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REVIEW

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Promoting landscapes with a low zoonotic disease risk through forest restoration: The need for comprehensive guidelines

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Abstract

1. Zoonotic diseases represent 75% of emerging infectious diseases worldwide, and their emergence is mainly attributed to human-driven changes in landscapes. Land use change, especially the conversion of natural areas to agricultural use, has the potential to impact hosts and vector dynamics, affecting pathogen transmission risk. While these links are becoming better understood, very few studies have investigated the opposite question—how native vegetation restoration affects zoonotic disease outbreaks.
2. We reviewed the existing evidence linking native vegetation restoration with zoonotic transmission risk, identified knowledge gaps, and, by focusing on tropical areas, proposed forest restoration strategies that could help in limiting the spread of zoonotic diseases.
3. We identified a large gap in information on the effects of native vegetation restoration on zoonotic diseases, especially within tropical regions. In addition, the few studies that exist do not consider environmental aspects that can affect the outcomes of restoration on disease risk, such as the land use history and landscape structural characteristics (as composition and configuration of native habitats). Our conceptual framework raises two important points: (1) the effects of forest restoration may depend on the context of the existing landscape, especially the percentage of native vegetation existing at the beginning of the restoration; and (2) these effects will also be dependent on the spatial arrangement of the restored area within the existing landscape. Furthermore, we propose important topics to be studied in the coming years to integrate zoonotic disease risk as a criterion in restoration planning.

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4. *Synthesis and application*. Our results contribute to a more comprehensive forest restoration planning, comprising multiple ecosystem services and resulting in healthier landscapes for both people and nature. Our framework could be integrated into the post-2020 global biodiversity framework targets.

KEYWORDS
diseases, emerging infectious diseases, forest loss, forest restoration, human health, landscape planning, landscape structure, zoonoses

1 | INTRODUCTION

Zoonotic diseases (those originating from animals; Slingerbergh et al., 2004) comprise 75% of the known emerging pathogens (Taylor et al., 2001). Representing a significant threat to global public health, they cause millions of deaths each year (Parrish et al., 2008), and result in significant economic damages. Most zoonotic pathogens are transmitted to humans either directly from animal hosts or indirectly via vectors (Gray et al., 1998), which places animals in a central role in disease dynamics. Therefore, their presence and densities in the environment are determinants of pathogen distribution and transmission risk to humans (Estrada-Peña et al., 2014).

Deforestation, forest fragmentation and land use change have the potential to impact the dynamics of these diseases (Gottdenker et al., 2014; Jones et al., 2013; Morand, 2022) being linked with increased outbreaks of zoonotic diseases worldwide (Chaves et al., 2018; Guégan et al., 2021; Morand & Lajaunie, 2021; Rulli et al., 2017). Human-driven changes can decrease the habitat suitability for many species, leading to a simplification of fauna communities (Curtis et al., 2022; Vázquez-Reyes et al., 2017), in a process known as biotic homogenization (McKinney & Lockwood, 1999). As a consequence, sensitive species are filtered out and replaced by disturbance-adapted generalists, which are more likely to be disease hosts (Gibb et al., 2020). In addition, wildlife stressed by the new environmental condition can present declines in immune function, becoming more susceptible to zoonotic pathogen infection (Reaser et al., 2021) and, increasing transmission risk to humans. Although there is support for the existence of a dilution effect—when high biodiversity reduces transmission risk (Keesing et al., 2006)—in some situations an opposite effect may occur, with species diversity leading to a higher transmission risk (Randolph & Dobson, 2012; Wood et al., 2014).

There is a growing understanding of the connections between forest loss, land use change and the emergence of zoonotic diseases. These factors are increasingly recognized as major drivers of zoonotic disease transmission in recent years (Patz et al., 2004; Swei et al., 2020). However, there is a notable lack of research into the outcomes of restoration efforts (i.e. initiatives aimed at restoring ecological functionality; Besseau et al., 2018) on zoonotic disease risks (Morand & Lajaunie, 2021). Extensive evidence suggests that restoration can provide substantial benefits that enhance the quality of life for humans (Keenleyside et al., 2012; Reaser et al., 2021). Restored landscapes can also be important for the persistence of native forest species (Strassburg et al., 2019), guiding the establishment of complex interactions between biota, biophysical features and processes that compose an ecosystem (Falk et al., 2007). Since forest and biodiversity loss are the main drivers of zoonotic disease outbreaks (Keesing & Ostfeld, 2021; Loh et al., 2015), restoration may have profound impacts on the transmission risk of these diseases. However, knowledge about these relationships needs to be better organized to be considered in forest restoration and eco-epidemiology studies.

