Coexistence Nexus in practice: Operationalizing One Health across agroecological landscapes and zoonotic risk in Central America

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Abstract

Reconciling biodiversity conservation, agricultural systems, and human health remains a central sustainability challenge, yet these dimensions are often addressed in isolation. Here, we extend coexistence theory beyond its traditional focus on biodiversity conservation by integrating agricultural production and zoonotic risk within a One Health perspective. In doing so, we link biodiversity, food production systems, land-use dynamics, and disease emergence within a common spatially explicit analytical framework. Using Central America as a case study, we combine multi-pathogen occurrence data with spatial indicators of anthropogenic pressure, livestock density, biodiversity, and climate in a Bayesian spatiotemporal modeling framework to identify patterns of zoonotic emergence. Our results reveal strong spatial clustering of emergence risk and highlight non-linear relationships, particularly with livestock density, indicating that zoonotic emergence arises from interacting socio-ecological pressures rather than isolated drivers. We further identify convergence zones where environmental change, agricultural systems, and host diversity overlap, generating elevated levels of socio-ecological vulnerability. Importantly, we show that spatial integration of these dimensions provides a tractable approach for operationalizing the coexistence framework, allowing the identification of high-priority areas for surveillance and intervention. While our analysis focuses on environmental and production-related indicators rather than the full multidimensional scope of food security, it captures key interfaces through which biodiversity, agriculture, and health interactions unfold. Overall, this study demonstrates how integrating spatial epidemiology with social-ecological theory can help identify leverage points for reducing zoonotic risk while supporting more resilient and sustainable landscapes. By grounding the One Health perspective in spatially explicit analysis, it offers a practical pathway for informing land-use planning and regional disease surveillance strategies.

1. Introduction

Reconciling biodiversity conservation with agricultural development and human health has emerged as one of the defining sustainability challenges of the 21st century. Nowhere is this tension more acute than in Central America, a region simultaneously marked by exceptional biological richness and persistent socioeconomic vulnerability. The continued expansion of agricultural frontiers into some of the globe's most biodiverse regions brings human populations, livestock systems, and wildlife communities into increasingly close contact, creating conditions that heighten exposure to zoonotic diseases (Jones, et al. 2013; Tajudeen, et al. 2022), while also exacerbating existing structural pressures such as food insecurity and governance limitations (Sibrian, et al. 2021; King, et al. 2016; Xavier, et al. 2022). The convergence of these processes not only threatens the integrity of ecological systems, but also generates complex geographies of risk whose impacts extend beyond national borders.

Central America's mosaic of ecosystems, from humid tropical forests to dry corridors, highland cloud forests, and extensive agroecosystems, forms a dynamic interface where environmental change, agricultural practices, and health risks intersect. These diverse landscapes host a wide range of biological communities, many of which act as reservoirs for pathogens with zoonotic potential. At the same time, land-use change, livestock distribution, and climatic variability reshape patterns of human-animal interaction and environmental suitability, influencing the conditions under which disease emergence occurs. Understanding these intertwined dynamics requires moving beyond isolated perspectives and instead examining how ecological and agricultural systems jointly structure zoonotic risk.

Recent conceptual advances in the study of social-ecological systems offer a useful entry point for addressing this challenge. Building on work that frames agroecological landscapes as dynamic systems capable of existing in alternative states, ranging from conflict to coexistence, researchers have introduced the notion of "coexistence parameters" (Crespin et Simonetti 2020), referring to the social and ecological factors that can be managed to reduce biodiversity impacts or increase tolerance to them, thereby shifting systems toward states where agricultural production and biodiversity conservation can be jointly maintained (Jouzi, Leung et Nelson 2022). Expanding on this perspective, Crespin and Moreira-Arce (2026) outline an agroecological systems model of coexistence in which these dimensions are multidimensional and dynamically interacting. However, the role of zoonotic risk remains

77 insufficiently integrated within this framework (Hirst et Halsey 2023), despite growing evidence that
78 the same drivers shaping biodiversity and agricultural systems also influence pathogen emergence
79 (Case, et al. 2022).
80 For example, forest fragmentation can simultaneously reduce ecosystem services, displace wildlife
81 hosts, and increase human exposure to vectors (Ortiz, et al. 2021). Likewise, livestock systems may
82 amplify transmission processes by increasing host density and contact rates (Klous, et al. 2016), while
83 certain agroecological configurations may instead buffer disease transmission through the maintenance
84 of ecological interactions that regulate pathogen circulation. These processes suggest that zoonotic
85 emergence is not driven by single factors, but by constellations of interacting pressures unfolding across
86 space and time. More importantly, this challenge extends beyond the traditional One Health perspective.
87 While One Health has long emphasized the interconnections between human, animal, and environmental
88 health, less attention has been paid to how food production systems interact simultaneously with
89 biodiversity conservation and zoonotic risk. We argue that agricultural production is not merely a
90 background driver of environmental change but a central component of socio-ecological systems that
91 shapes both ecosystem integrity and disease emergence. Integrating these dimensions within a common
92 frameworks therefore represents a critical step toward understanding sustainability challenges through
93 a broader food systems and Planetary Health perspective.
94 Here, we examine the regional diversity of Central America both as a challenge and as an opportunity
95 for operationalizing this integrated perspective. Despite shared ecological continuities, each country
96 exhibits distinct combinations of land-use change, agricultural practices, governance structures, and
97 health system capacities. These differences shape not only national vulnerabilities but also
98 transboundary dynamics of risk. Vector-borne diseases such as dengue or chikungunya do not respect
99 political borders (Charles, et al. 2021), just as ecological processes extend beyond them. Similarly, land-
100 use changes in one country may alter disease ecology across a wider region (Ortiz, et al. 2021), while
101 agricultural and socioeconomic pressures can reshape exposure pathways through migration dynamics
102 (Dodd, et al. 2020). A regional and spatially explicit perspective is therefore essential.
103 Our analysis builds on this foundation to bridge conceptual and empirical approaches. Specifically, we
104 investigate how environmental conditions, agricultural systems, and ecological communities jointly

structure the spatial distribution of zoonotic disease emergence, and where these factors converge to generate socio-ecological vulnerability hotspots. To do so, we combine spatial indicators of land use, livestock density, biodiversity, climate, and anthropogenic pressure with multi-pathogen occurrence data within a Bayesian spatiotemporal modeling framework.

While this approach does not directly capture all dimensions of food security (such as access, utilization, or stability) it provides a tractable representation of the environmental and production contexts in which interactions between biodiversity, agriculture, and health take place. By linking these dimensions through spatial analysis, we translate the coexistence framework into an operational tool capable of identifying areas where risks accumulate and interventions may have the greatest impact.

Ultimately, this study contributes to bridging the gap between conceptual innovation and applied sustainability research. By explicitly integrating zoonotic dynamics within a coexistence perspective and grounding the analysis in spatially explicit data, we provide a more coherent understanding of how socio-ecological systems shape disease emergence. In doing so, we highlight opportunities to design interventions that are better aligned with the complexity of real-world landscapes, where biodiversity conservation, agricultural practices, and human health are inextricably connected.

2. Methods

Study design and analytical framework

To investigate how environmental conditions, agricultural systems, and ecological communities jointly shape zoonotic disease emergence, we adopted a spatially explicit analytical framework linking multi-pathogen occurrence data with indicators of land use, livestock distribution, biodiversity, and climate. The analysis was structured to address two complementary objectives: (i) identifying the environmental correlates of zoonotic emergence across pathogens, and (ii) examining how these relationships translate into risk for a focal species with well-known ecological dynamics.

This approach combines a regional, multi-pathogen perspective with a species-specific analysis, allowing us to capture both generalizable patterns and pathogen-specific mechanisms within a consistent modeling framework.

