

Macroecological approaches for the prediction of zoonotic disease risk

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Moreno Di Marco¹✉, Lara Marcolin¹, Andrea Tonelli¹✉, Eloise Skinner² & Elena Catucci¹

Outbreaks of zoonotic pathogens have become more frequent as human modification of the natural environment accelerates pathogen spillover from wildlife to humans, yet much remains to be investigated around the mechanisms that regulate pathogen outbreaks. This Review explores the current use of macroecological variables (that is, emergent ecosystem properties) for modelling zoonotic disease risk. We identify important research gaps and discuss untapped opportunities for using a wider spectrum of variables to achieve improved modelling of zoonotic disease risk and, consequently, surveillance. We present a set of operational recommendations and guidelines for potential integration of macroecological approaches within a broader One Health framework.

Zoonotic risk prediction has recently gained prominent attention in global pandemic preparedness strategies¹, and the mechanisms that lead wildlife-borne pathogens to generate human outbreaks have been widely discussed^{2,3}. In recent decades, zoonotic outbreaks have become more frequent, and more likely to escalate to large-scale epidemics and pandemics^{2,4}, despite the overall improvement in global human health. This increasing frequency of reported zoonotic outbreaks is not just a consequence of intensified monitoring, as several studies have demonstrated a recent increase in the rate of spillover events—the transmission of a pathogen from animals to humans—that give rise to large-scale outbreaks^{2,4,5}. This increased rate is the result of human population growth, an increment in human mobility and the overall escalation of anthropogenic pressure on natural environments, which create more opportunities for animal-to-human transmission and can lead to higher susceptibility of animal hosts³.

The rapid increase in emerging zoonotic disease events², and the potentially enormous number of unknown viruses with zoonotic potential⁵, mean that epidemic and pandemic preparedness require predictive models that are built on risk mechanisms⁶. Certain mechanisms that drive zoonotic risk are well known, and include land-use change⁷, deforestation⁸, wildlife trade⁹ and livestock production¹⁰. These mechanisms alter the natural circulation of pathogens within wildlife communities (for example, by altering the distribution and abundance of hosts¹¹) and/or the human–wildlife interface which

determines the risk of pathogen spillover¹². Yet, much remains to be explored around ecological mechanisms that drive the risk of pathogen spillover and outbreak. In fact, zoonotic risk models generally only account for a limited number of predictive variables that represent drivers of risk—vegetation type, land-use change, population density and so on—and disregard many important ecological mechanisms such as variation in host competence and which generate pathogen dilution or amplification^{13,14}. This is particularly evident when considering emergent properties of ecological systems, so-called macroecological properties. Macroecology focuses on the distribution of species, their abundance and their ecological functions at large scales, examining both spatial and temporal trends^{15–19}. Macroecology builds on, and integrates, several other disciplines such as ecology, evolution, biogeography and genomics. The potential of using a macroecological approach for the study of infectious diseases has already been advocated²⁰, under the assumption that pathogen ecology is closely linked to the distribution, abundance and interactions of their hosts, all of which are regulated by macroecological processes. Yet, despite rapid progress of emerging infectious disease (EID) research in the past decade²¹, the consideration of macroecological aspects potentially connected to zoonotic risk remains scant. This is reflected in the limited use of macroecological variables for predictive purposes in zoonotic research, and for monitoring programmes as part of One Health and pandemic prevention strategies⁶.

¹Department of Biology and Biotechnologies “Charles Darwin”, Sapienza University of Rome, Rome, Italy. ²Centre for Clinical Research, Faculty of Health, Medicine and Behavioural Sciences, The University of Queensland, Brisbane, Queensland, Australia. ✉e-mail: moreno.dimarco@uniroma1.it; andrea.tonelli@uniroma1.it