Understanding possible trade-offs and defining win–win restoration strategies are essential to ensure landscapes with low zoonotic transmission risk to humans. Zoonotic diseases have complex transmission cycles, with each pathogen responding differently to changes in the landscape (Lambin et al., 2010). With the launch of the 'United Nations Decade on Ecosystem Restoration', which has the goal to massively accelerate global restoration of degraded ecosystems by 2030, comprehending the effects of restoration on zoonotic disease dynamics have become imperative. Moreover, the post-2020 global biodiversity framework has several targets mentioning an increase in native vegetation and nature-based solutions, which will require restoration efforts with adequate spatial planning to guarantee biodiversity conservation and the provision of ecosystem services. Therefore, in this paper we review the existing evidence linking all types of restoration with zoonotic disease risk (general findings of the Systematic review). We propose forest restoration strategies for tropical areas that could limit the spread of zoonotic diseases (conceptual framework) and identify knowledge gaps to be studied in the future years (cutting-edge opportunities for research). We focused on forest areas because our literature review indicated a huge gap in studies in this region; and they are the most pathogen-rich areas in the world (Olival et al., 2017). We believe that this structure allows the understanding of the problem, shows the knowledge compiled so far and presents the conceptual framework of the potential responses of zoonosis transmission to tropical forest restoration.

2 | SYSTEMATIC LITERATURE REVIEW

2.1 | Methodology

Our literature review was organized in five steps (Arksey & O'Malley, 2005; Levac et al., 2010): (1) *Identifying the research questions*: This literature review aimed to answer the question: what

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is the current state of evidence on the links between restoration and zoonotic disease risk? Or what are the effects of restoration on zoonotic transmission risk? (2) *Identification of relevant articles*: We conducted a comprehensive scientific literature search in two steps. First, we used the 'naïve keywords' (forest restoration OR restor* AND disease OR zoon*) and (forest restoration OR restor* AND disease OR zoon* OR emerging infectious disease OR emerging AND infectious AND disease) in the Scopus database. We ran the search on 24 August 2022 and imported the results into R using the LITSEARCHR package (Grames et al., 2019). This package uses the Rapid Automatic Keyword Extraction algorithm (Rose et al., 2010) to create a pool of possible keywords relevant to a field of study. Employing this package, we removed duplicates and used *extract-terms* function to systematically extract all potential keywords from the article titles, keywords and abstract. The important keywords were identified in a keyword co-occurrence network: ("ecological restoration" OR "ecosystem services" OR "forest management" OR "forest restoration" OR "genetic diversity" OR "forest ecosystem" OR "restoration effort") AND ("forest health" OR "emerging infectious disease" OR zoono*). The script and the generated analytics for the keyword search are available on GitHub (https://github.com/paulaprist/Restoration_diseases.git).

The final search using this keywords combination was performed on 24 August 2022 in Scopus and resulted in 2289 articles. We chose to use only Scopus, because our naive search indicated that this platform returned not only a larger number of articles, but also all resulting articles from other platforms (Web of Knowledge and Pubmed). To ensure we were covering as many studies as possible, we used the results from our first search and from the *litsearchR* search, which resulted in a total of 2878 unique articles. The searches were conducted in English and with no restriction on year.

Our analysis for inclusion was a multi-step process. A preliminary scanning of the titles and abstracts was performed by two reviewers, and the articles that were unrelated to our objectives were discarded. In this first step all articles that made mention of environmental variables, biodiversity and zoonotic diseases in their titles and/or abstracts were selected for the second phase. As a result, 93 of 2878 unique articles were included for full reading and were then further evaluated by the two reviewers, who jointly decided on their inclusion or exclusion. Any discrepancy was discussed in a meeting with all co-authors to debate whether the article met our selection criteria (Figure 1).

(3) *Article selection*: For the final inclusion criteria we selected only articles that could indicate a correlation between restoration and zoonotic disease risk. Our inclusion criteria for the topic restoration were defined as any papers that refer to any native vegetation restoration type (e.g. controlling invasive species, maintaining tree diversity, etc., with the aim of returning composition and structure to a more natural state). For zoonotic diseases we included any papers that evaluated vectors, hosts or reservoir abundance, even if no prevalence measurements were taken in these animals or in humans. (4) *Data management*: A spreadsheet was created to extract and summarize the data from the selected articles. This table included: authors; year of publication; title; location; year, size, age and type of restoration; disease; host or vector species; response found. (5) *Analysing, summarizing and reporting the results*: the analysis and synthesis of literature included only qualitative analysis (i.e. content analysis).

2.2 | General search findings

We read 93 articles relating environmental variables, restoration and/or to zoonotic diseases, and found that only 14 met our criteria and thus entered the final analysis (Table S1). These studies were performed in six countries between the years 2012 and 2021. Most of the studies were performed in the United States ($n = 7$), followed by Hong Kong ($n = 2$). Chronologically there was minimal variation in the number of published studies, with an average of one article published each year (with the exception of 2012 and 2021, with respectively five and three articles) (Figure 2). Furthermore, the number of pathogens explored was restricted, with most studies evaluating only one pathogen, or a group of pathogens transmitted by the same vector in a single study (i.e. mosquito-borne diseases or tick-borne diseases). The exception was the United States, which not only had the largest number of studies, but also the greatest diversity