Study area and data sources

The study was conducted across six Central American countries (Belize, Costa Rica, El Salvador, Guatemala, Honduras, and Nicaragua), forming a biologically rich and environmentally heterogeneous region. This area spans tropical lowlands, intensively cultivated agricultural landscapes, densely populated urban corridors, and mountainous forested ecosystems. The climate is predominantly tropical, with marked wet and dry seasons shaped by altitudinal gradients and contrasting oceanic influences. Land-use patterns vary widely, ranging from expanding croplands and peri-urban settlements to protected forests and coastal wetlands, creating a dynamic interface between human, livestock, and wildlife populations.

To represent this diversity, we integrated spatially explicit covariates from multiple open-access data sources (Supplementary Information 1), including socio-demographic indicators (NASA SEDAC, WCS), land-cover and vegetation metrics (Sentinel-2), crop distributions (MapSPAM), livestock densities (Global Livestock of the World), climatic variables (NASA POWER), and wildlife richness layers (IUCN). Together, these datasets characterize the main environmental and agroecological gradients shaping human–animal–environment interactions across the region. While these variables do not directly capture all dimensions of food security, they provide consistent proxies for the configuration and intensity of production systems, which represent key interfaces through which zoonotic risks emerge.

Zoonotic occurrence data were obtained from the OMSA–WAHIS database (Supplementary Information SI1), including records for 21 pathogens over a 21-year period (2005–2025). Within this framework, we conducted a focused analysis of the New World screwworm fly (*Cochliomyia hominivorax*), a parasitic species strongly dependent on climatic conditions, livestock availability, and land-use patterns. This species provides a biologically grounded case study for examining how regional drivers translate into risk for a specific pathogen of major veterinary and economic relevance.

Spatiotemporal data structure

All variables were harmonized onto a regular 10 × 10 km grid, with each grid cell evaluated annually over a 21-year period (2005–2025), forming a consistent cell–year panel for analysis. Zoonotic disease occurrence was represented as yearly counts of reported outbreaks aggregated to each grid cell. Cells with no reported events were retained to represent background environmental conditions,

acknowledging that these observations may reflect both true absence and variability in detection or reporting intensity.

Climatic variables (mean temperature, total precipitation, and wind speed) were derived at annual resolution, allowing direct temporal alignment with outbreak data. Other environmental and socio-demographic variables were available at discrete time points. For these datasets—including population density, land cover, crop distributions, livestock densities, and the Human Footprint Index—annual values were assigned based on the closest available year. This approach preserves the structure of the original datasets while avoiding the introduction of artificial trends through interpolation, resulting in covariates that evolve stepwise over time and capture medium-term changes in land use and agricultural systems. Wildlife richness was treated as time-invariant, reflecting longer-term ecological patterns.

All variables were standardized (z-scores) prior to analysis. The final dataset consisted of 9,169 grid cells observed over 21 years, yielding a harmonized spatiotemporal panel of environmental conditions and zoonotic emergence events.

Statistical modeling approach

To quantify the relationship between environmental factors and zoonotic emergence, we implemented a Bayesian hierarchical modeling framework using the Integrated Nested Laplace Approximation (INLA). Given the count nature of outbreak data and their strong overdispersion, observations were modeled using a negative binomial distribution.

Let Y_i denote the number of outbreaks observed in grid cell i. The response was modeled as:

$$Y_i \sim \text{Negative Binomial}(\lambda_i, \kappa)$$

where λ_i is the expected number of outbreaks and κ is the dispersion parameter.

The log-expected value was specified as:

$$\log(\lambda_i) = \alpha + \sum_{j=1}^{p} \beta_j X_{ij} + r_i + v_i + u(t_i)$$

where α is the intercept, X_{ij} are the standardized covariates, and β_j their coefficients. The term r_i represents unstructured random effects capturing residual heterogeneity, while v_i models spatially

structured variation. Temporal dynamics are captured through $u(t_i)$, specified as a first-order random walk (RW1), which accounts for residual interannual variation not explained by the time-varying covariates included in the model.

Spatial dependence was modeled using the stochastic partial differential equation (SPDE) approach, which approximates a continuous Gaussian random field through a triangulated mesh. Priors for spatial and temporal components were defined using penalized complexity priors, favoring simpler structures unless supported by the data.

To limit multicollinearity, we retained one representative variable for each major climatic dimension based on variance inflation factor (VIF) analysis, selecting mean temperature, precipitation, and maximum wind speed.

Spatial modeling and mesh construction

The spatial field was defined over a triangulated mesh covering the study area. Mesh construction followed a two-step procedure, with vertices placed at sampling locations and additional nodes added to ensure full spatial coverage and minimize boundary effects.

An initial spatial range of 400 km was selected to capture regional-scale patterns of zoonotic emergence. Inner and outer mesh resolutions were defined proportionally to this range to balance spatial precision and computational efficiency. Sensitivity analyses using alternative ranges (100 km and 700 km) yielded consistent results, supporting the robustness of the selected configuration.

Model evaluation and predictive performance

Predictive performance was evaluated using a five-fold cross-validation scheme, with 80% of the data used for training and 20% for testing in each fold. Performance was assessed using the log pseudo-marginal likelihood (LPML), derived from conditional predictive ordinates, as a measure of out-of-sample predictive ability.

Discriminative performance was further evaluated using the Area Under the Receiver Operating Characteristic Curve (AUROC) and the Area Under the Precision-Recall Curve (AUPRC), the latter being particularly informative given the rarity of emergence events (≈0.53% of observations). Confidence intervals were obtained via bootstrap resampling.

To reflect operational constraints, model performance was also assessed using ranked-risk thresholds corresponding to the top 1% and top 5% of predicted high-risk locations. For each threshold, we calculated precision, recall, lift, and the number of true positives detected per unit of inspection effort, providing a surveillance-oriented interpretation of model outputs.

Separate evaluations were conducted for the full multi-pathogen dataset (all-zoonoses model) and for the subset of *C. hominivorax* observations, enabling both general and pathogen-specific assessments.

Inference and interpretation

Model outputs are reported as posterior means and 95% Bayesian credible intervals. To facilitate interpretation, regression coefficients were transformed into relative risks (RR), representing the multiplicative change in expected outbreak counts associated with a one-unit increase in each standardized covariate.

Effects were considered statistically supported when the 95% credible interval did not overlap zero (or one for RRs). Given the observational nature of the data, estimated relationships are interpreted as statistical associations rather than direct causal effects.

3. Results

Model performance was evaluated separately for two complementary modeling frameworks: (i) the all-zoonoses model, which integrates emergence data across multiple pathogens to identify broad environmental correlates of zoonotic risk, and (ii) the *C. hominivorax* model, a species-specific analysis examining the determinants of emergence for this focal parasite.

For the all-zoonoses framework, model performance was compared across spatial configurations using neighborhood radii of 100, 400, and 700 km, with year included as a fixed covariate in all cases (Table 2). Predictive performance was consistent across spatial scales, with similar LPML values and discrimination metrics (AUROC ≈ 0.89; AUPRC ≈ 0.12). The 400 km configuration was retained for inference, as it provided the most stable LPML estimate while capturing regional-scale spatial structure in reported emergence patterns. Results from this model are used to characterize general associations between environmental conditions and zoonotic occurrence across pathogens.

For *C. hominivorax*, predictive performance improved when cattle density was modeled as a non-linear RW2 effect. The 400 km RW2 specification yielded the highest predictive accuracy among species-

specific models (AUROC = 0.97–0.98; AUPRC = 0.26). Because this model was fitted to a restricted dataset of confirmed cases, its LPML values are not directly comparable to those of the all-zoonoses model; however, the discrimination metrics indicate a strong ability to identify high-risk locations for this species.

