied</i>	25 (23%)	Deforestation:6 Fragmentation:15 Conversion:6 Reforestation:5	Large:9 Small:14 Both:2	Median: 0 Interquartile:0

Table 6

Distribution of articles by effects on vectors presence, forest dynamics, spatial and temporal dimensions.

Type of effects	Number of articles (%)	Nb. of articles by forest dynamics	Nb. of articles by spatial dimensions	Median and interquartile of forest temporal scale variables
All articles	111			
<i>Forest surface increases vector</i>	19 (17%)	Deforestation: 5 Fragmentation:12 Conversion:3 Reforestation:5	Large: 7 Small:12 Both:0	Median: 0 Interquartile:0
<i>Forest surface decreases vector</i>	20 (18%)	Deforestation: 9 Fragmentation: 17 Conversion:2 Reforestation:4	Large:14 Small:3 Both:3	Median: 0 Interquartile:1.25
<i>Non-linear relationship</i>	5 (5%)	Deforestation: 2 Fragmentation: 4 Conversion: 0 Reforestation: 2	Large:2 Small:1 Both:2	Median: 0 Interquartile:0
<i>Non-significant relationship</i>	6 (5%)	Deforestation: 0 Fragmentation:5 Conversion:1 Reforestation:1	Large:4 Small:2 Both:0	Median: 0 Interquartile:0
<i>Dependant effects</i>	10 (9%)	Deforestation: 2 Fragmentation: 6 Conversion: 3 Reforestation: 1	Large:2 Small:5 Both:3	Median: 0 Interquartile:3
<i>Non studied</i>	51 (46%)	Deforestation:10 Fragmentation: 39 Conversion: 7 Reforestation: 7	Large:31 Small:16 Both:4	Median: 0 Interquartile:7

Table 5: Distribution of articles by effects on pathogens presence, forest dynamics, spatial and temporal dimensions.

Table 6: Distribution of articles by effects on vectors presence, forest dynamics, spatial and temporal dimensions.

Different trends were observed by forest dynamics when comparing the entire sample of papers to a subset comprising only empirical studies. Figure 6 shows an illustration for the pathogen presence. In a context of fragmentation, more articles found a protective effect of the forest in proportion when the entire sample of articles was analysed compared to the empirical studies. The same trend applied for the vector presence (See additional file 3: Figure S5).

The limited availability of studies addressing reforestation and conversion makes it difficult to draw conclusion on their impact on disease transmission. Dependent effects were identified across various studies, with authors acknowledging and considering these dependencies in their analyses. A list of these dependent effects included factors related to spatial scale and the buffer size, factors related to the vector species or stages, the pathogen species, the location sites and the biogeographic region, the neighbouring effects, the structure or configuration of forest, the host composition or the proportion of exposed human.

Apart from the forest dynamics, impacts on pathogen and vector presence also depended on the continent of the studied sites (see Fig. 7). In proportion, a protective effect was more observed in North America and Asia compared to Europe. It was difficult to assess South America, Africa and Oceania given the low number of studies. In Europe, increasing forest surface was more observed as a risk factor.

Discussion

The purpose of this scoping review was to provide an overview of the literature on the links between forest dynamics and acari-borne disease risk. More precisely this review collated all pathogens, vectors, hosts and forests variables. It described how these variables were used and what were the major observed impact of forest dynamics on acari-borne disease risk in the world. We conducted a literature review search of three international databases. We screened 413 articles published between 1953 and May 2023 and we included 111 of them in this scoping review.

The literature is mainly composed of empirical studies and produce observational data, highlighting the emerging nature of the study field. The temperate forests of North America were the most studied followed by European temperate forests and tropical forests of Southeast Asia. The influence of forest dynamics on acari-borne diseases remained a primarily Western-centric concern. Among acari vectors living in the forest, *Ixodes* ticks transmitting Lyme disease in a context of temperate forest fragmentation was the most investigated. Studies were more pathogen oriented even if a small proportion of studies used vector density as a proxy to estimate the hazard. Humans were not systematically considered even if they are a key element of the system and essential to estimate exposure and risk. Variables used to

describe forest ecosystem varied considerably and the temporal aspect was challenging to consider. We identified four major theoretical backgrounds from the collected articles as habitat suitability [21, 22], island biogeography theory [23], community composition ecology with the dilution effect hypothesis [24] and landscape ecology with ecotone [25] centred studies. The influence of forest dynamics on the risk of acari-borne disease transmission is still debated within the scientific community, reflecting a lack of consensus in terms of observed effects, methodologies and theoretical frameworks used to investigate a complex relationship.

Forest effects and the influence of ecological background

According to habitat suitability theories and niche modelling studies, forests and forested areas serve as habitats for a lot of acari vectors studies (see [12] for a meta-analysis). Forest ecosystems provide a stable microhabitat required for the vector's survival and support diversified vertebrate communities that serve as hosts for vectors and reservoirs for pathogens. The absence of forests should result in the absence of vectors and decreasing risk of disease transmission. Those statements are supported in several articles examining either vector presence [26–28] or vectors and pathogens combined [29] in all forest dynamics considered. Modelling studies performed by Robinson et al. [30] for pathogens and by Li et al. [31] for ticks and pathogens corroborated these empirical findings. However, this statement must be nuanced as several authors also found co-dependant effects for the vector presence [32, 33] and for the pathogen presence with the meta-analysis of Walsh et al. [34]. Our scoping review emphasized that forests may protect against disease transmission under specific conditions involving forest configuration factors as shown in the studies of Dong et al. [35] and Wongnak et al. [36].