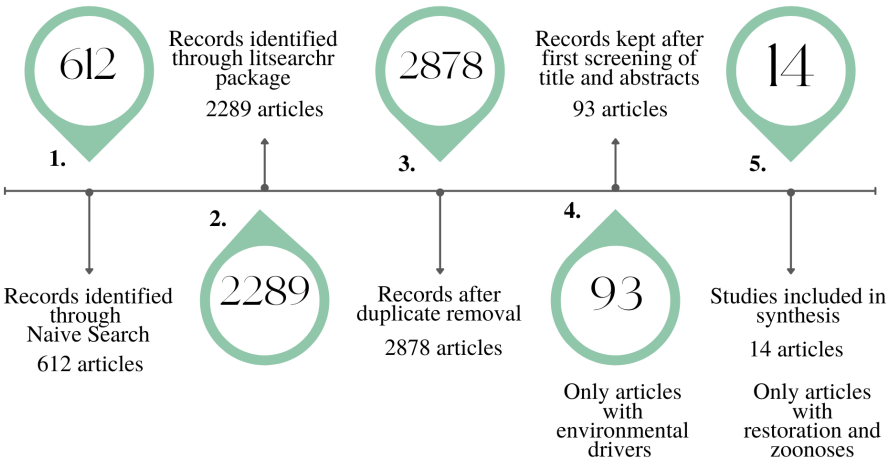

FIGURE 1 Framework for the literature review process, including the number of articles selected in each phase.

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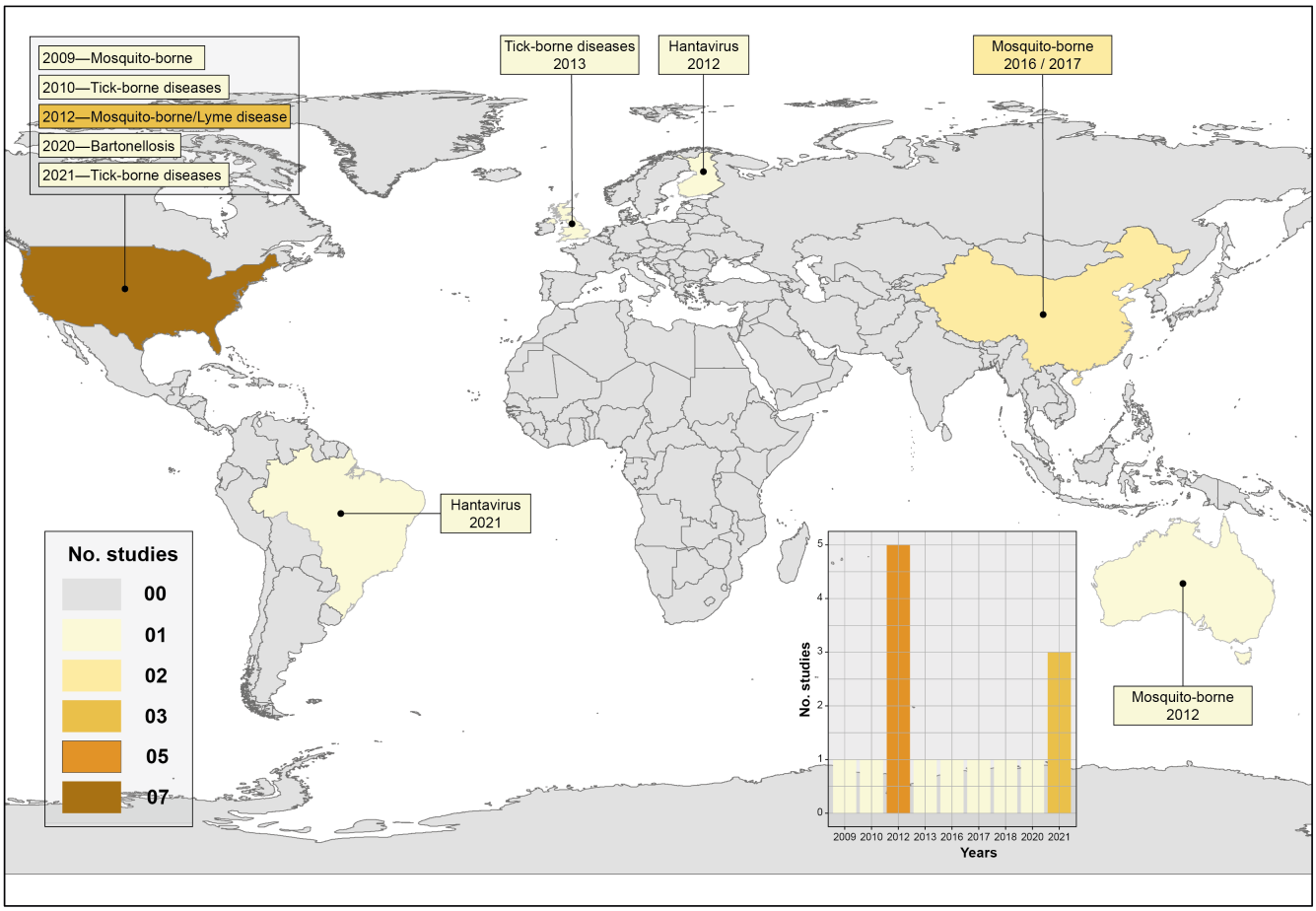

FIGURE 2 Number of studies evaluating restoration and zoonotic diseases, published per geographic location, year and zoonoses and number of studies published in each year.

of zoonoses addressed ($n = 4$). Tick-borne pathogens (*Borrelia burgdorferi*, *Babesia* spp., *Anaplasma* spp. and *Rickettsia* spp.) appeared in five studies, with two addressing specifically Lyme disease risk. Mosquito-borne diseases (diseases transmitted by *Aedes*, *Anopheles* and *Culex* species) appeared in five, while hantaviruses twice. *Bartonellosis* appeared only once.