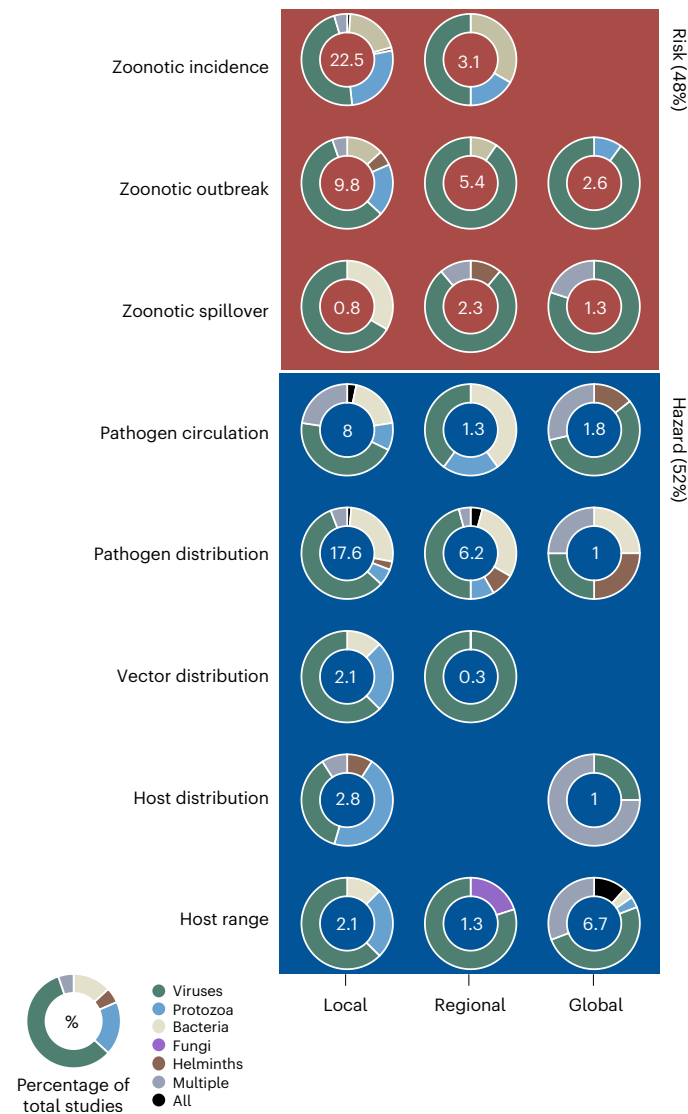


Fig. 1 | Conceptual mapping of zoonotic modelling research in the past decade. ‘Hazard’ represents articles that assessed the potential presence of pathogens and ‘Risk’ represents articles that also considered human exposure to pathogens. The articles analysed in our literature review are summarized on the basis of their geographic scale (x axis) and research aim (y axis). Each combination of geographic scale and research aim is depicted by a circular plot. In each circle, we report the overall percentage of articles, whereas the target pathogen types of each study are shown in different colours.

In this Review we critically assess how zoonotic risk models have incorporated different types of predictor variables, including socio-economic, environmental and macroecological parameters, to address specific research aims. We identify a consistent gap in the use of macroecological variables, such as host diversity, evolutionary history and ecological integrity, despite growing theoretical support for their relevance. We then synthesize the conceptual basis for incorporating these variables into zoonotic risk research, drawing on principles from animal ecology, biogeography and disease ecology. Building on this, we provide a dual contribution: first, we outline key conceptual and practical barriers that have limited the uptake of macroecological approaches in zoonotic risk modelling and, second, we present a set of recommendations and guidelines to support better integration of macroecology into One Health research and policy. Our aim is to inform when and how macroecological principles (and variables) can be most effectively used to aid zoonotic risk research for guiding disease monitoring and preparedness plans.

Current zoonotic disease modelling

The use of modelling approaches for zoonotic disease prediction has grown rapidly in recent years, to address the increased need for anticipating future disease outbreaks and inform both management and policy strategies²². Several recent reviews have looked at trends and patterns in zoonotic research, exploring different themes around the environmental and anthropogenic drivers of zoonotic disease emergence^{23–25}. Here we took a broader perspective, providing a comprehensive overview of current approaches used as part of zoonotic disease modelling—spanning from pathogen circulation in wildlife to outbreak risk in humans. We then focused on the use of the macroecological variables that are potentially linked to zoonotic disease risk, an area that has received limited attention in the One Health literature and virtually no systematic treatment.

We identified 387 scientific articles published in the past decade (2014–2024) that present modelling exercises to predict zoonotic diseases (Supplementary Methods 1 and Supplementary Table 1). To compile the literature database, we first screened all papers on the basis of their title and abstract to identify studies that explicitly referred to, or whose content indicated, modelling of zoonotic diseases. In this context, we consider zoonotic diseases as infectious diseases that are transmitted from a non-human animal to humans (either directly or indirectly). We then reviewed the full texts of the shortlisted articles to confirm their relevance. These articles have been separated into two categories: those addressing zoonotic disease hazard—focused on the presence of a pathogen, often inferred from the distribution of host and/or vector species—and those addressing zoonotic disease risk—which additionally incorporate elements of human exposure to such a pathogen, including socio-economic conditions that may lead to zoonotic transmission²⁶. We found an equivalent proportion of articles addressing hazard versus risk (Fig. 1 and Supplementary Fig. 1), and a dominance of local-scale analyses compared with regional or global studies (at around 2:1).

Approximately half of the reviewed articles pursued two main aims (Supplementary Fig. 1): predicting the spatial distribution of pathogens (that is, ‘hazard’ under our definition) and predicting the disease incidence in terms of either the number of human cases or infected areas (that is, ‘risk’ under our definition). The remaining articles addressed a broader set of modelling objectives, including predictions of zoonotic outbreak occurrence, pathogen circulation and host range. In this regard, whereas the reviewed articles encompassed a wide range of pathogens (viruses, bacteria, protozoa and metazoa; Fig. 1), viruses were by far the most investigated group, and vector-borne diseases received the highest attention overall (52% of all articles). In this context, we consider vector-borne diseases to be human diseases caused by pathogens that are transmitted by a vector (for example, a mosquito, a tick, a flea), usually through biting. Within the subset of studies that model vector-borne diseases (Supplementary Fig. 2), we found a slightly stronger focus on disease risk, with the majority aiming at predicting disease incidence or disease outbreak.

Surprisingly, we found that articles predicting zoonotic spillover are much less common than others in the recent literature (<5%), even if some highly influential articles addressed this topic, for example, making spatial predictions of the risk of zoonotic disease emergence at a global scale^{4,27}. These approaches build on the known (or approximate) time and location of zoonotic EID events, and the characteristics of these locations, to predict where new events are more likely to occur. Further developments extended this framework to predict future scenarios of risk, on the basis of the predicted change in biological and anthropogenic factors that drove the EID risk in the past^{28,29}. Additional research has applied such models to understand the role of specific aspects of anthropogenic pressure, such as hunting levels³⁰, or specific environmental variables, such as ecological integrity³¹.