These results evoked the theory of island biogeography by considering forests and forest fragments as habitats for vectors and pathogen reservoirs, further supported by niche modelling studies. Large and well-connected forest patches should support a highly diversified plant and animal communities, which may significantly enhance disease maintenance and transmission. Fragmentation, particularly in temperate forests, has received important attention in this field. A part of the studies observed a positive correlation between larger and highly connected patches of forest and the abundance of vectors and pathogens [37, 38]. However, Brownstein et al. [39] observed a similar correlation for human cases but not for the field-collected ticks, suggesting other factors at stake. Wang et al. [40] also corroborated those findings in reforestation context observing that forest connectivity alone did not significantly affect the presence of pathogens but became significant when combined with other factors such as host assemblage or the infection status of neighbouring areas. These findings support Reperant's conceptualization of hosts, themselves seen as biogeographic islands for pathogens [41]. Such results were reported in tropical environments by Esser et al. [42] where larger forest fragments were associated with more diverse wildlife communities, consequently supporting larger and more diverse tick communities.

Studies investigating forest dynamics under the scope of community compositions help understanding these complex heterogeneous effects. Forest composition and configuration, alongside forest structure,

can induce vertebrate community reassembly by modifying ecological niches and food resources [43]. A prevailing hypothesis suggests that only generalist species can easily adapt to perturbations, while specialist species struggle to acclimate to anthropized habitats emerging from forest dynamics [44]. Generalist species like rodents and deer were the main reservoirs of pathogens and vectors hosts playing a major role in acari-borne disease transmission. In a temperate forest marked by fragmentation resulting from fire, MacDonald et al. [45] observed varied responses among small mammal communities. These responses depended on the species and their level of habitat specialization. Concurrently, they found a high level of tick burden following fire perturbation. Consistent with those results, Morand et al. [46] showed that tropical forest dynamics as conversion or reforestation will also reshape the rodent and pathogen community composition according to their level of specialization and synanthropy. High synanthropic rodents were more associated with fragmented landscape where highly specialised forest rodents decreased. However, in this study *Orientia tsutsugamushi*, the agent of scrub typhus, decreased with ongoing fragmentation and forest conversion to agricultural land, which may be at odds with the results of MacDonald et al. [45]. Razali et al. [1] made the hypothesis that forest remnant with more disturbed surrounding areas contribute to higher intensity of ectoparasites' infections, as an indication of a stressful condition of the animals. Although the authors found a non-significant relationship and this hypothesis could not be verified either by Nadolny and Gaff [47].

Habitat suitability, island biogeography and community composition frameworks are often complementary and used in a synergy with the dilution effect hypothesis. The dilution effect is defined as "the net effect of species diversity reducing disease risk by any of a variety of mechanisms" [48]. The dilution effect hypothesis is commonly referred in disease ecology and particularly in the Lyme disease. Many authors attempted to link these ecological mechanisms to forest dynamics. The study by Allan et al. [49] demonstrated that in fragmented landscapes, biodiversity tended to be lower, leading to higher pathogen density in vectors. These observations were also consistent in tropical forests such as the case of Kyasanur Forest Disease [50]. Linske et al. [51] found the opposite trend with a higher biodiversity in fragmented landscape significantly associated with a higher tick and pathogen presence. LoGiudice et al. [52] also failed to establish a significant relationship between forest patch size and prevalence, or between forest patch size and the population of white-footed mice, despite observing a negative yet non-significant trend. Based on this literature, fragmentation had largely been examined within the framework of the dilution effect and thought to be used as a proxy for biodiversity. The dilution effect had found consistent support in the literature [53]. However, directly associating habitat disturbance like fragmentation and biodiversity loss may show conflicting results by underestimating confounding factors and fail to accurately represent local community ecology [53, 54]. In this trend, our scoping review shows an overrepresentation of protective effect of the forest in reviews compared to empirical studies.

The ecotone and interface framework offer a nuanced perspective on why fragmentation may not always have detrimental effects on biodiversity but may still have contrasted results in term of disease risk. These hypotheses suggest that fragmentation may create new niches at the interface between two different habitats. Those niches can support high species richness but also greater encounter probability with alternative hosts compared to the interior of large forest patches [51, 55]. Goethert et Telford [56]

found that ticks from the edge fed on a greater diversity of hosts than those from the thicket and that prevalence of pathogen was higher at the edge. All previously discussed ecological mechanisms enhance our understanding of the abundance of either the vector or the pathogen, and then assisting to quantify the hazard. However, the risk of vector-borne disease not only encompasses the hazard but also the exposure and the coping capacity [57]. Exposure reflects the probability of getting potential vector-infected bites. Ecotone and interface resulting from forest dynamics, by creating spatial overlap between tick-infested areas and human visits, increase then the exposure and so the risk [58–61]. Jackson, Hilborn, et Thomas [62] observed that Lyme disease human cases had a quadratic relationship with the percentage of forest cover. However, human cases also significantly increased with the percentage of forest edge, meaning that when forest cover is equivalent, the interspersed between two habitats is of great importance for disease risk. Those results were confirmed by McClure et Diuk-Wasser [63] and put back the forest configuration at the core of the debate. In a context of fragmentation or deforestation, even if an important surface of a niche vanishes, it creates more and more opportunities of exposure between species that do not usually encounter or even between wildlife, domestic animals and humans. The results of our scoping review aligned with this hypothesis with the overall negative effect of deforestation on disease risk.