Together, these models provide complementary perspectives: the all-zoonoses model captures general patterns of zoonotic emergence at the regional scale, while the *C. hominivorax* model characterizes species-specific spatial responses within the same environmental context. All subsequent analyses, including fixed-effect estimates, spatial predictions, and temporal patterns, are therefore based on the selected 400 km configurations.

Fixed covariates

Fixed-effects results indicate that climatic and ecological variables show the strongest associations with zoonotic disease occurrence across livestock systems, whereas socio-demographic factors and most land-cover variables display weaker or more uncertain relationships (Tables 3–4).

In the all-zoonoses model, temperature exhibits a negative association with emergence risk (posterior mean = −0.35; RR = 0.71, 95% BCI: 0.68–0.74), while precipitation shows a positive association (posterior mean = 0.25; RR = 1.29, 95% BCI: 1.18–1.41). Wind speed presents a weak and uncertain effect (posterior mean = 0.05; RR = 1.05, 95% BCI: 0.82–1.36). Mammal–bird richness is positively associated with emergence risk (posterior mean = 0.76; RR = 2.13, 95% BCI: 1.43–3.18).

Among anthropogenic variables, cropland shows a modest negative association (posterior mean = −0.21; RR = 0.81, 95% BCI: 0.67–0.97), whereas built-up and water areas show no statistically supported effects. Population density is not associated with emergence risk (posterior mean = −0.08; RR = 0.92, 95% BCI: 0.78–1.10), while the Human Footprint Index displays a strong positive association (posterior mean = 0.78; RR = 2.19, 95% BCI: 1.61–2.99). This relationship may reflect a combination of increased environmental pressure and heterogeneity in surveillance or reporting intensity across the region.

The pathogen-specific *C. hominivorax* model (Table 4) shows broadly similar patterns, with stronger effect sizes for several covariates. Temperature shows a more pronounced negative association (posterior mean = −0.55; RR = 0.57, 95% BCI: 0.53–0.62), and precipitation a stronger positive

association (posterior mean = 0.28; RR = 1.32, 95% BCI: 1.18–1.49). Mammal–bird richness is also positively associated with emergence (posterior mean = 1.01; RR = 2.75, 95% BCI: 1.52–5.06).

In contrast, socio-demographic and most land-cover variables show weak or uncertain effects, with the exception of cropland, which retains a negative association (posterior mean = −0.23; RR = 0.79, 95% BCI: 0.63–0.99). The Human Footprint Index also shows a positive but more moderate association (posterior mean = 0.59; RR = 1.81, 95% BCI: 1.14–2.88).

Across both models, climatic conditions and wildlife richness show the most consistent associations with reported zoonotic occurrence, while anthropogenic variables exhibit more variable effects. The species-specific model for *C. hominivorax* displays stronger and more structured responses to these gradients, consistent with its narrower ecological niche.

Identifying emergence risk

Across the study region, both the all-zoonoses model and the *Cochliomyia hominivorax*–specific model show similar large-scale spatial patterns, with elevated emergence risk concentrated in southern Mexico, Guatemala, Honduras, and Nicaragua (Figures 1–2). In both models, these high-risk areas are associated with low spatial uncertainty and narrow 95% credible intervals, indicating strong model support. Differences emerge in the spatial extent and definition of predicted hotspots. The all-zoonoses model shows a broader distribution of elevated risk, accompanied by greater uncertainty in peripheral regions. In contrast, the *C. hominivorax* model identifies more spatially concentrated hotspots with sharper boundaries. Combining predicted risk with uncertainty allows the identification of both reliable hotspots (i.e. areas of high risk and low uncertainty) and more uncertain hotspots, where elevated risk is associated with wider credible intervals. Outside these areas, predicted risk remains low and shows limited spatial structure. These spatial patterns are consistent with threshold-based classification results (Table S1). The top 1% risk threshold identifies a small number of high-precision hotspots, whereas the top 5% threshold captures a larger number of areas with lower certainty.

Non-linear relationship with cattle density. Livestock-related emergence risk shows a pronounced non-linear association with cattle density across all models (Figure 3). For all zoonotic events combined (Figure 3A), the estimated effect increases sharply at low cattle densities, reaches a maximum at intermediate densities (approximately 80,000–100,000 animals), and then declines at higher densities.

This decline is accompanied by wider credible intervals, indicating greater uncertainty at very high cattle concentrations.

A similar pattern is observed in the *C. hominivorax* model (Figure 3B), with a steeper increase toward the peak and a more pronounced decline at higher densities. Overall, these results may indicate that intermediate cattle densities are associated with higher levels of reported emergence, whereas both low-density and high-density systems show lower estimated risk.

Temporal effect

Temporal dynamics differ between the all-zoonoses and the *C. hominivorax* models (Figure 4). In the all-zoonoses model (Figure 4A), the temporal random effect shows moderate interannual variability with an overall increasing trend across the study period. After a relatively low baseline around 2006–2008, the effect increases progressively, with a more pronounced rise after 2020. This pattern suggests an increase in reported zoonotic emergence over time, although it may reflect a combination of ecological processes and changes in surveillance capacity or reporting practices.

In contrast, the *C. hominivorax* model (Figure 4B) shows a distinct temporal structure. From 2005 to approximately 2018, the temporal random effect remains close to zero with wide credible intervals, consistent with very low numbers of reported cases during this period. A slight fluctuation is observed around 2010, but the trajectory remains generally flat until the late 2010s. Beginning around 2018–2020, the temporal effect increases sharply, followed by a rapid rise in the final years of the series, accompanied by narrower credible intervals.

Taken together, these results indicate that while reported zoonotic emergence across pathogens shows a gradual increasing trend, *C. hominivorax* is characterized by a prolonged period of low occurrence followed by a rapid increase in recent years. This contrast highlights differences in temporal dynamics between aggregated multi-pathogen patterns and species-specific emergence signals.

4. Discussion

Our results provide empirical support for an expanded coexistence framework in which biodiversity conservation, agricultural production, and health are not treated as separate policy domains but as interacting components of a common socio-ecological system (König, et al. 2020; Fiasco et Massarella

2022; Massarella, et al. 2022). By explicitly linking zoonotic emergence to the original food-biodiversity nexus, this study advances the operationalization of coexistence theory and offers a spatially explicit framework for analyzing the interactions between food production systems, environmental change, and disease risk. At the same time, our findings emphasize that these relationships should be interpreted as statistical associations rather than direct causal mechanisms, reflecting the complexity of underlying ecological and epidemiological processes.

Across the region, zoonotic risk is not randomly distributed but concentrated in areas where human activity, livestock presence, and wildlife diversity intersect. The consistent associations observed with the Human Footprint Index, cattle density, and mammal-bird richness point to these interfaces as recurrent conditions under which emergence becomes more likely (Mancini, et al. 2024; Barreto et Prist 2025). From a One Health perspective, these zones correspond to areas where interactions among human, animal, and environmental health are intensified. However, part of these patterns may also reflect variation in surveillance effort and reporting capacity, particularly in areas with higher human footprint, where detection systems are more developed. Distinguishing between biological risk and detection bias therefore remains a key challenge for interpretation.

Our findings further reveal asymmetries among coexistence parameters, with some pressures amplifying risk and others potentially mitigating it. While higher human footprint is associated with increased emergence risk (RR = 2.19), cropland cover shows a modest negative relationship (RR = 0.81), suggesting that not all anthropogenic transformations have equivalent effects. One interpretation is that differences in land-use configuration, rather than simple intensity, shape the degree of human-animal contact and environmental disturbance. At the same time, the positive association with wildlife richness (RR = 2.13) highlights a well-known tension in disease ecology: biodiverse systems may both sustain ecological functions and provide reservoirs for pathogen persistence. However, this pattern should be interpreted cautiously, as species richness does not directly capture host competence or transmission pathways, and may also correlate with unobserved environmental gradients.