Table 1 | List of macroecological properties with potential to inform zoonotic risk modelling, including examples of specific variables, literature references (where these have been used) and related data sources

Macroecological property	Macroecological variable	Rationale	References	Example data sources
Compositional diversity	Alpha diversity (species richness)	A higher number of wild species leads to a higher number of potential hosts but also a potential dilution effect	14,95	Biogeographic modelling Infrastructure for Large-scaled Biodiversity Indicators (BILBI) ⁹⁶ IUCN Red List (www.iucnredlist.org) Area of Habitat ⁹⁷
	Beta diversity	A higher compositional turnover leads to a higher probability of pathogen spillover among hosts	98	
	Gamma diversity	The same rationale as for alpha diversity (see above)		
Species abundance	Species abundance and spatio-temporal dynamics	Spatio-temporal patterns and dynamics of species abundance affect the distribution of zoonotic pathogens, especially density-dependent ones	11,98	TetraDENSITY 2.0 ⁹⁹
	Abundance–occupancy relationships	Biological homogenization increases zoonotic risk (more abundant and widespread species are competent hosts for pathogens; an increase in occupancy increases pathogen sharing)	11,77	
	Evenness (the relative numerosity of species in a community)	An unbalanced populations composition may favour generalist species, which are more prone to host pathogens	11	
Ecological integrity	Biodiversity habitat index	A high ecological integrity reduces zoonotic risk	31	Biodiversity Intactness Index ¹⁰⁰ Biodiversity Habitat Index ¹⁰¹
	Biodiversity intactness index			
	Contextual intactness			
	Defaunation Index			
Fragmentation	Landscape configuration and fragmentation	Properties of patches determine the localized disease risk, whereas configuration and connectivity drive patterns of pathogen spread	12,69	LandFrag ¹⁰²
Functional diversity	Functional diversity (diversity of life histories, diversity of morphologies and diversity of diets)	Functional diversity reduces the exposure of wildlife to pathogens	79,95	COMBINE: a COalesced Mammal dataBase of INtrinsic and Extrinsic traits ¹⁰³
Phylogenetic diversity	Phylogenetic diversity	Phylogenetic relatedness increases the probability of pathogen sharing among hosts	90	VertLife.org (https://vertlife.org/)
Structural diversity	Enhanced vegetation index	Structural diversity captures the ecological complexity and habitat dynamics that influence pathogen and host distribution, as well as human–wildlife interactions	43	Enhanced Vegetation Index ¹⁰⁴

In addition to studies predicting zoonotic incidence, pathogen distribution or spillover risk, approximately 10% of the reviewed articles aimed at identifying the potential host range of pathogens. By predicting host–pathogen associations, these studies aimed at disentangling eco-evolutionary patterns that drive the definition of viral carrier status³² or, more generically, at predicting the association between potential hosts and pathogens^{21,23,33}. These exercises typically build on the life-history and/or phylogenetic characteristics of known host species to identify unknown potential hosts. This task is critical, as the current knowledge of host–pathogen associations is severely limited and is biased towards certain well-studied systems³⁴. Predictions of host competence can serve a number of purposes, and have often been used to produce maps of zoonotic hazard which can provide guidance for monitoring and surveillance efforts³⁵. Further developments regarding these approaches have also been oriented towards the prediction of future scenarios of hazard under climate change^{26,36}.

Zoonotic research uses a multitude of analytical techniques: at least a dozen modelling approaches have been adopted in recent scientific articles (often more than one approach in the same article;

Supplementary Fig. 1). Recent studies have shown that the use of machine learning applications is growing in the literature on zoonotic modelling³⁷, and we found that this was indeed the second-most common approach after linear models. Machine learning applications are already widely used in other fields such as biodiversity³⁸ and climate science³⁹. Similar to zoonotic disease modelling, these fields face several challenges in terms of data availability, biases and limited knowledge of some of the underlying process dynamics. In this context, machine learning tools enable the analysis of large, complex datasets and provide predictions based on known data attributes and emerging data patterns, using flexible model structures.

Recent zoonotic modelling exercises have used a wide spectrum of variables, with climate and land-use variables being the most commonly adopted by far (over two-thirds and over half of articles, respectively). This reflects the common knowledge that habitat conditions influence the spread of pathogens by altering the distribution, phenology and abundance of both zoonotic hosts and vectors. For example, habitat suitability of fruit trees and mammal frugivore richness were found to correlate with Ebola virus outbreaks⁴⁰, underscoring the

importance of considering complex trophic interactions within ecosystems. Land conversion has also been demonstrated to be a strong driver of the risk of disease emergence in natural environments^{11,41}. Many studies have focused on the influence of habitat condition on vector-borne diseases such as malaria, dengue, Zika and others^{42,43}. These studies have consistently found strong correlations between disease incidence and both climatic conditions and land-use change, the latter often favouring the creation of suitable microhabitat conditions for the reproduction of mosquitoes (such as stagnant water in rural and urban areas). For example, higher malaria incidence was associated with deforestation activities in Borneo and the Brazilian Amazon^{42,44}. Likewise, Santos et al.⁴⁵ found a direct relationship between deforestation, vector presence and the occurrence of visceral leishmaniasis in both humans and dogs in Brazil.

Forest loss alters habitat suitability, favouring vector proliferation and enhancing transmission risk when there is proximity between deforested areas and human settlements. Alongside land-use change, climate change is also known to play a key role in extending the transmission season and spatial range for both malaria and dengue⁴⁶, across Africa and the Americas for the former and across the Eastern Mediterranean and Western Pacific for the latter. Recent studies have demonstrated the synergistic effects of land-use and climate change over vector-borne disease transmission. For example, rising global temperatures and land conversion are projected to dramatically expand the geographic range and seasonal suitability for *Aedes* mosquitoes, exposing up to a billion more people to *Aedes*-borne viruses in the future^{47,48}.

Current use of macroecological variables

Macroecology is the branch of ecology that focuses on broad-scale patterns, processes and emergent properties of complex systems^{16,49,50}. Examples of variables adopted in macroecological analyses include species richness, functional diversity and ecosystem properties such as integrity and fragmentation. The aim of macroecology is to understand the general drivers and patterns underlying biological phenomena across different spatial and temporal scales. This theoretical orientation can be adopted by several applied disciplines. For example, macroecological approaches have been promoted for applications related to biodiversity conservation⁵¹, to support a more comprehensive assessment of threats to biodiversity, including their synergistic effect, and the identification of effective conservation monitoring and action. Macroecological theories and methods have also been adopted in carbon science, to understand the link between emergent properties of ecosystems and their carbon content⁵², and to predict the risk of carbon loss associated with ecosystem alteration⁵³.