Forest dynamics and the challenges of temporal and spatial scales.

The diversity of approaches, theories and hypotheses is not enough to explain the conflicted results. Studying forest dynamics impact on disease risk is also challenging because of different temporal and spatial scales intertwining. Concerning the spatial scale, there is a difference between entomological hazard that is usually measured at patch scale and human exposure that is investigated at broader scale by the public health surveillance system. Several authors pointed out the dependency of their results with the spatial scale studied as well for the pathogen [64, 65], for the vector [32, 66] or for both [67]. McClure et Diuk-Wasser [63] built a model to connect both. This difference has also been more widely acknowledged by Salkeld et al. [68] in their meta-analysis. Studies that relied on county-level health data were not incorporated for two reasons. First, infection dynamics operate at fine spatial scales and therefore data at coarse county or region levels may not be indicative of local pathogen transmission patterns. Second, sampling effort can be very heterogeneous at the regional level making it harder to obtain an accurate measure of biodiversity. Those scaling effects had already been acknowledged in ecology [69, 70]. In epidemiology, it is also common to study short ecological processes. Our scoping review showed that very few authors considered the age of forest in their analyses. Forest cycles ran over a very long period compared to the lifetime of humans, wildlife and even more vectors. Shah et al. [61] highlighted that further untangling mechanisms would require a more detailed data set on land-cover history, scale and context. Ehrmann et al. [71] concluded that historical forest continuity on its own was not significant but considering the resulting functionality of the forest stand was important. Few authors [47, 72] considered the temporal forest successions by describing the forest as a gradient from monoculture or non-forested areas to second growth forest and to old growth or pristine one. Both took place in North America and both showed that infection prevalence or vector abundance was associated with an intermediate stage (second growth forest in regeneration after habitat change or pine-mixed

hardwood forest). Our scoping review showed that matching heterogeneous spatial and temporal scaled data is challenging and rarely done yet promising.

Forest dynamics typology and its inclusion in forest cycles

The forest dynamics keywords found, as deforestation, fragmentation, conversion and reforestation, were consistent with the literature and succeeded in encompassing many articles in the scope. However, this typology may lead to some biases. Thinking in terms of forest stages opens new perspectives in terms of forest functionality. For example, a fragmented forest is not necessary synonym of a habitat loss as it can be described in a context of reforestation even if the total habitat amount would increase [6].

Reforestation can also result in a second growth forest, with an intermediate perturbed area, favouring generalist species and potentially vector-borne diseases. This idea has been modelled by McClure and Diuk-Wasser [63] and empirically studied by several authors [62, 73], who found a nonlinear quadratic response of forest dynamics on disease risk. The quadratic response suggests a threshold from which, biodiversity starts to mitigate disease transmission. Such a response had been observed in forest pest invasion [74]. This threshold is difficult to evaluate in term of forest stage/age. We would then gain to be more precise about what kinds of forest are we talking about. The FAO gave a common international definition of forest, although, very few authors pointed out which definition of forest they used. The studies gathered in our scoping review included all sorts of forest worldwide in a very wide range of ecosystems with different structures and functionalities. This great diversity of forests may explain the heterogeneous results observed in term of disease regulation, making comparisons harder. A proper work of description might be more efficient in explaining the results.

Place of scrub typhus and strong determination in forest dynamics according to geographical localisation.

Surprisingly, studies on scrub typhus were few in our dataset. We made a complementary search to assess the lack of studies investigating forests, chigger mites and scrub typhus. We confirmed that this acari-borne disease was much more associated to keywords like fallow, shrubland or bush. Those habitats can be seen as intermediated stages or as ecotones in forest evolution and dynamics [75]. The results of Morand et Lajaunie [76] showed that it is not meaningless to study them under this scope. Our scoping review provides a new perspective of research exploring scrub typhus in a context of forest dynamics. Another perspective is the lack of conversion and deforestation in temperate context and reforestation and fragmentation in tropical context.

Relevance

Exploring the state of the art on forest dynamics and acari-borne diseases is a topical issue because, in a very changing world, forest cover is also under important process of change. Winkler et al. [75] as well as Grantham et al. [15] observed a net gain of forest in the northern part of the world and a net loss in the southern part as well as a disparate level of functional integrity. Ecological, social and political drivers lead those changes. Among these changes, new agricultural practices like agroforestry or agricultural abandonment that create unsettled new areas favour shrubland encroachment. Those intermediate

stages can eventually evolve back to forest[75]. On the contrary, agriculture extension producing international goods (soybean, beef, sugar can, oil palm and cocoa) cause major deforestation[75]. Environmental policies also impact forest cover. The REDD + initiative (Reducing Emissions from Deforestation, forest Degradation, and other forest activities) leading to reforestation has been internationally supported by the Paris Agreement with the objective of carbon reduction up to -1.1 ± 0.5 GtCO₂e/yr fixed at 2030 [77]. Climate change is also causing a significant and yet hard to predict forest cover change (range shift, drought, pest vulnerability, increase of exceptional event frequencies like storm, fires, etc) [78]. This makes those forest dynamics impact studies more relevant than ever.