More broadly, the relatively weak and inconsistent effects observed for several land-use and crop-specific variables suggest that zoonotic emergence is unlikely to be driven by single factors in isolation (Chaves, et al. 2022). Instead, it appears to arise from particular constellations of pressures acting

simultaneously across space and time (Jagadesh, Combe et Gozlan 2022). From this perspective, coexistence can be understood not as a fixed outcome, but as a dynamic position within a multidimensional socio-ecological space (Combs, et al. 2021; Crespin et Simonetti 2020), where systems may shift toward more stable or more vulnerable configurations depending on how these pressures interact.

The non-linear relationship observed with cattle density illustrates this complexity particularly clearly. Risk increases sharply at low to intermediate densities before declining at higher densities, a pattern that is especially pronounced for *C. hominivorax*. This species-specific response is consistent with its biology as an obligate parasite dependent on host availability (Long, et al. 2026). At intermediate densities, livestock abundance may increase host exposure and facilitate transmission, whereas at higher densities the transition toward more intensive management systems (potentially including improved veterinary care and vector control) may reduce infestation opportunities. However, alternative explanations cannot be excluded, including differences in reporting practices between production systems or unmeasured aspects of livestock management.

Temporal dynamics further reinforce the importance of cautious interpretation. While the all-zoonoses model suggests a gradual increase in emergence over time, the sharp resurgence observed for *C. hominivorax* after 2018-2020 aligns with its documented re-emergence following near-eradication (Valdez-Espinoza, et al. 2025). At the same time, part of the observed temporal signal may reflect improvements in surveillance systems, changes in reporting practices, or increased awareness, rather than purely ecological processes. Disentangling these effects remains difficult in observational datasets and highlights the importance of interpreting temporal trends as combined signals of biological and institutional dynamics.

By operationalizing the coexistence framework through spatial analysis, our approach provides a practical means of identifying areas where environmental pressures, agricultural systems, and disease dynamics converge. These “socio-ecological vulnerability hotspots” offer a useful basis for prioritizing surveillance and intervention efforts. However, it is important to note that our analysis relies primarily on environmental and production-related indicators, and does not explicitly capture all dimensions of food security, such as access, utilization, or stability. As a result, the identified hotspots should be

interpreted as areas of elevated environmental and epidemiological vulnerability rather than comprehensive measures of food system outcomes.

However, this limitation should not obscure one of the central contributions of the framework. Beyond its implications for zoonotic surveillance, our approach highlights the need to reconsider agricultural production as a central component of socio-ecological sustainability rather than simply a driver of environmental change. Agricultural systems are often viewed primarily through their impacts on biodiversity loss and disease emergence. Yet our results suggest that the configuration of agroecological landscapes can simultaneously influence biodiversity conservation, production systems, and zoonotic risk. This perspective moves beyond a simple biodiversity-health linkage and instead emphasizes the interconnected nature of food production, ecosystem integrity, and health outcomes within shared landscapes. In this respect, the Coexistence Nexus framework aligns not only with One Health principles but also with broader Planetary Health and food-system resilience agendas, where the challenge is not merely to reduce disease risk, but to sustain ecological and productive systems capable of supporting long-term human well-being.

At the policy level, the strong spatial clustering of risk underscores the limitations of uniform, region-wide intervention strategies (Combs, et al. 2021). Instead, the observed heterogeneity supports more targeted approaches, in which surveillance and mitigation efforts are adapted to local configurations of risk. This may involve prioritizing high-certainty hotspots for intensive monitoring, while using more precautionary strategies in areas where uncertainty remains high. Coordinating agricultural, environmental, and public health policies within such a framework can help embed disease prevention within broader sustainability strategies (Clifford Astbury, et al. 2023).

Finally, while Central America provides a compelling case study, the transferability of this framework should be considered with caution. The specific relationships identified here are shaped by regional ecological, agricultural, and institutional contexts. Nonetheless, the broader approach of linking spatial epidemiology with socio-ecological theory may offer a useful template for other regions facing similar interactions between biodiversity change, agricultural systems, and zoonotic risk (Mahon, et al. 2024).

In conclusion, this study highlights the importance of integrating a One Health perspective into analyses of socio-ecological systems. Rather than representing a simple trade-off between production and

conservation, the coexistence nexus emerges as a dynamic system shaped by interacting environmental and anthropogenic pressures. Identifying how these pressures combine to generate patterns of zoonotic emergence provides a basis for more targeted and context-sensitive interventions. As such, the value of this framework lies less in predicting specific outcomes than in helping to identify where and how interventions may be most effective within complex and evolving landscapes.

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Table 1: Standardized covariates used in the model including mean, quartiles, Median and variance inflation factor (VIF).

	Covariate	Mean	Q2.5%	Q97.5%	Median	VIF value
Socio-demographic (From NASA SEDAC's and WCS)	Population density (persons/km2)	0.001	-0.305	-0.003	-0.201	1.801
	HFI (/10km)	-0.025	-0.756	0.533	-0.053	2.882
Land cover area (from sentinel 2)	Forest (Ha)	-0.051	-0.473	-0.089	-0.373	1.294
	Water (Ha)	0.009	-0.201	-0.176	-0.199	1.309
	Built up (Ha)	-0.018	-0.557	0.131	-0.339	2.543
	Crops (Ha)	-0.016	-0.267	-0.252	-0.267	1.883
Dominant crops (from MapSPAM)	Banana (Ha)	-0.016	-0.135	-0.131	-0.135	1.204
	Beans (Ha)	0.055	-0.516	0.086	-0.390	1.369
	Maize (Ha)	0.059	-0.488	0.110	-0.315	1.785
	Coconut (Ha)	0.003	-0.140	-0.029	-0.140	1.054
	Palm Oil (Ha)	-0.009	-0.288	-0.195	-0.288	1.237
	Rice (Ha)	-0.026	-0.175	-0.161	-0.174	1.308
	Sugar cane (Ha)	0.009	-0.206	-0.152	-0.203	2.072
Livestock's (from Global Livestock of the World, GLW)	Cattle (Nb/10km)	0.017	-0.714	0.386	-0.258	1.431
	Chicken (Nb/10km)	-0.007	-0.279	-0.042	-0.223	1.398
	Sheep (Nb/10km)	0.014	-0.111	-0.073	-0.097	1.960
	Goat (Nb/10km)	0.025	-0.297	0.000	-0.180	2.224
	Pig (Nb/10km)	0.004	-0.156	-0.043	-0.113	1.206
Climatic variables (from Nasa Power)	Temperature (◦C)	0.000	-0.609	0.755	0.213	1.771
	Precipitation (mm)	0.000	-0.739	0.736	-0.299	1.485
	Wind speed (knots)	0.000	-0.831	0.555	-0.166	1.804
Wild animal richness	Mammal bird richness	-0.052	-0.645	0.624	0.132	1.635

Table 2: Comparison of spatial model performance based on the logarithmic pseudo-marginal likelihood (LPML) and predictive accuracy metrics. For each model, LPML, AUROC, and AUPRC values are reported as medians with their associated ranges across repeated model fits. All-zoonoses models were fitted using neighborhood radii of 100, 400, and 700 km to assess sensitivity to spatial structure. The *C. hominivorax* models were fitted on a subsampled dataset restricted to confirmed *C. hominivorax* cases and are therefore not directly comparable to the all-zoonoses models. Two specifications are shown: one including cattle density as a fixed effect, and one modelling cattle density using a non-linear RW2 effect.