The use of macroecological variables as part of zoonotic disease modelling has already been advocated²⁰. Still, our literature review shows that only one in four papers included macroecological variables in their modelling procedure, a percentage that is much lower compared with other environmental variables (such as climatic or land-use variables). We defined a list of macroecological variables with strong potential to inform zoonotic risk modelling (Table 1), and we compared it with the results of our literature review. Most articles using macroecological variables aimed at modelling pathogen distribution, pathogen circulation or zoonotic incidence (Fig. 2). Articles focusing on pathogen distribution showed the widest use of macroecological variables overall, although this was often limited to host species abundance or host species richness. Species richness has been identified as an important driver of zoonotic transmission dynamics⁵⁴, whereby high species richness may reduce pathogen circulation in wildlife communities through a phenomenon known as the 'dilution effect'⁷⁴. We found a much lower use of species richness in papers focusing on vector-borne diseases, where species abundance was much more common (Supplementary Fig. 2). Overall, less than 5% of the articles included more complex macroecological variables, such as those representing elements of ecosystem structure or functional diversity.

Key ecological metrics such as species richness and evenness, community structure and ecological integrity enable the complexity of ecosystems to be captured. These metrics can provide an accurate representation of the factors that influence disease dynamics, providing critical information on how zoonotic risk is distributed across landscapes and enhancing our ability to anticipate and mitigate it. We argue that there are important opportunities for using a wider spectrum of macroecological variables in zoonotic disease modelling, as has been done successfully in other fields. When looking at the use of macroecological variables in zoonotic risk articles, we identified several research gaps, that is, instances where risk modelling could benefit from the inclusion of currently underutilized variables (Fig. 3). This is the case, for example, of functional diversity and ecosystem integrity, which are rarely used for zoonotic modelling. These research gaps represent promising avenues for future investigation at the interface between macroecology and zoonotic risk research. However, not every macroecological variable is useful for every modelling purpose. For example, we did not find articles using ecosystem structural diversity to predict the host range of a pathogen, which makes sense as the latter typically responds to evolutionary, physiological and ecological characteristics of the host species³², rather than to the physical properties of an ecosystem.

Incorporating emergent ecological properties into spatial prediction models of zoonotic risk offers a nuanced understanding of the conditions under which pathogens are likely to spill over from wildlife to humans. Several models have been developed to predict the spatial risk of zoonotic diseases, mainly based on socio-economic and environmental conditions. For example, Skinner et al.⁴³ have recently analysed the relationship between cumulative human pressure and the occurrence of six vector-borne diseases across Brazilian municipalities, using machine learning. They found that human pressure is indeed an important predictor of disease occurrence, but the actual relationship differed on the basis of the disease ecology (sylvatic versus urban). We argue that such relationships are also mediated by ecosystem properties, such as species richness or intactness, which can be represented by macroecological variables. Using a case study on cutaneous leishmaniasis, one of the diseases analysed in ref. 43, we empirically demonstrate how the integration of macroecological variables into a zoonotic risk model can provide additional information on the main drivers of disease occurrence and enhance the model predictions (see next section).

A case study on macroecological modelling

We tested whether the inclusion of macroecological variables can further support the explainability and improve the predictive capacity of a model that aims to determine the risk of a zoonotic disease. To achieve our aim, we used the data on cutaneous leishmaniasis in Brazil, published by Skinner et al.⁴³. In their original paper, Skinner and colleagues used eight environmental and socio-economic variables—temperature, precipitation, number of wet days, pasture, cropland, forest area, human footprint and population size—to predict the occurrence of cutaneous leishmaniasis in different municipalities of Brazil, using random forest machine learning models. We followed a similar analytical procedure and built a random forest model that included the above-mentioned variables—we refer to this as the 'original model' (Supplementary Methods 2). Afterwards, we extended the model by embedding five additional macroecological variables among those we discussed (Table 1): host richness, functional richness, biodiversity intactness index, enhanced vegetation index and forest loss. We refer to this extended model as the 'macroecological model'. Both models were validated using spatial block-validation.

When comparing the performance of the two models we found that the predictive ability of the macroecological model (TSS = 0.46) exceeded that of the original one (TSS = 0.42), especially in terms of sensitivity, which is the ability to correctly predict municipalities affected