In general, a small number of studies addressed the effects of restoration on zoonotic disease risk, supporting what was found by Speldewinde et al. (2015). This gap is even more pronounced in tropical areas, with almost nothing published on the subject. The results found were contradictory, indicating that the responses are difficult to interpret and may be pathogen and locality specific. However, none of the studies considered landscape aspects, such as the amount of native vegetation and the configuration of the remaining patches before and after the restoration process, both which can be key to understanding and managing species distributions (Saura, 2021) and subsequent zoonotic risk.

In temperate regions, a global analysis revealed that outbreaks of zoonotic and vector-borne diseases were linked with increases in forest cover (Morand & Lajaunie, 2021). Studies in small scales presented contradictory results, showing no effect (Conte et al., 2021), increased (Dalgleish & Swihart, 2012) or even reduced risk (Morlando et al., 2012). Yet, these studies did not evaluate the increment of forest cover per se, but compared areas restored by specific managements with unrestored areas. The findings were: restoration through timber harvest presented no effect on tick-borne disease risk (Conte et al., 2021), reintroduction of blight-resistant chestnut increased zoonotic risk (Dalgleish & Swihart, 2012) and restoration through active management and through removal of invasive species presented decreases in Lyme disease (Morlando et al., 2012) and ehrlichiosis (Allan et al., 2010) risk. In addition, rodents in young forests were more likely to be infected with hantavirus than in mature forests (Voutilainen et al., 2012), suggesting a potential time lag in response, where zoonotic risks could be elevated initially before eventually decreasing.

Furthermore, in these temperate regions, where restoration occurs in open habitats, such as peatlands and prairies, the restoration to its natural conditions seems to have the potential to control vector abundances and reduce the transmission risk of tick-borne pathogens (Gilbert, 2013). However, rodents infected with *Bartonella* can also be found in these restored areas (Beckmann et al., 2020) which can increase disease risk if their populations achieve high abundances. Restoration impacts in temperate regions extend beyond terrestrial environments and are seen in salt

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marsh waterscapes, where restoration techniques that alter tidal channels and ponds to minimize flooding and encouraging habitation of vector predators have decreased the abundance of vectors resulting in potential health benefits (Jacups et al., 2012; Rochlin et al., 2009, 2012).

Although tropical regions are highly biodiverse, pathogen rich and considered the most important targets for large-scale restoration initiatives (Climate Focus, 2017; Kerr, 2001), there is a large knowledge gap in this region about the effects of forest restoration on zoonotic diseases (Figure 2). One study showed a potential positive effect of forest restoration in decreasing the abundance of rodents that transmit hantavirus, however, it was based on a hypothetical restoration scenario (Prist et al., 2021), and its results have yet to be validated. Two studies showed that green roofs installed in urban areas in Hong Kong have been successful in reducing the abundance of insect vectors compared to ordinary roofs (Wong & Jim, 2016, 2017). This indicates that this 'nature-based solution' could have positive health outcomes even when performed at small spatial scales and in urban areas.

3 | CONCEPTUAL FRAMEWORK FOR TROPICAL FOREST AREAS

Given the large gap in existing knowledge about restoration and zoonotic diseases, we developed a conceptual framework that hypothesizes how restoration of tropical forest environments may affect the zoonotic transmission risk to humans. This conceptual framework was developed for tropical forest regions and considers that zoonotic risk will be dependent on the amount of vegetation in the landscape at the time of restoration, and the spatial arrangement of the restored areas. In this sense, we hypothesized what would be the risks of disease transmission after forest restoration performed in two different strategies and in landscapes with varying amounts of forest cover (low, intermediate and high, Figure 3).

The conceptual framework assumes that vectors, hosts and reservoirs play important roles in pathogen transmission to humans (Lessler et al., 2016). The framework also assumes that their abundance is modulated by changes in both composition and configuration of native vegetation (Chaves et al., 2021; Prist et al., 2021), with different species having similar patterns of response (Chaves et al., 2021; Mendoza et al., 2019; Prist et al., 2021). Finally, we focus on zoonotic and infectious diseases common to rural areas, due to large-scale restoration projects often being developed in these environments.

Disease risk was considered as the potential transmission of a zoonotic pathogen to humans, which requires contact between hosts, vectors and humans. In both restoration strategies, the increase in the amount of forest cover is the same. However, in strategy 1, restoration is performed to increase the size of existing fragments, decreasing the amount of forest edge. In strategy 2, the goal is to increase connectivity by creating stepping stones and/or forest corridors, also boosting forest edges.

To hypothesize how different forest cover could affect zoonotic risk transmission, we rely on the presence of thresholds of biodiversity response to landscape changes (Andrén, 1994; Banks-Leite et al., 2014; Pardini et al., 2010), which can guide restoration prioritization and expected benefits (Banks-Leite et al., 2014; Tambosi et al., 2014). Most of the studies have shown that in tropical areas, species require at least 30% of native habitat for community integrity maintenance (Andrén, 1994; Arroyo-Rodríguez et al., 2020; Banks-Leite et al., 2021; Boesing et al., 2018). Although there is no consensus on this value (which can range from 20% to 50%), we are basing our framework on these studies, assuming the values found in Pardini et al. (2010). However, it should be noted that habitat requirements can vary according to the geographic region and landscape context.