MODEL	LPML	AUROC (IC 95)	AUPRC (IC 95)	PREVALENCE
ALL-ZOONOTIC 400	**-0.03** (0.0008)	**0.89** (0.88 ; 0.91)	**0.12** (0.10 ; 0.14)	**0.53**
ALL-ZOONOTIC 100	**-0.03** (0.0008)	**0.89** (0.87 ; 0.91)	**0.12** (0.10 ; 0.15)	**0.53**
ALL-ZOONOTIC 700	**-0.03** (0.0008)	**0.89** (0.87 ; 0.91)	**0.12** (0.10 ; 0.15)	**0.53**
***C.HOMINIVIRAX* (+ CATTLE FIXED EFFECT)**	**-0.03** (0.02)	**0.96** (0.96 ; 0.97)	**0.12** (0.10 ; 0.16)	**0.38**
***C.HOMINIVIRAX* (+ CATTLE RW2 EFFECT)**	**-0.017 (0.0004)**	**0.98 (0.97 ; 0.98)**	**0.26 (0.23 ; 0.30)**	**0.38**

Table 3: Posterior mean estimates, 95% Bayesian credible intervals (BCI), and corresponding relative risks (RR) for socio-demographic, land-cover, livestock, climatic, and wildlife covariates included in the final spatial model. Relative risks were obtained by exponentiating posterior mean coefficients and represent the multiplicative change in prevalence associated with a one-unit increase in each standardized covariate, holding all other variables constant. Covariates were classified as having a positive or negative effect when their 95% BCI did not overlap zero (or RR did not overlap 1); effects were considered non-significant otherwise.

	Covariate	***Posterior mean***	***Q025***	***Q975***	***RR (95% BCI)***	***Significative effect***
Socio-demographic	Population density	-0.08	-0.25	0.09	0.92 (0.78 ; 1.10)	-
	HFI	**0.78**	**0.48**	**1.09**	**2.19 (1.61 ; 2.99)**	**Positive**
Land cover area	Built up	-0.06	-0.31	0.19	0.94 (0.73 ; 1.21)	-
	Cropland	**-0.21**	**-0.40**	**-0.02**	**0.81 (0.67 ; 0.97)**	**Negative**
	Water	-0.17	-0.40	0.05	0.84 (0.67 ; 1.05)	-
Climatic variables	**Temperature**	**-0.35**	**-0.39**	**-0.30**	**0.71 (0.68 ; 0.74)**	**Negative**
	Precipitation	**0.25**	**0.17**	**0.34**	**1.29 (1.18 ; 1.41)**	**Positive**
	Wind speed	0.05	-0.20	0.31	1.05 (0.82 ; 1.36)	-
Wild animal richness	**Mammal-bird richness**	**0.76**	**0.36**	**1.16**	**2.13 (1.43 ; 3.18)**	**Positive**

Table 4: Posterior mean estimates, 95% Bayesian credible intervals (BCI), and corresponding relative risks (RR) for socio-demographic, land-cover, livestock, climatic, and wildlife covariates included in the final spatial model for the *C. hominivorax* case study. Relative risks were obtained by exponentiating posterior mean coefficients and represent the multiplicative change in prevalence associated with a one-unit increase in each standardized covariate, holding all other variables constant. Covariates were classified as having a positive or negative effect when their 95% BCI did not overlap zero (or RR did not overlap 1); effects were considered non-significant otherwise.

	Covariate	***Posterior Mean***	***Q025***	***Q975***	***RR (95% BCI)***	***Significative effect***
Socio-demographic	Population density	-0.24	-0.59	0.03	0.79 (0.55 ; 1.12)	-
	HFI	**0.59**	**0.13**	**1.06**	**1.81 (1.14 ; 2.88)**	**Positive**
Land cover area	Built up	0.14	-0.29	0.57	1.15 (0.75 ; 1.77)	-
	Cropland	**-0.23**	**-0.46**	**-0.005**	**0.79 (0.63 ; 0.99)**	**Negative**
	Water	-0.16	-0.44	0.12	0.85 (0.64 ; 1.13)	-
Climatic variables	**Temperature**	**-0.55**	**-0.63**	**-0.48**	**0.57 (0.53 ; 0.62)**	**Negative**
	Precipitation	**0.28**	**0.16**	**0.40**	**1.32 (1.18 ; 1.49)**	**Positive**
	Wind speed	0.12	-0.22	0.46	1.13 (0.80 ; 1.58)	-
Wild animal richness	**Mammal-bird richness**	**1.01**	**0.42**	**1.62**	**2.75 (1.52 ; 5.06)**	**Positive**

Captions

Figure 1: Spatial predictions of all zoonotic emergence risk and associated uncertainty. Panels show (top left) the posterior mean of emergence risk estimated using the INLA model, (top right) the spatial uncertainty expressed as the standard deviation of the latent field, (bottom left) the width of the 95% credible interval, and (bottom right) the resulting hotspot classification combining risk and uncertainty, distinguishing reliable hotspots (high risk and low uncertainty), uncertain hotspots (high risk and high uncertainty), and areas with no detected hotspot.