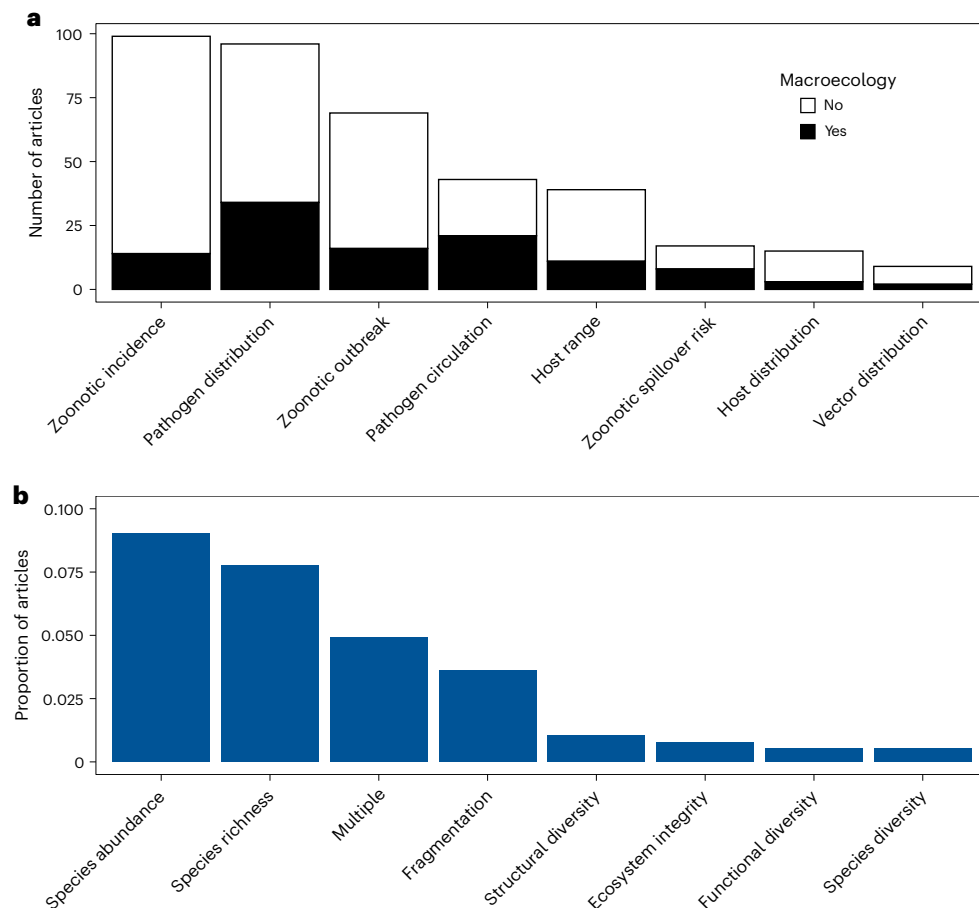


Fig. 2 | Use of macroecological variables across scientific articles that present zoonotic modelling exercises. a, Total number of articles with a given research aim (full bar), and the number of articles including macroecological variables (black portion of the bar). **b**, Proportion of articles that use specific macroecological covariates.

by the disease (Supplementary Discussion and Supplementary Table 2). Macroecological variables indeed played a crucial role in building the model, as we found functional richness and host richness to be among the most important predictors of cutaneous leishmaniasis, which were ranked, respectively, as the first and fourth most influential variables (Fig. 4). Host richness captures the number of mammalian hosts of *Leishmania*, which affects the risk of spillover to humans, whereas functional richness represents the total diversity of host functional strategies in a municipality. Other macroecological variables were less important for model prediction, but still comparable to the importance of some of the original variables, such as cropland extent (which is customarily used in zoonotic modelling). Notably, the importance of functional richness was comparable to that of the human population, a well-known driver of zoonotic disease risk. Our findings underline the potential of incorporating macroecological variables into zoonotic risk modelling, to aid model prediction and interpretation.

The potential of macroecological variables

Host species diversity

Ecologically complex ecosystems, with high species richness, support hosts with diverse immune strategies and competence levels that can reduce pathogen prevalence and mitigate zoonotic risk⁵⁵. Such communities are less likely to be dominated by a few species acting as dominant reservoirs for zoonotic pathogens¹¹. Yet, there are other dimensions of species diversity which are important for zoonotic transmission, albeit rarely considered. For example, phylogenetic diversity, which accounts for the evolutionary relationships among species, represents a potential barrier against zoonotic spillover. Indeed, communities with high

phylogenetic diversity are less susceptible to pathogen cross-species transmission due to the broad range of physiological and immunological traits among distantly related species⁵⁶. Combining a wide range of species interactions with a broad spectrum of evolutionary traits, high species richness and high phylogenetic diversity may reduce pathogen prevalence and the risk of zoonotic spillover from host communities.

The relative abundance of competent hosts changes with species richness, generating complex (often idiosyncratic) responses of zoonotic risk to this variable⁵⁷. This underscores the importance of considering community structure and dynamics when modelling zoonotic transmission. For example, diversity metrics that incorporate evenness (that is, the relative abundance of different species in a community) may enhance disease risk predictions by better capturing the probability of encounter between pathogens and each host species if encounter rates are proportional to host abundance⁵⁵. Recent studies have found that decreasing evenness generally leads to high disease risk for both frequency-dependent and density-dependent pathogens^{29,58}. In communities with reduced evenness, a few dominant species tend to prevail, often those with the highest rates of intraspecific contact and viral sharing⁵⁹. Widespread and abundant species, in particular ecological generalists, are more prone to interact with various hosts and humans, increasing pathogen sharing and creating novel opportunities for pathogen spillover^{60,61}. Accordingly, species evenness may improve the model prediction capability more than species richness alone⁵⁸. Similarly, our case study (see previous section) shows that functional diversity—representing the spectrum of ecological roles of organisms within a community⁶²—might play a critical role in disease risk modelling.