Limitations

Our scoping review encompassed only articles written in English which lead to an underrepresentation of non-English speaking countries (especially Chinese, Russian, and Japanese). Very few studies concerned chigger-borne diseases regarding reforestation or conversion, which made hard to draw conclusions on the link between forest dynamics and these diseases. Finally, as already explained, the forest descriptions and definitions available along with the very varied contexts in the collected articles rendered difficult to statistically test the impact of forest dynamics on acari-borne risk. More broadly, the scoping review with its methodology could not bring evidence on a particular effect or intervention as pointed out by Arksey and O'Malley [18]. It rather aimed to summarise and disseminate research findings and to identify research gaps. If we are not specifically testing a certain impact of forest dynamics, this scoping review can still be seen as a first step to check full systematic review feasibility.

Conclusion

As far as we know, no previous literature review performed such comprehensive analysis of the links between forest dynamics and acari-borne diseases worldwide. This article provides a large picture of forest cover variations and impacts on the presence of vectors and pathogens and how forest ecosystem, wildlife, vectors, pathogens and humans are intertwined. Landscape ecology coupled with a systemic and transdisciplinary approach appears promising in this field of research. Such studies could facilitate decision-making both in the field of public health and biodiversity conservation.

Declarations

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Authors' contributions

All authors conceptualized the study and took part in designing the protocol. NB and KCM performed the data extraction. NB ran the analysis. KCM, CP and SM contributed to the interpretation of the results. NB

wrote the manuscript under the supervision of KCM, CP and SM. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analysed during this study are included in this published article and its supplementary information files.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no financial or non-financial competing interests.

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Figures

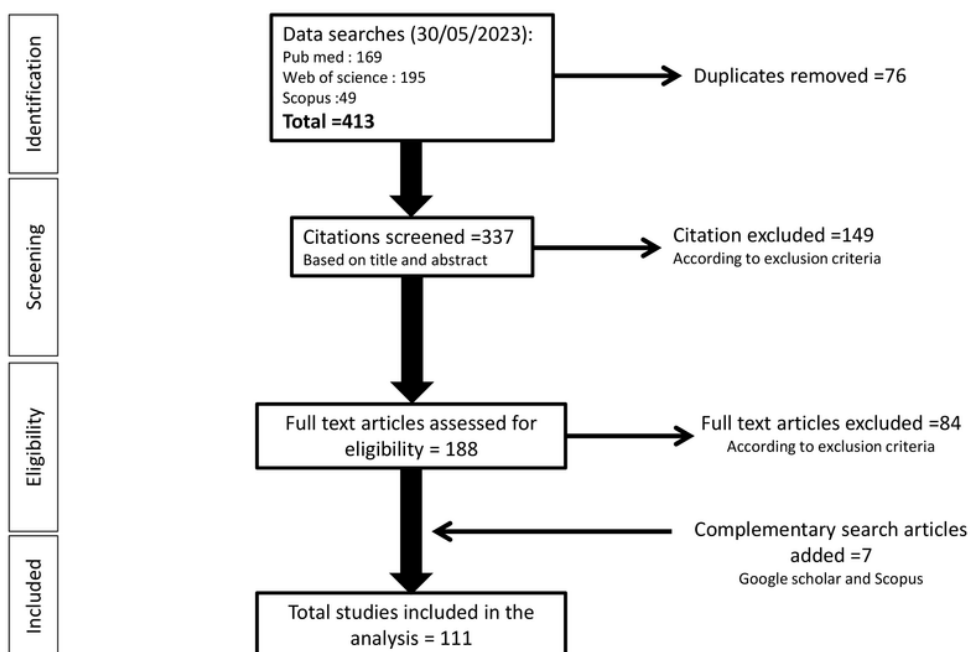


Figure 1

Flow diagram for scoping review of forest dynamics impacts on acari-borne disease literature.

Caption Fig.1: This flow diagram is based on PRISMA-ScR methodology.