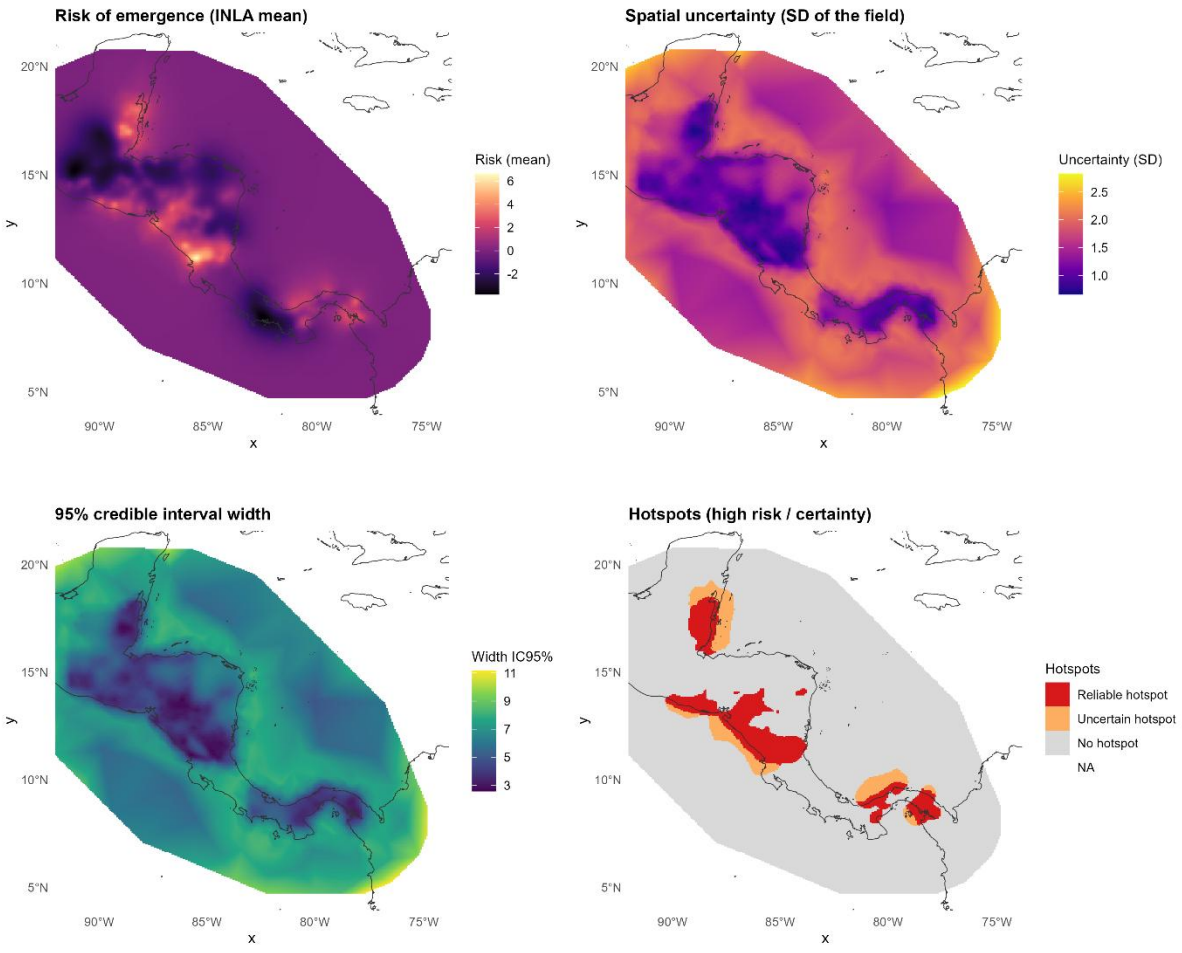


Figure 2: Spatial predictions of *Cochliomyia hominivorax* emergence risk and associated uncertainty. Panels show (top left) the posterior mean of emergence risk estimated using the INLA model, (top right) the spatial uncertainty expressed as the standard deviation of the latent field, (bottom left) the width of the 95% credible interval, and (bottom right) the resulting hotspot classification combining risk and uncertainty, distinguishing reliable hotspots (high risk and low uncertainty), uncertain hotspots (high risk and high uncertainty), and areas with no detected hotspot.

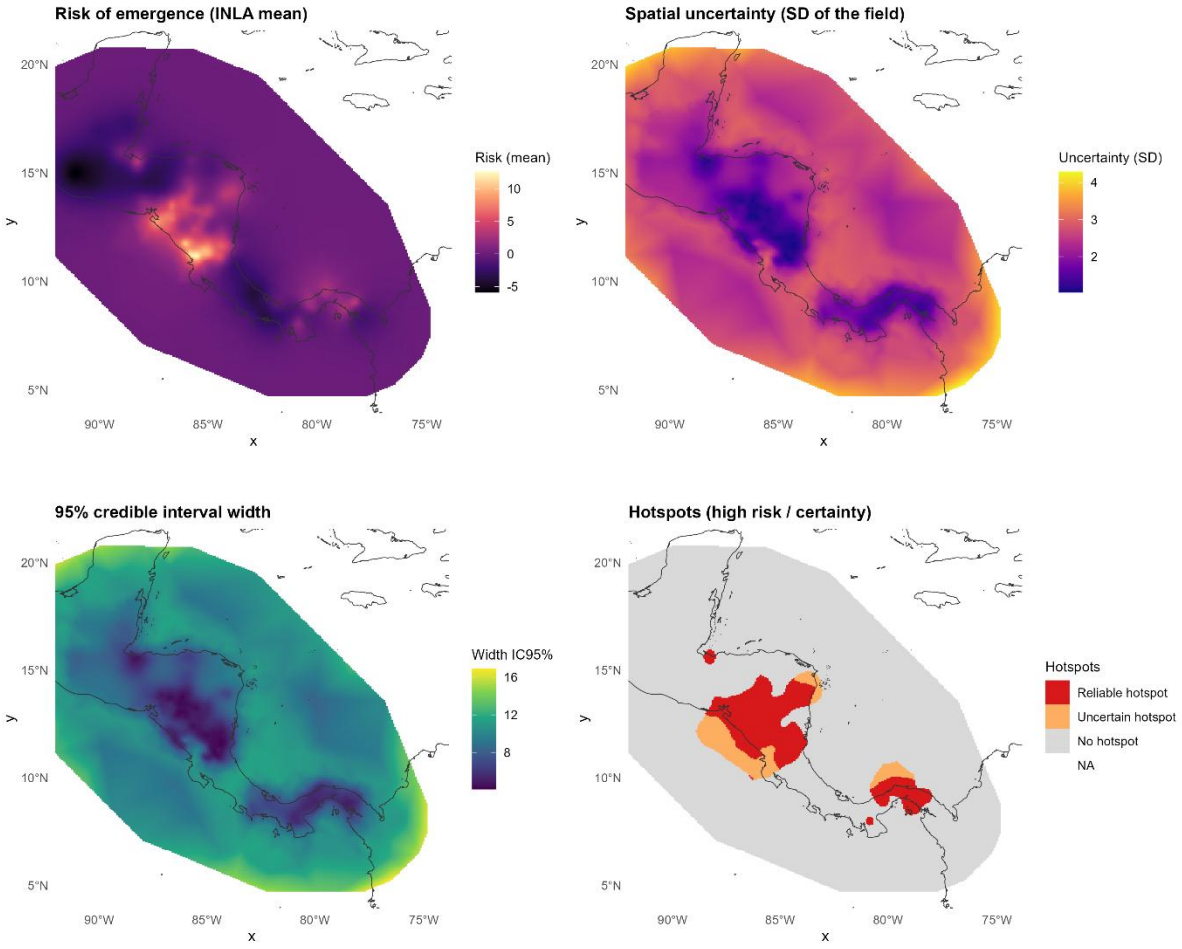


Figure 3: *Nonlinear effect of cattle density on zoonotic occurrence risk.* (A) Posterior smooth effect of cattle density on the probability of zoonotic diseases (all etiologies combined), estimated using a second-order random walk (RW2) model. (B) Corresponding effect estimated only for *Cochliomyia hominivorax* cases. Solid lines represent the posterior mean and shaded regions show the 95% credible intervals.