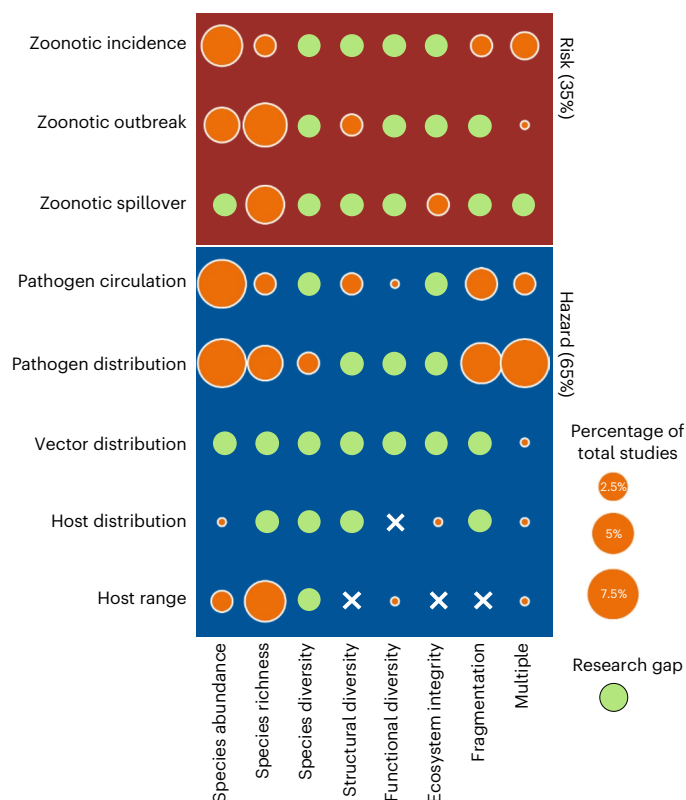


Fig. 3 | Conceptual mapping of macroecological properties used in articles pursuing different aims. The circle size represents the percentage of articles with a certain aim (as identified in Fig. 2) and including a certain macroecological variable (horizontal axis). White cross symbols denote the lack of a theoretical connection between the aim and the variable, that is, data are not expected. Green circles represent potential gaps in the use of macroecological variables.

Ecosystem and landscape configuration

Landscape ecology has its roots in the study of the links between spatial patterns and processes, and macroecology can provide the theoretical background for investigating the relationship between landscape alteration and the risk of zoonotic disease^{63,64}. The spatial structure and configuration of a landscape drive ecological processes and functions within ecosystems^{65,66}, including pathogen circulation and zoonotic spillover, but these characteristics are often neglected in the zoonotic disease literature. In fact, landscape ecology has often been found to regulate vector-borne disease risk⁶⁷, especially when altered by anthropogenic pressure⁶⁸. Landscape composition and structure determine the connectivity of host populations within and between habitat patches⁶⁹, and consequently the circulation of pathogens and the potential for cross-species transmission.

The analysis of habitat fragmentation, associated with land-use change, can improve the ecological understanding of the dynamics of pathogen transmission. Forest fragmentation, for example, is a known driver of the transmission of Lyme disease, as host species are more abundant in landscapes that are characterized by smaller habitat patches and a higher edge/area ratio⁷⁰. The so-called edge effect alters populations and communities along the boundary of a habitat. By increasing habitat edges, habitat fragmentation also increases the contact rate between human and wildlife populations, resulting in a higher overall disease transmission risk, as seen for Ebola virus⁷¹. This is also problematic when fragmentation is determined by an expansion of urban and suburban areas, favouring the presence of generalist and synanthropic species that are highly competent reservoirs of zoonotic pathogens⁷².

An important, yet often neglected, element of landscape configuration is ecological integrity: an ecosystem's capacity to maintain its

composition, structure and functions within a natural range of variation⁷³. Ecological integrity metrics encompass a range of indicators that reflect broader aspects of ecosystem health, such as habitat degradation, fragmentation and the overall impact of human activities on natural systems. Human-induced pressures influence both the diversity and abundance of species^{74,75}, disrupting pathogen ecology and increasing zoonotic risk^{12,31}. Instead, pristine ecosystems reduce zoonotic risk by maintaining their ecological and evolutionary functions with minimal human disturbance^{31,76}. Preserving large contiguous landscapes with high ecological integrity is a fundamental principle of conservation biology, with strong co-benefits for the reduction of zoonotic disease risk via integrated management^{31,41}. Incorporating ecological integrity metrics into zoonotic risk modelling also enables a more comprehensive understanding to be achieved of how anthropogenic-driven environmental changes influence zoonotic disease dynamics³¹.

Life-history and evolutionary variables

Life-history theory has been used extensively in studies aimed at identifying 'hotspots' of pathogen hazard, which are defined as areas with a high probability of pathogen presence due to the presence of many potential host species. Such efforts have traditionally been focused on drawing conclusions about life-history traits linked to host status⁷⁷⁻⁷⁹, in addition to unveiling the potential host range of a given pathogen^{24,32,37}. Such studies are based on evidence of an eco-immunological relationship between species' strategies along the fast-slow continuum of life histories⁸⁰ and their susceptibility to diseases. Different life histories are associated with different investments in immune defences, driven by an evolutionary trade-off between reproduction and immunity⁸¹⁻⁸³. In several vertebrate taxa, life history also covaries with traits that influence species' interactions with the environment, other hosts and humans^{84,85}. Such traits, which include body size, behaviour and biogeography, have been found to be linked to components of host competence⁸⁶, exposure to pathogens⁸⁷, the potential for pathogen maintenance⁸⁸ and zoonotic transmission⁸⁹; collectively, these characteristics have influenced the phylogeography of pathogens⁹⁰ and the pathogen-sharing patterns between species⁵⁹.

Species' traits may also affect the epidemiological characteristics of a community of species. As life-history traits impact both infection outcomes and transmission dynamics at the species level, the functional diversity of a community may also influence the infection risk when assemblage composition is a key predictor of the pathogen transmission dynamics²⁹. Indeed, an alteration of the host community composition can profoundly alter the dynamics of pathogen transmission by affecting the dilution dynamics¹⁴. In a recent study, functional divergence within European bird assemblages was found to be negatively associated with H5Nx occurrence, indicating that increased diversity of traits may reduce infection risk in a community⁹¹. Applying life-history theory to disease surveillance may improve hazard-monitoring strategies, supporting the identification of surveillance priorities in areas where community assemblages are dominated by potential hosts of zoonotic pathogens.