Landscapes (large areas, with sizes >3600 ha) with a high amount of forest cover (~>50%) are expected to have low abundances of disease hosts and reservoirs (Chaves et al., 2021; Pardini et al., 2010; Prist et al., 2021) and low contact rates with humans, resulting in low transmission risks. This happens because these landscapes can harbour a high diversity of species, heterogeneous communities and the presence of habitat specialist species (Estavillo et al., 2013; Hanski, 2011; Pardini et al., 2010; Radford et al., 2005). Notably, in these landscapes several pathogens can still be present, but at lower prevalence and with minimized chances of transmission to humans given the decreased rates of human–wildlife contact.

In landscapes with an intermediate amount of forest cover (~40%), the persistence of habitat specialist species becomes dependent on the configuration of the remaining habitat (Banks-Leite et al., 2014; Estavillo et al., 2013; Pardini et al., 2010; Villard & Metzger, 2014). Connectivity among patches is practically lost, restricting dispersal and recolonization of species (Estavillo et al., 2013; Hanski, 2011). Aspects such as patch size, amount of edge habitat and isolation become extremely important and will determine the abundance of disease hosts and reservoirs. For example, in landscapes within this threshold, forest edge extension (the total length of boundary between two habitat types, per unit of core area) can reach its maximum, boosting contact rates and increasing the potential for infectious disease emergence (Bloomfield et al., 2020; Faust et al., 2018).

Landscapes with low levels of forest cover (~<10%) would be at higher risk for zoonotic transmission, since community structure tends to be homogeneous and can be dominated by a few generalist species (i.e. disease vectors and reservoirs) that become super abundant (Chaves et al., 2021; Prist et al., 2021). If immersed in an agricultural matrix, these impoverished meta-communities could form the ideal landscape for pathogen transmission; contact rates between humans, domestic animals and wildlife are increased, rising spillover risk. It is worth pointing out that for some diseases, this landscape could also present a low risk. This would happen if faunal communities were oversimplified to harbour all the species needed to complete the life cycle of some zoonoses.

Performing a forest restoration following **strategy 1**, where restoration increases the size of forest fragments, the expected

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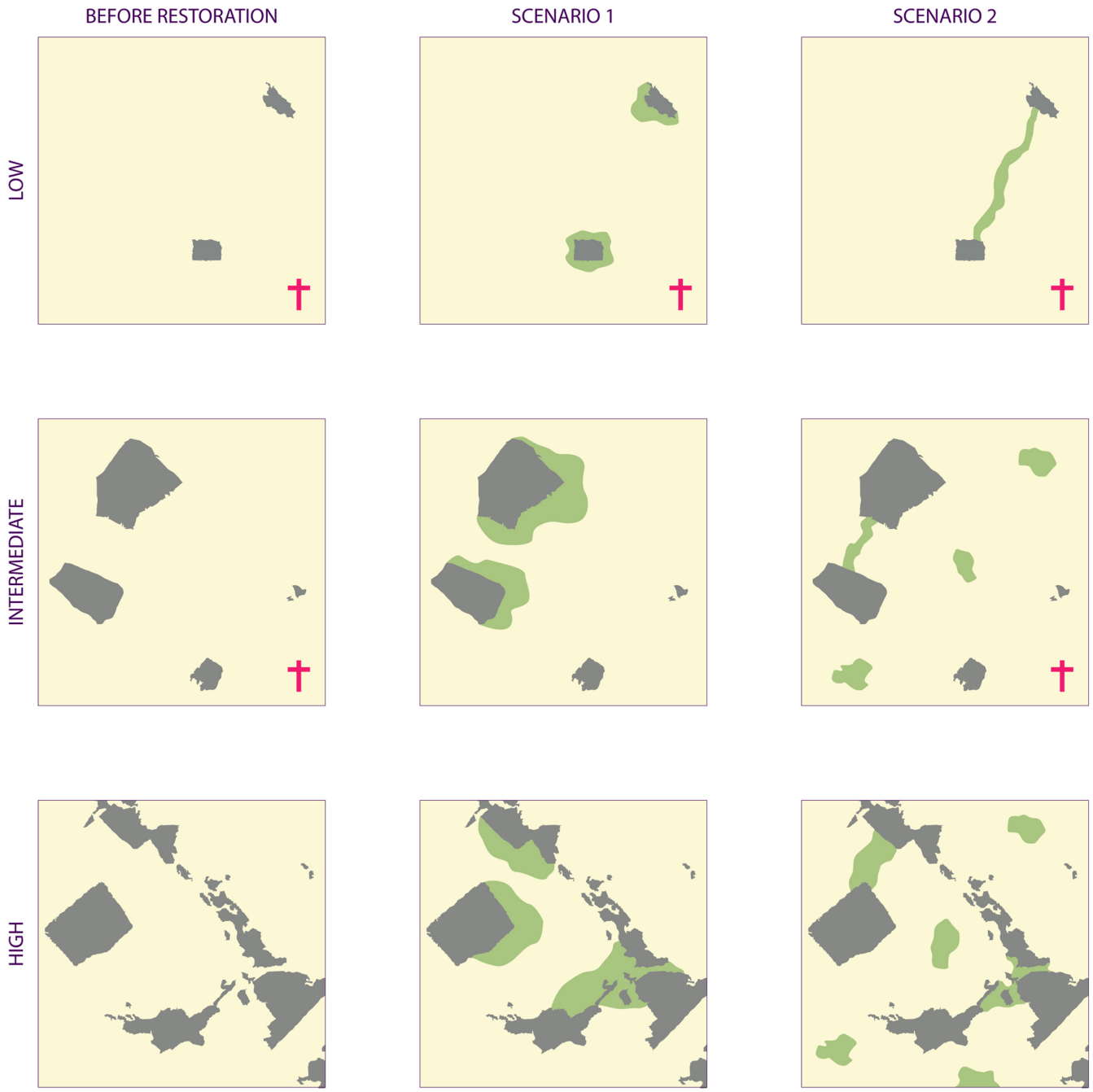