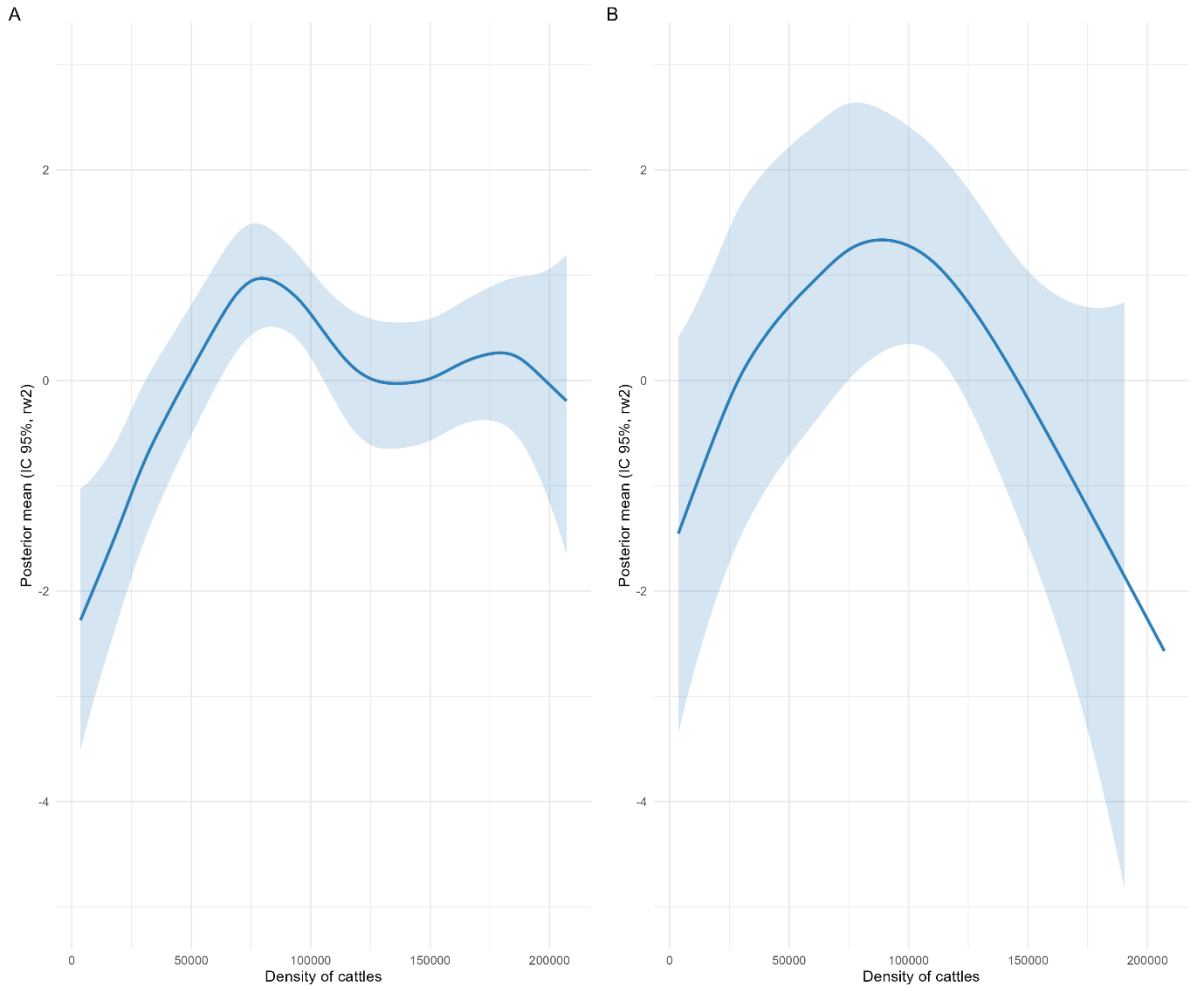
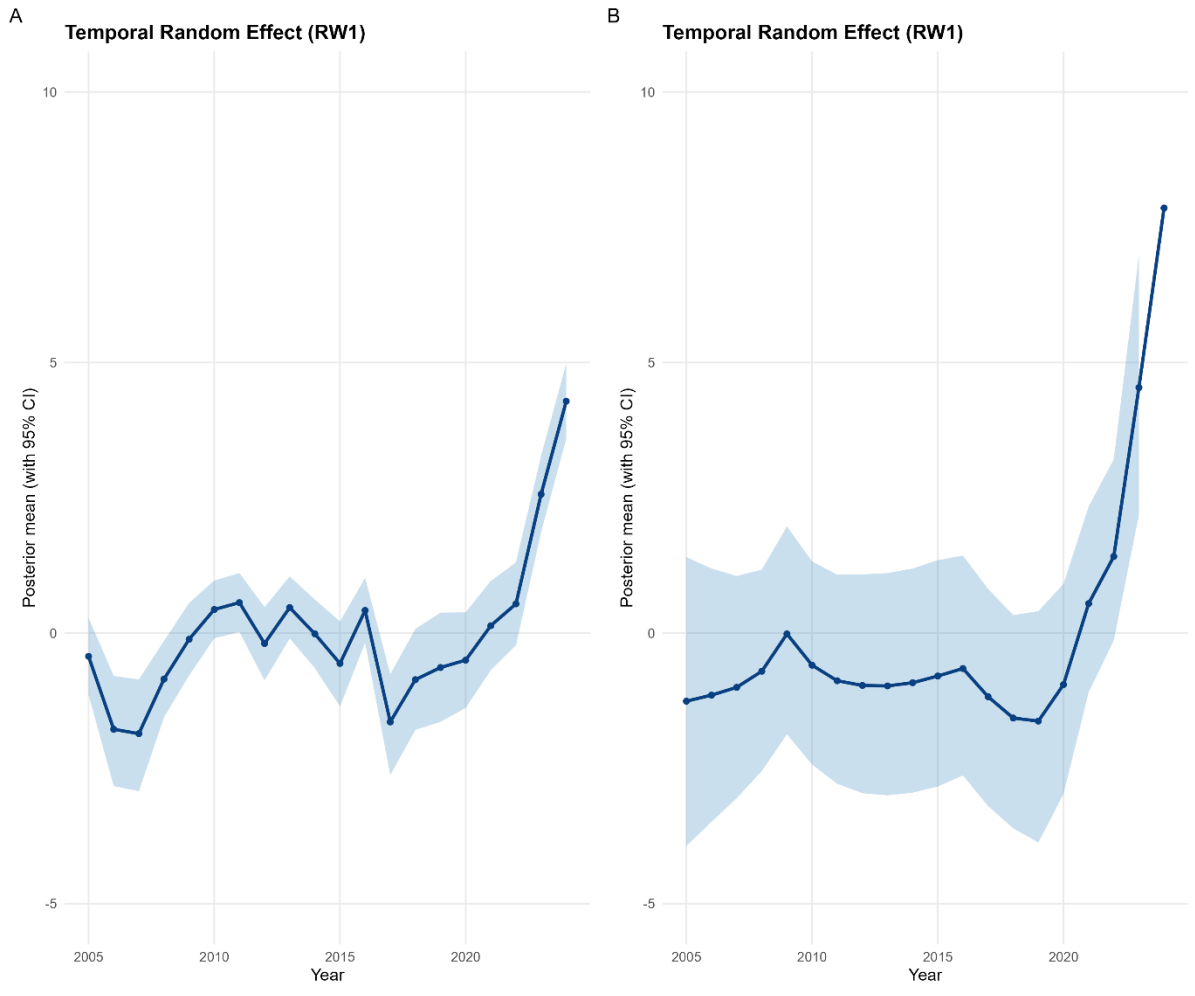


Figure 4. Temporal random effects for zoonotic emergence models (RW1). (A) Posterior temporal random effect for the all-zoonoses emergence model, showing moderate inter-annual fluctuations and a gradual long-term increase across the study period, with a sharp rise beginning around 2020. (B) Posterior temporal random effect for the *Cochliomyia hominivorax*-specific model, characterized by near-zero and highly uncertain effects prior to 2018–2020—reflecting the species' historical near-extinction in Central America—followed by an abrupt and well-supported increase in recent years. Shaded bands represent 95% Bayesian credible intervals (BCIs). Both models were estimated using a first-order random walk (RW1), allowing flexible, data-driven reconstruction of temporal trends.



Box 1: From trade-offs to coexistence: A three-dimensional sustainability framework

Reconciling biodiversity conservation with food security and food production is a key sustainability challenge, traditionally framed as a trade-off requiring optimization (Fischer, et al. 2017). Crespin & Simonetti (2021) introduced the concept of *coexistence parameters*, which are the social and ecological factors that can be managed to reduce conflict and shift systems toward states where food security and biodiversity conservation are simultaneously achieved. Such framework conceptualizes the *coexistence niche* as an n-dimensional space located at the intersection of food security and biodiversity components (Crespin et Moreira-Arce 2026).

However, this two-axis model remains incomplete because it lacks a critical third dimension. related to health. As demonstrated by recent global crises, the drivers of biodiversity loss and food insecurity are inextricably linked to zoonotic risk and public health (Hirst et Halsey 2023). Including zoonotic dynamics within the coexistence model thus highlights a key frontier for sustainability science. This manuscript proposes a theoretical expansion of the *Agroecological Systems Model of Coexistence* by formally integrating a third orthogonal axis-health-aligned with the One Health (OH) paradigm (WHO 2022).