Boosting disease modelling with macroecology

Although the link between biodiversity conservation and the prevention of infectious disease emergence has been challenging to acknowledge at societal and political levels⁹², their synergy is becoming more and more evident to the scientific community⁶. Conservation efforts may indeed reduce human encroachment and contact with wildlife, thus reducing the likelihood of zoonotic disease events^{24,42,93}. Macroecological theories and methods are already used to help overcome some of the key challenges faced by biodiversity conservation, such as threat quantification and species monitoring⁵¹; however, much remains to be explored around the use of macroecology for zoonotic risk prediction.

Despite the potential value that macroecological approaches can bring to predicting and understanding zoonotic disease risk, our

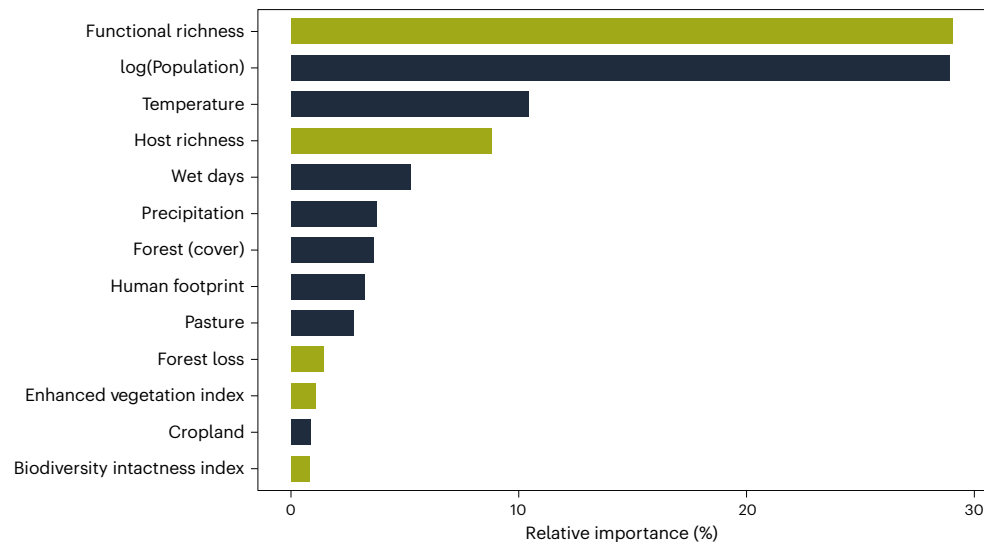


Fig. 4 | Relative predictive importance of explanatory variables in the macroecological model. The dark blue bars indicate the environmental and socio-economic variables comprising the original model used in ref. 43, and the green bars denote additional variables included in the macroecological model.

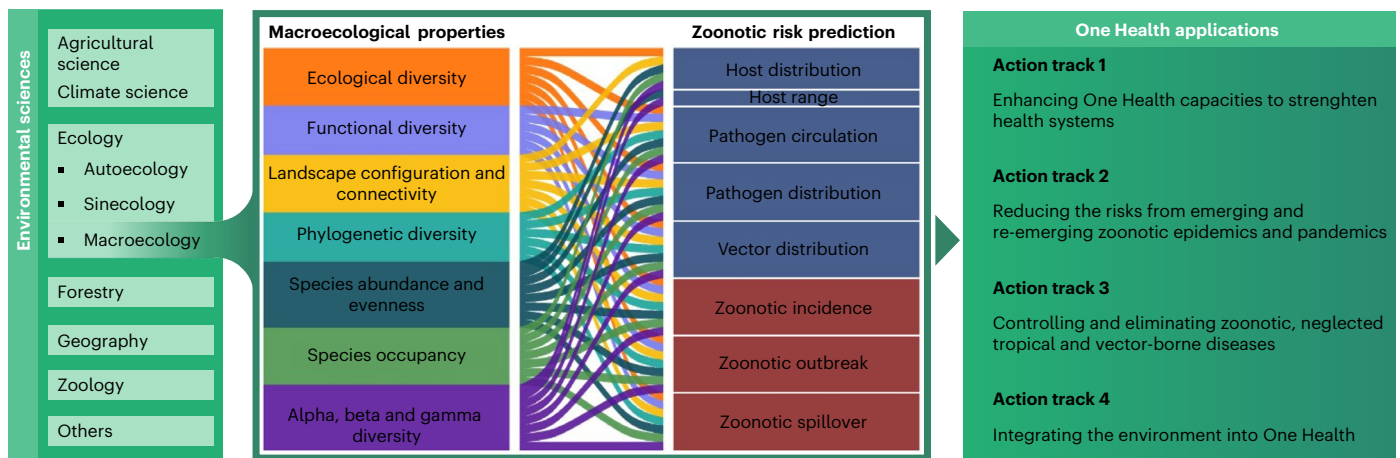


Fig. 5 | Mapping the use of macroecological variables in the context of One Health applications, to improve the integration of environmental science into zoonotic risk prediction. One Health applications are reported in terms of the main action tracks proposed in the One Health Joint Plan of Action¹.

findings highlight that they are underutilized (Fig. 3). There are a few possible reasons for this. First, data availability may be seen as a potential impediment to the inclusion of certain macroecological variables in zoonotic risk research. Yet, this same issue also affects other research fields that have already adopted macroecological variables, such as conservation biology⁵¹. In fact, we provide several example datasets that are currently available for sourcing (or calculating) macroecological variables (Table 1). Second, there is an inherent complexity in the interpretation of several variables that can represent ecosystem elements, which are often indirectly connected to the risk of disease emergence (such as host functional diversity). This, however, should not be a limitation but rather an opportunity to improve our epidemiological understanding of zoonotic diseases. For example, many epidemiological studies that include climatic and environmental drivers to assess disease transmission use the normalized difference vegetation index (or NDVI) as a proxy for environmental conditions. This shows that there is recognition that the environment is an important element to consider for the transmission of zoonotic diseases, even if that metric acts more as an instrumental variable than a contributing driver of disease transmission. A third reason for the limited adoption of macroecological approaches is their scale of application.