FIGURE 3 Conceptual framework showing the expected results of forest restoration according to two different strategies in three landscapes with different amounts of forest cover (low, intermediate and high). Strategy 1 increases the size of forest fragments, while strategy 2 increases landscape connectivity, promoting restoration through the creation of stepping stones and forest corridors. Dark green shows already existing forest fragments; light green represents restored areas, while the red crosses show landscapes that may be at higher risk of transmission after forest restoration initiatives when compared to their previous situation. Landscapes without crosses either have potentially decreased risk, or almost no change, as in high forest cover landscapes, where risk is low before restoration and has the potential to remain low after intervention.

outcomes are: (1) landscapes with high amounts of forest cover could present no changes in the transmission risks because they already have a low pathogenicity. This is due to the abundance of vectors and hosts and the low contact rates with humans. Increases in forest cover should not alter the abundance of vectors, reservoirs and host species.

(2) Landscapes with an intermediate amount of forest cover could present reductions in transmission risks. In these landscapes, large forest patches in conjunction with landscape configuration are essential to maintain forest specialist species (Estavillo et al., 2013; Pardini et al., 2010). Increasing the area of forest patches through restoration could increase patch size, reduce

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isolation and improve species diversity. This can reduce the abundance of host species and, consequently, contact rates and transmission risks. Furthermore, species that specialize in open habitats, such as the hantavirus reservoir *Necromys lasiurus*, would lose their suitable habitat as the amount of forest increases, consequently reducing their abundances (Prist et al., 2021), and potentially decreasing transmission risk.

(3) Landscapes with low amounts of forest cover could present increases in their pathogenicity. In such landscapes, forest-dependent species tend to be extinct and disease reservoirs and vector species could thrive. A small increase in the amount of forest cover could lead to an increase in the ideal habitat for generalist species and boost transmission risks. This can happen if specialized forest species from neighbouring landscapes do not recolonize these newly restored areas. Furthermore, if the initial forest cover is too low to allow for the presence of vectors and hosts, any increment could allow potential hosts and vectors to return, increasing their abundance and consequently transmission risk.

In restoration programs following **strategy 2**, when restoration increases landscape connectivity, the following outcomes are expected: (1) Landscapes with high amounts of forest cover could present no change in the transmission risk of zoonotic diseases, due to the same hypothesis presented in strategy 1.

(2) Landscapes with an intermediate amount of forest cover could present negative effects, boosting contact rates with humans and domestic animals and increasing transmission risk. The increase in the amount of forest edge resulting from restoration could not only raise the abundance of reservoirs and vectors, but also facilitate their movement (Prist et al., 2022). In tropical areas, forest edges act as conduits of interactions between pathogen hosts, reservoirs and humans, facilitating the physical encounter between them and increasing transmission risk (Bloomfield et al., 2020; Faust et al., 2018). Notably, tropical forest edges are a major launchpad for novel human viruses (Dobson et al., 2020). This effect could be avoided if the restored areas are created by forming wide corridors, with enough size to allow for the dispersion and recolonization of forest specialist species. For example, Prist et al. (2022) argue that forest corridors longer than 250 m could be sufficient to stop the spread of yellow fever virus in the Brazilian Atlantic Forest.

(3) Landscapes with a low amount of forest cover could present increases in transmission risks by extending forest edges densities and the number of suitable habitats for disease hosts and vectors. This is a similar mechanism to what is expected in strategy 1. In addition, an increase in connectivity will likely increase forest fragmentation, further contributing to increases in the abundance of disease hosts and transmission risk (Wilkinson et al., 2018). This scenario is also consistent with the intermediate disturbance hypothesis, which states that local species diversity is low in high disturbed areas (Connell, 1978). In this situation, only a few species survive to dominate the new environmental condition (Connell, 1978).

Despite the low abundance of vectors and reservoirs, as well as minimal contact rates with humans, the risk of disease transmission still exists in high forest cover landscapes. Avoiding any form of contact with wild animals is the best way to prevent pathogen spillover to humans. Moreover, although our framework indicates a general trend, there may be cases, in which the increase in forest cover, regardless of the strategy employed, may lead to an increased spillover risk, such as when the diversity of pathogens and parasites is positively correlated with the diversity of free-living species. Monitoring programs should always be implemented to allow for early responses and the implementation of mitigation and control actions.