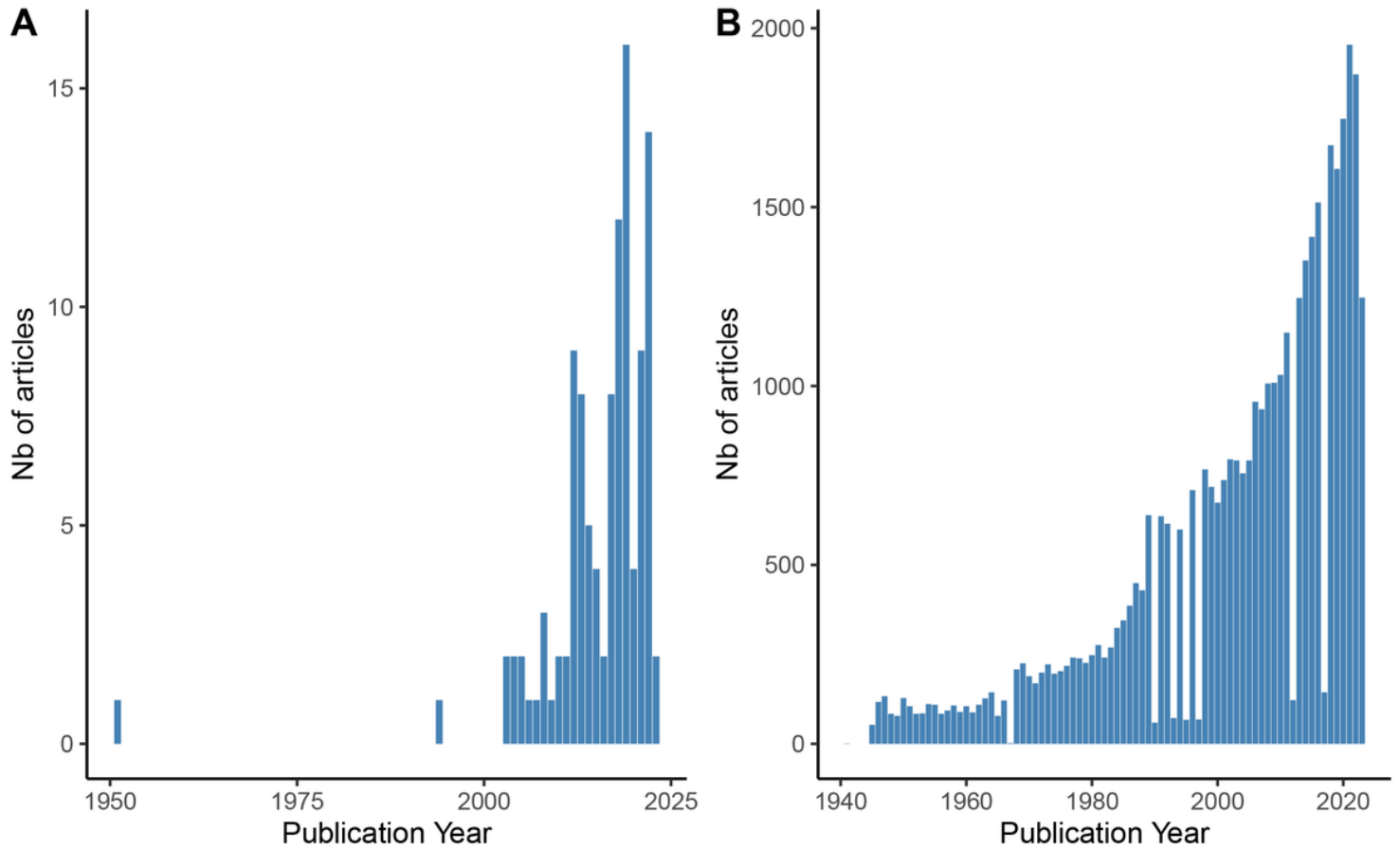


Figure 2

Chronological charts depicting the publication periods of the articles.

Caption Fig.2: (A) represents the articles collected thanks to the request and included in the scoping review and (B) the articles extracted from PubMed with the broad request “tick-borne disease” as an element of comparison.

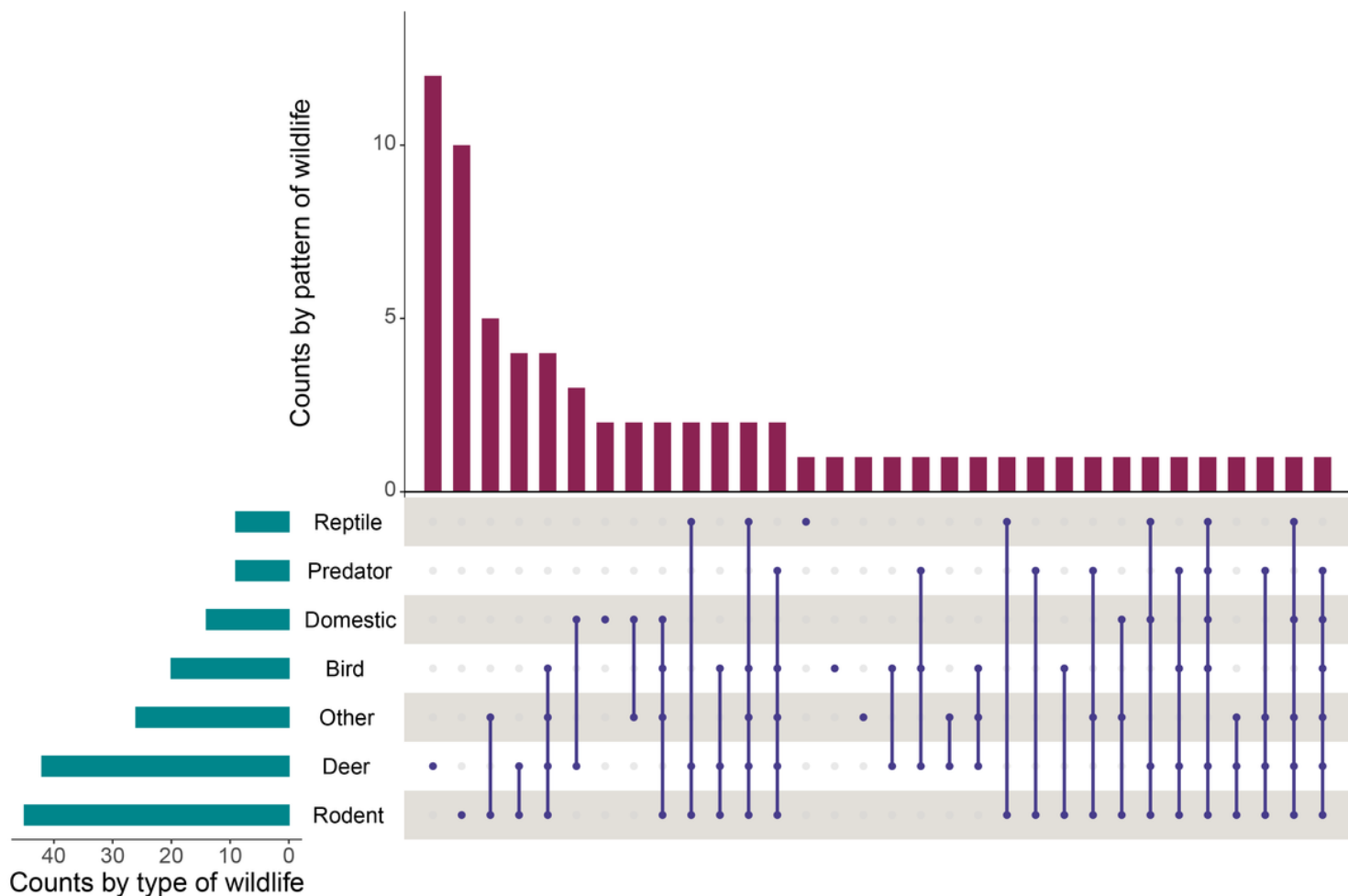


Figure 3

Upset plot of the studied wildlife distribution.