Macroecological properties are, by definition, more relevant at larger spatial scales. This means that zoonotic risk analyses performed at very local scales (for example, within a municipality or within a single protected area) are unlikely to benefit from using these variables. Yet, we argue that several macroecological variables—including ecosystem integrity, community evenness and host richness—are relevant even at a national or subnational scale, that is, the scales most typically used in zoonotic risk studies (for example, see ‘A case study on macroecological modelling’ above).

Integration into the One Health framework

We propose two levels of guidance for improving the use of macroecological approaches within zoonotic disease research as part of a One Health framework. The first level consists of a set of recommendations that are focused on system-wide priorities and capacity-building opportunities aligned with the One Health Joint Plan of Action¹. The second level outlines practical guidelines to assist researchers in determining when macroecological variables are most likely to be informative in the modelling of disease risk. We provide four main recommendations for advancing the inclusion of macroecology as part of the broader One Health framework (Fig. 5).

First, we recommend that the use of macroecological variables be extended in zoonotic risk studies, to include variables that are known to represent the essential elements of host community diversity, landscape configuration and phylogenetic and functional divergence among species. To evaluate whether the inclusion of such variables is appropriate, we further outline general guidelines and principles to support this assessment on a case-by-case basis (see the guidelines below).

Second, we recommend an improvement in the reporting of zoonotic surveillance data from national and subnational monitoring, to enable a deeper understanding of zoonotic disease risk through its potential correlation with macroecological variables; this specifically concerns the standardization of ‘negative’ results, a general issue in disease ecology.

Third, we recommend that the availability of spatially resolved historical records of zoonotic disease emergence and incidence be enhanced, to enable better understanding of the temporal links between environmental change and zoonotic disease risk (including any lag effect). In particular, this requires the downscaling of coarse-grained information on disease emergence events from past decades.

Fourth, we recommend that macroecology be integrated as part of One Health capacity building, to enable One Health professionals to gain essential knowledge of the ecological principles that facilitate understanding the environmental aspects of zoonotic disease risk. The acquisition of macroecological knowledge as part of a country’s One Health task force would help our understanding of how zoonotic risk responds to emergent ecosystem properties, and to anticipate the undesired consequences of environmental change.

Whereas macroecological variables offer powerful insights into ecosystem-level drivers of zoonotic disease risk, they are not universally applicable. As with any model design, their inclusion should be guided by the specific aims, the spatial and temporal scale, and the underlying assumptions of the study and modelled entities. We therefore present four general guidelines about when, and how, to include macroecological variables in zoonotic disease models.

First, macroecological variables are most relevant when models aim to capture emergent, system-level dynamics. Models that focus on ecosystem degradation, land-use change or biodiversity-related hypotheses should consider incorporating metrics such as ecological integrity, structural diversity or fragmentation. These variables provide a way to represent ecological processes that may influence zoonotic risk through host availability, community composition or pathogen-sharing potential. Therefore, their inclusion is particularly appropriate when the research goal is to understand why risk emerges in specific ecological contexts.

Second, the use of macroecological variables should be evaluated particularly in multi-host, ecologically complex systems. Diseases that involve multiple reservoir hosts, vectors or environmental persistence are shaped by ecological interactions that are not easily captured by traditional covariates. In these systems, macroecological variables (such as species richness or functional diversity) can account for processes such as amplification, dilution or the dominance of generalist species in degraded habitats. This is particularly important when transmission depends on the structure and function of the host community, rather than on individual species.

Third, broad spatial and/or temporal scales are those best suited to macroecological integration. At large spatial scales, emergent ecological patterns such as fragmentation or biogeographic gradients can be reliably measured and meaningfully linked to disease patterns. Likewise, in models for projecting future risk under climate or land-use change, macroecological variables can help to account for shifts in ecological structure and function. As shown in ‘A case study on macroecological modelling’, these variables often help to explain the residual variation that remains after conventional environmental predictors have been included.

Finally, we suggest that the use of macroecological variables should be avoided in localized studies without ecological mediation. In studies where transmission is dominated by direct and well-characterized mechanisms, such as human behavioural exposure or a single species-spillover model, macroecological variables are unlikely to add substantial value and their inclusion may complicate interpretation of the model and increase the risk of spurious associations.

Prevention of pathogen spillover and emergence is the most cost-effective strategy for anticipating zoonotic disease outbreaks, and the prediction of disease emergence and circulation is key to defining effective monitoring and prevention strategies. In this context, the prevention of zoonotic disease transmission is also recognized as a priority by the new World Health Organization Pandemic Treaty⁹⁴. Advancing the use of macroecological principles and variables for zoonotic risk prediction can go a long way in supporting this goal under a One Health framework.

Data availability

Details of reviewed articles are provided in Supplementary Table 1. Data for running the case study are available via GitHub at <https://github.com/and-tonelli/ZoonoticRiskMacroecology>.

Code availability

Codes for running prediction models presented in the case study are available via GitHub at <https://github.com/and-tonelli/ZoonoticRisk-Macroecology>.

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Author contributions

M.D.M. conceived of the original idea. M.D.M., L.M., A.T. and E.C. designed the study and planned the analysis. L.M., A.T. and E.C.

collected the data. L.M., A.T., E.C. and M.D.M. analysed the data. All authors contributed to the interpretation of the findings. M.D.M. wrote the initial draft with support from all authors. All authors contributed to revising the paper and approved the final paper.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Moreno Di Marco or Andrea Tonelli.

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