4 | CUTTING-EDGE OPPORTUNITIES FOR RESEARCH REGARDING FOREST RESTORATION IN TROPICAL AREAS

4.1 | Nonlinearities in zoonosis emergence

Evidence of nonlinearity in biodiversity response to landscape changes has already been shown (Banks-Leite et al., 2014; Pardini et al., 2010; Vidal et al., 2019). However, studies verifying the presence of critical thresholds in spillover risk are still lacking (Kilpatrick et al., 2017). In tropical regions, when forest cover is reduced below 30% of the landscape, abrupt changes in species composition have been observed. In this situation a shift happens, from a specialist-dominated community to one composed primarily of generalist species, many of which are classified as pathogen hosts (Banks-Leite et al., 2014; Pardini et al., 2010; Prist et al., 2021). We can thus hypothesize that a critical threshold should exist for spillover risk in this region, which is related to changes in biodiversity and in the species community composition (Prist et al., 2017). Studies testing the existence of critical thresholds would be important to understand how many forested areas can be converted before crossing the threshold. After this point, restoration actions may not be able to reduce zoonotic spillover risk due to the drastic changes in community composition. In addition, some studies propose that in landscapes below this threshold, local species richness and abundance is dependent on patch size and the remaining habitat configuration (Andrén, 1994; Fahrig, 2003; Pardini et al., 2010; Prist et al., 2012). There are negative effects of habitat fragmentation and configuration on species richness and abundance (and consequently on richness and abundance of disease hosts and vector species), and these habitat configuration effects are distinct from those of habitat amount (Saura, 2021). Better understanding of these responses will allow for proper spatial planning of landscapes, ensuring that landscapes with low pathogenicity are formed, whether above or below the threshold.

Likewise, matrix quality can affect population dynamics and threshold values (Arroyo-Rodríguez et al., 2020), determining dispersion capacity of reservoirs/hosts, which further influences the magnitude of transmission. Some studies show that vector and reservoir species can move farther in fragmented landscapes (Diffendorfer et al., 1995; Pires et al., 2002), resulting in higher transmission risk

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in these areas (Hahn et al., 2014; Prist et al., 2022). Understanding which matrix types facilitate or restrain the movement of different pathogen hosts, or how far they can move in nonhabitat environments is fundamental to understanding transmission dynamics and designing healthy landscapes for humans.

4.2 | Trade-offs among different zoonotic diseases and ecosystem services should be evaluated before proposing any landscape management strategy

A landscape considered healthy for one zoonoses will not necessarily be the best one for the provision of other ecosystem services. One study in Brazil showed that there are possible trade-offs, and that a landscape considered ideal for providing disease regulation can be unsuitable for other services, such as pest control and pollination (Prist et al., 2022). Studies considering co-occurring zoonoses in the same landscape and even interactions with different ecosystem services, are essential to understanding these trade-offs and to define the most cost-effective landscape management strategies.

4.3 | Much more than the structure of the landscape, the choice of the tree species for restoration is very important

High-quality reforestation can be considered a nature-based solution to the problems of biodiversity loss, climate change (Seddon et al., 2020) and possibly to human health (Prist et al., 2021). However, to achieve these goals, the restoration must be well planned. If host and vector preferences are not considered in such restoration projects it might attract pathogen-hosting wildlife to new food and habitat resources, thereby increasing the risk of human exposure to zoonotic pathogens (Dalgleish & Swihart, 2012; Reaser et al., 2021). Regardless of the type of intervention planned—active or passive (Hobbs & Cramer, 2008)—the focus should always be on native species, since invasive alien plants may provide optimal habitat for zoonotic hosts and vectors that increase disease risk (Allan et al., 2010; Stone et al., 2018). The Nipah virus for example, was associated with the planting of mango trees next to pig enclosures, which attracted bats and led to the spread and amplification of the virus (Breed et al., 2006). In addition, selection of appropriate sites for forest recovery, and the composition and configuration of the elements of the new landscape are also essential for restoration to have the desired effect. The type of intervention required will depend on the type and extent of the ecosystem damage and it can range from removal of invasive species to substantial alteration of the physical environment (Hobbs & Cramer, 2008). Here we are focusing only on a discussion regarding the recovery of native vegetation through the increase in the amount of forest cover and are not interested in the type of method applied to achieve this outcome.

4.4 | Temporal dynamics of restoration are likely to affect the expected human health outcomes

There are several formations that an ecosystem can go through during the restoration process (Suding et al., 2004), which result in different outcomes for the risk of zoonotic disease transmission (Speldewinde et al., 2015). Therefore, we expect that there will be a time lag before the ecosystem service of zoonosis regulation is provided by reforested areas. In general, forest restoration can recover around 44% (from 15% to 85%) of species richness and composition when compared to unrestored areas (Crouzeilles et al., 2017; Lennox et al., 2018; Rey Benayas et al., 2009) on a time scale of 40 years (Lennox et al., 2018). This recovery time can vary with the speed of the restoration process, the landscape context, land use history, potential recolonization of species (Morales-Díaz et al., 2019; Pardini et al., 2010) and the type of restoration implemented.