Caption Fig.3: The upper chart represents the number of articles in y axis according to the pattern of studied wildlife in x axis. For example, 12 articles only examine deer population, while four of them consider both rodents and deer. The chart on the left-hand side, represent the overall number of articles by wildlife types. For example, in total, rodents are investigated in 45 articles, and reptiles only in nine articles.

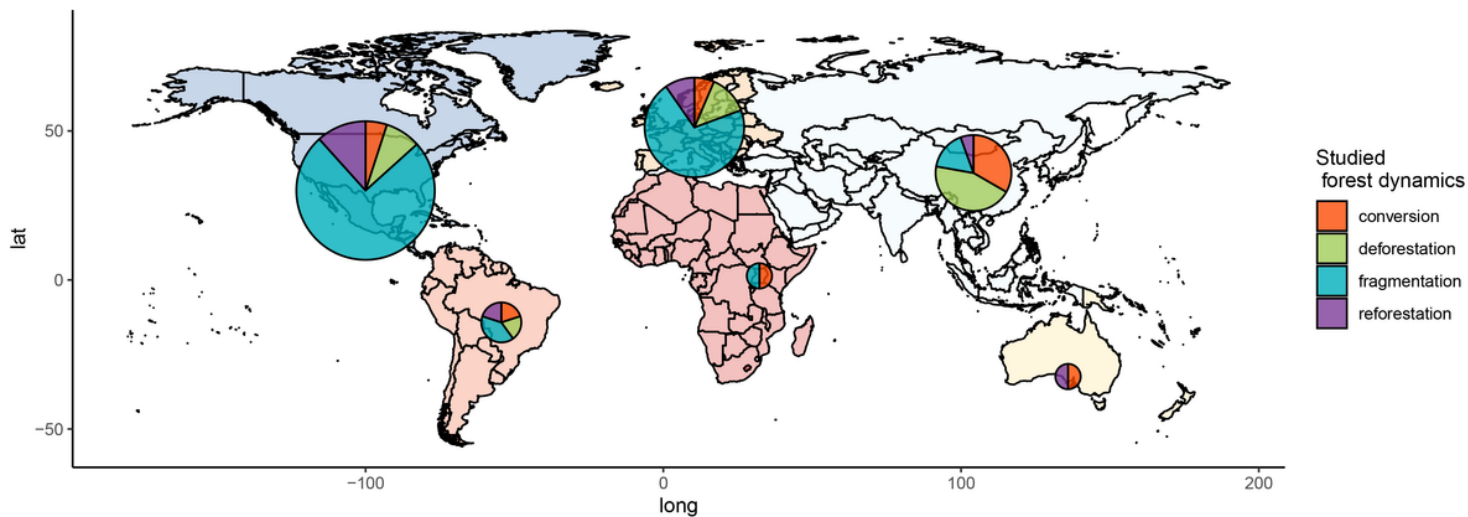


Figure 4

Proportion of forest dynamics studied worldwide (n=111).

Caption Fig.4: The size of the pie chart reflects the number of articles.