Adopting the comprehensive OH definition, the new Health axis is deconstructed into three interdependent components that interact with the original two axes: *Human health*, *Animal health*, and *Environmental health*. Human health encompasses physical health (e.g., free from zoonotic diseases) and mental well-being, the latter often derived from "nature's contributions to people" (NCP) (Díaz, et al. 2018). This component interacts directly with food security access (socioeconomic stability) and biodiversity structure (exposure to green spaces). Animal health integrates the physical health and welfare of both domestic and wild animals, recognizing that high stress in animal populations (driven by habitat fragmentation or intensive agriculture) can compromise immunity and increase pathogen shedding (Hayek 2022). Environmental health refers to the integrity of the physical and biological matrix (e.g., soil, water, air) that acts as the foundational "system context" for human and animal health outcomes. For a complete breakdown of the conceptual components, their specific interactions, and potential parameters within the nexus, see Table 1.

Identifying the points of intersection between these three axes (see Fig.1) allows us to pinpoint the specific coexistence parameters that simultaneously reduce biodiversity impacts, secure food supplies, and mitigate disease risks. For example, managing connectivity through biological corridors is a key coexistence parameter, it restores environmental health and buffers human health risks by regulating vector populations (Ortiz, et al. 2021) (Prist, et al. 2023), while maintaining crop pollination services (food security). Similarly, diversified agroecological systems act as a coexistence parameter by providing stable food while conserving ecological relations that dilute pathogen prevalence among wildlife reservoirs, thus safeguarding animal health (Crespin et Simonetti 2020).

To operationalize this framework, we propose a pragmatic approach grounded in integrated vulnerability mapping. By superimposing data layers for each axis, such as deforestation rates (biodiversity), availability and access indicators (food insecurity) (Sibrian, et al. 2021), and zoonotic risk interfaces (disease burden) (Charles, et al. 2021), we can identify *socio-ecological vulnerability hotspots* where risks converge geographically. This mapping allows us to determine where intervention is most needed to push the local system towards a *basin of coexistence*, a dynamic attractor in phase space where the system remains stable in a state of coexistence despite external shocks (Crespin et Moreira-Arce 2026). By treating human, animal and environmental health as integral components of the coexistence niche, this integration transforms the framework into a comprehensive instrument for regional resilience.

730 **Table 1.** Conceptual axes that interact to create the human-nature coexistence nexus.
731 Interactions within the nexus can give way to potential coexistence parameters.

Conceptual Axis	Component	Description	Interactions within the Nexus
Biodiversity	1. Compositional	Identity and variety of genes, species, and populations (e.g., pathogen reservoirs, crop varieties).	→ Food Security: Genetic diversity serves as a buffer for crop resilience (Quantity) and dietary diversity (Quality). → Animal Health: Wild populations act as reservoirs; high diversity can dilute pathogen prevalence (dilution effect). → Human Health: Zoonotic spillover risk increases when compositional balance is disrupted (e.g., loss of predators).
	2. Structural	Physical arrangement of habitats (e.g., forest connectivity, patch size, fragmentation).	→ Environmental Health: Intact structures prevent erosion and regulate microclimates. → Human Health: Fragmentation increases "edge effects," heightening human exposure to vectors like ticks/mosquitoes. → Food Security: Landscape structure determines arable land availability and water retention (Quantity).
	3. Functional	Ecological processes (e.g., nutrient cycling, pollination, predation, water filtration).	→ Food Security: Pollination and soil fertility are critical ecosystem services for crop yields (Quantity). → Environmental Health: Water filtration and air purification directly support the "system context" for health. → Animal Health: Predation regulates reservoir populations, preventing disease outbreaks.
Food Security	1. Quantity (Availability)	The supply of food (calories) dependent on production systems and land use.	→ Biodiversity: Expansion of production often degrades Structural biodiversity (deforestation). → Animal Health: Intensification (crowding) increases stress and pathogen transmission in livestock. → Environmental Health: Agrochemical use can degrade soil and water quality.
	2. Quality (Utilization)	Nutritional value, food safety, and diet diversity required for healthy metabolism.	→ Human Health: Adequate nutrition supports immune function (Physical); nutritional deficiencies increase vulnerability to disease. → Biodiversity: Demand for diverse diets encourages the conservation of agrobiodiversity (Compositional) rather than monocultures.
	3. Access & Stability	Physical/economic access to food and the stability of that access over time.	→ Human Health: Poverty and food insecurity drive stress (Mental Health) and reliance on unsafe foods. → Biodiversity: Instability drives coping strategies like bushmeat hunting, impacting wildlife populations (Compositional). → Animal Health: Unregulated trade or hunting compromises wildlife welfare and health.

Health	1. Human Health	Physical: Freedom from disease/injury. Mental: Well-being and resilience.	→ Biodiversity: "Nature's contributions to people" (NCP) support mental well-being (Structural). → Food Security: Healthy populations are economically productive, ensuring stable food access (Access).
	2. Animal Health	Physical: Disease status of domestic/wild animals. Welfare: Freedom from distress (Five Freedoms).	→ Biodiversity: Disease outbreaks in wildlife (e.g., chytrid, distemper) can cause extinction events (Compositional). → Food Security: Healthy livestock ensures stable protein supplies; sick animals threaten food safety (Quality).
	3. Environmental / Ecosystem Health	Integrity of the physical environment (soil, water, air) that sustains life.	→ Biodiversity: A healthy matrix supports functional ecosystem processes (Functional). → Food Security: Degraded environments (e.g., salinized soil) collapse production systems (Quantity).

Box 2. Glossary of concepts for the expanded Coexistence Nexus Framework. The following terms are fundamental to the expanded conceptual model presented in Box 1 and detailed in Table 1.

Term	*Definition*
Agroecological Systems Model of Coexistence	The original conceptual framework that established the Food-Biodiversity nexus, composed of two multidimensional axes (Food Security and Biodiversity), which this manuscript expands upon (Crespin & Simonetti 2021).
Coexistence Niche	A multi-dimensional subspace where both food production and biodiversity conservation needs are met. It is an n-dimensional space located at the intersection of various components of food security and biodiversity (Crespin & Moreira-Arce 2026).
Coexistence Parameters	Social and ecological factors that can be actively managed to reduce conflict and shift a social-ecological system toward a state where food security and biodiversity are simultaneously achieved (Crespin & Simonetti 2021).
Coexistence Nexus	The expanded conceptual framework resulting from formally integrating the third orthogonal axis of Health (One Health) into the original Food-Biodiversity nexus (Crespin & Moreira-Arce 2026).
One Health (OH)	A comprehensive approach recognizing that the health of humans is inextricably linked to the health of animals and the environment (One Health High-Level Expert Panel et al. 2022).
Human Health	A component of the Health axis encompassing both physical health (e.g., freedom from zoonotic diseases) and mental well-being, the latter often derived from "nature's contributions to people" (NCP) (Díaz et al. 2018).
Animal Health	A component of the Health axis that integrates the physical health and welfare of both domestic and wild animals, including their disease status and freedom from distress and fear (One Health High-Level Expert Panel et al. 2022).
Environmental/Ecosystem Health	A component of the Health axis referring to the integrity of the physical and biological matrix (e.g., clean water, soil stability) that acts as the foundational "system context" for all other health outcomes (One Health High-Level Expert Panel et al. 2022).
Socio-ecological vulnerability hotspots	Specific geographic locations identified by integrated vulnerability mapping where critical risks from biodiversity erosion, food insecurity, and disease burden converge, requiring targeted intervention.
Basin of Coexistence	Not a physical place, but a dynamic attractor in phase space where a social-ecological system remains stable in a desired state of coexistence despite external shocks or perturbations (Crespin & Moreira-Arce 2026).