We also expect that the recovery time can vary among disease systems, with no single outcome for all zoonoses. Therefore, restoration projects should be carefully monitored throughout the entire process. In addition to tracking changes in the abundance of host and vector species, monitoring community composition over time is also critical. The order in which species recover may affect the structure of communities (Berg et al., 2015) and the establishment of host species interactions (Lira et al., 2019) impacting spillover risk. For this reason, it is crucial to understand the sequence of species gains to unravel their consequences and predict how these network interactions affect the provision of ecosystem services.

Most studies do not consider the temporal dimension, despite its importance for the sustainability of ecosystem service provision (Boesing et al., 2020). Long-term monitoring studies are essential: in a first instance, forest restoration could increase understorey density, boosting the amount of suitable environments for vectors and reservoirs (Morales-Díaz et al., 2019). However, after this critical period and with the advancement of the successional stage, species richness increases, and the community becomes more complex, potentially controlling the abundance of vectors and hosts. This scenario predicts a curvilinear relationship in which risk to humans increases with restoration age until it reaches an inflection point (yellow line in Figure 4), where, more commonly, forest structure and complex communities begin to buffer against transmission (Keesing & Ostfeld, 2021). Until this point is reached, monitoring, control and educational programs should be established in restored areas to reduce the chances of contact between humans, vectors and hosts to reduce transmission risks.

A time lag is but one of the possible outcomes of restoration on zoonotic disease risk. Here we present two more possible trajectories, which represent only hypotheses within several possibilities. In one possible trajectory (red line in Figure 4), spillover risk increases with restoration. This can happen, for example, in our restoration strategy 2 in low and intermediate forest cover landscapes. In these cases, studies understanding risk behaviours and wildlife exposure should be priority, so that risk reduction happens mostly by avoiding human–wildlife interactions. In another possible trajectory (green

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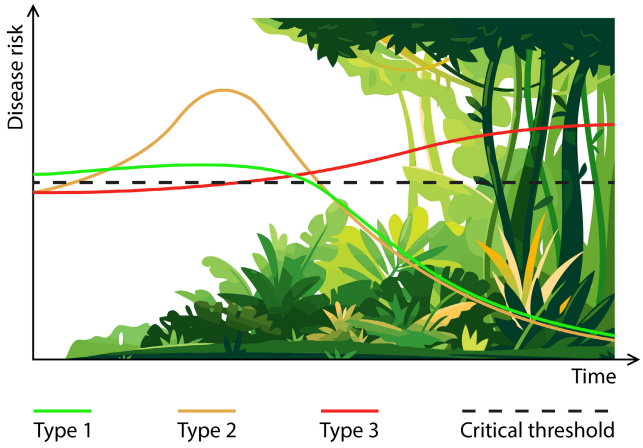

FIGURE 4 Possible time lag responses of zoonosis risk in relation to forest restoration. We hypothesize that different responses may occur throughout the restoration process (1) yellow line: risk to humans increases with restoration age until it reaches an inflection point where increasingly forest structure and biodiverse forest communities begin to buffer against transmission through the dilution effect; (2) green line: early stages of restoration may cause no effect on spillover risk, until over time, increased biodiversity and the formation of more complex communities lead to a decreased risk; (3) red line: spillover risk increases with restoration due to increases in host species richness and abundance.

line in Figure 4), early stages of restoration may have no effect on the spillover risk, until the forest reach threshold level of structural complexity that allows the species interactions that eventually reduce vector abundances and thus, transmission risk. In any case, long-term monitoring programs are essential to understand these behaviours and establish adequate control programs to avoid any negative outcomes.

5 | FINAL REMARKS

The aim of this article was, through a literature review, to understand how restoration affects the risk of zoonotic disease transmission to humans. This topic has growing significance considering new restoration projects are carried out every year in different parts of the world, which can have both positive and negative results for human health. The few articles found in the literature review generated contradictory results. In addition, there was minimal information about landscape aspects, such as habitat cover and configuration at and after restoration, and how they determine ecosystem service provision. In response to this knowledge gap and pressing need for guidelines in a scientific and political environment increasingly concerned about degraded landscapes, we developed a conceptual framework for tropical areas, that hypothesizes potential responses to zoonosis transmission, given the landscape context and spatial arrangement of forest restoration. Far from being a clear outcome, the goal of this model is to raise the discussion about how forest restoration can affect the transmission risk of these diseases. It is also guided by some of the many aspects that can affect these outcomes and should be incorporated into restoration studies.

AUTHOR CONTRIBUTIONS

Paula R. Prist, Mariana Morais Vidal, Cecilia Siliansky de Andreazzi and Leandro Reverberi Tambosi conceived and designed the research; Paula R. Prist, Mariana Morais Vidal, Cecilia Siliansky Andreazzi, Carlos Zambrana-Torrelio, Peter Daszak, Raquel L. Carvalho and Leandro Reverberi Tambosi draft and revise the manuscript for important intellectual content; and all authors finally approved the manuscript to be published.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. In addition, Raquel L. Carvalho is an Associate Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

This paper does not use any data.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Studies evaluated in the present review with country, disease studied, outcome measured, type of restoration and the response found. Light blue dots denote a positive effect of restoration on human health (decrease in transmission risk), orange dots denote a negative effect (increase in transmission risk), while grey dots denote a neutral effect.

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