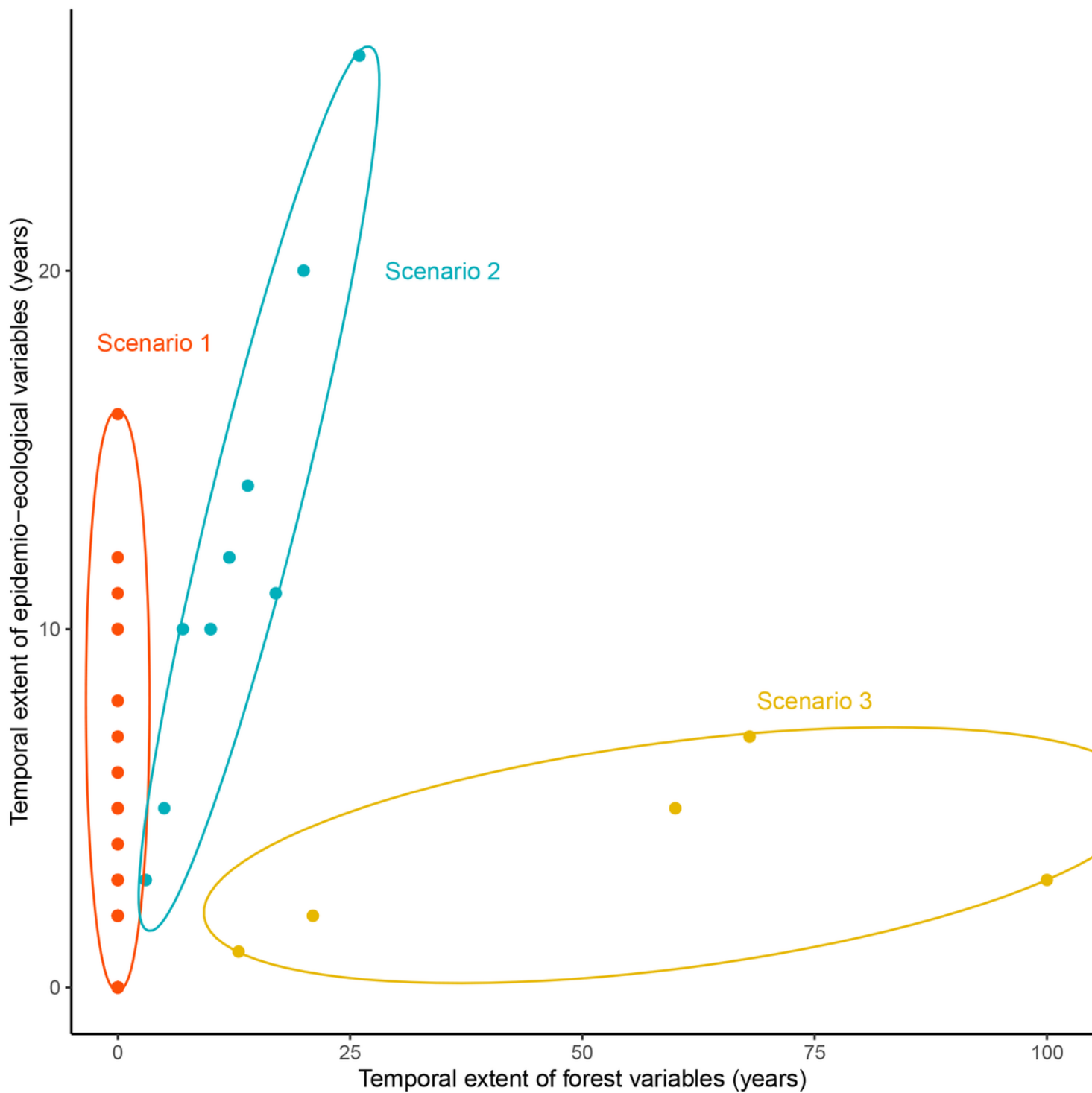


Figure 5

Temporal extent of eco-epidemiological data as a function of temporal extend cover by forest data.

Caption Fig.5: Three scenarios emerged from this chart. Scenario 1 encompasses studies incorporating both short and long-term epidemiological-ecological data alongside current forest data. Scenario 2 comprises studies aligning the temporal scope of their epidemiological-ecological data with that of their

forest data. Scenario 3 gathers studies with long-term forest data but shorter-term epidemiological-ecological data. This classification is established based on the insights provided by the chart.

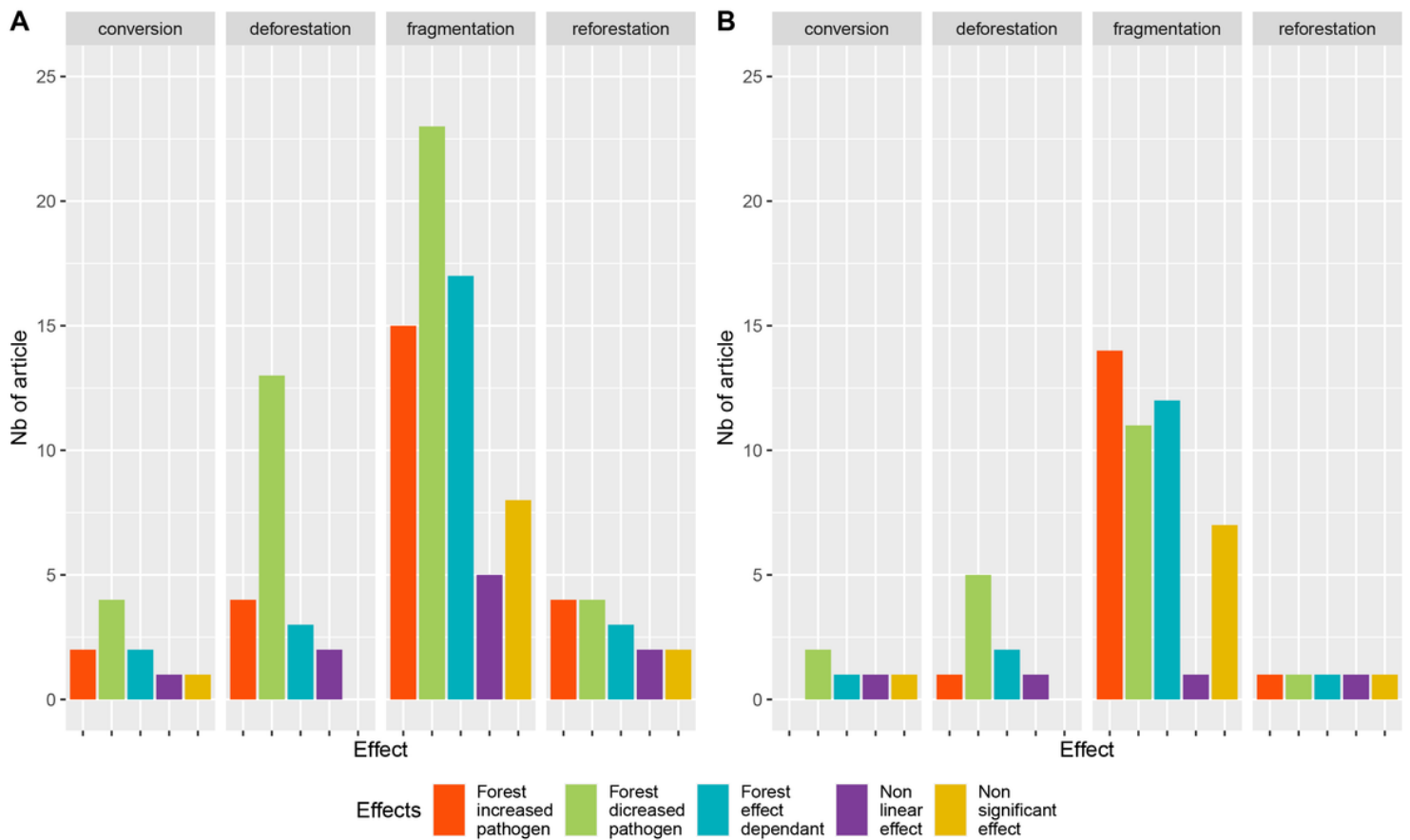


Figure 6

Differences in forest dynamics impacts distribution on the pathogen presence according to studies' type.

Caption Fig.6: (A) represents the distribution when considering all collected articles n=111 and (B) is the distribution when considering only empirical studies n=73.

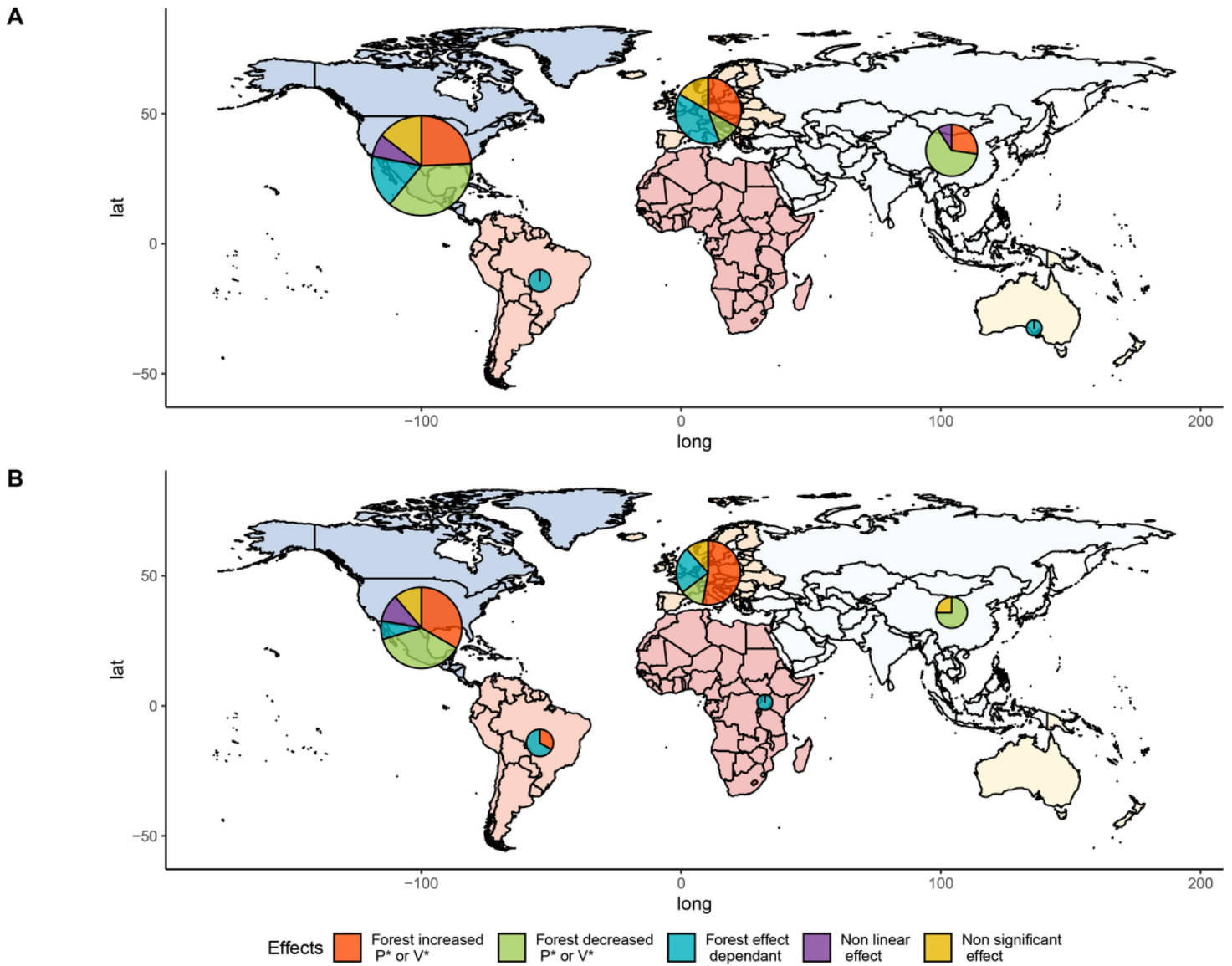


Figure 7

Observed forest effect composition according to the studied continent.

Caption Fig.7: (A) chart represents the impact of forest cover size on the pathogen presence (*P meaning pathogen) and (B) chart on the vector presence (*V meaning vector). The size of the pie chart represents the number of articles (n=111).

Supplementary Files

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