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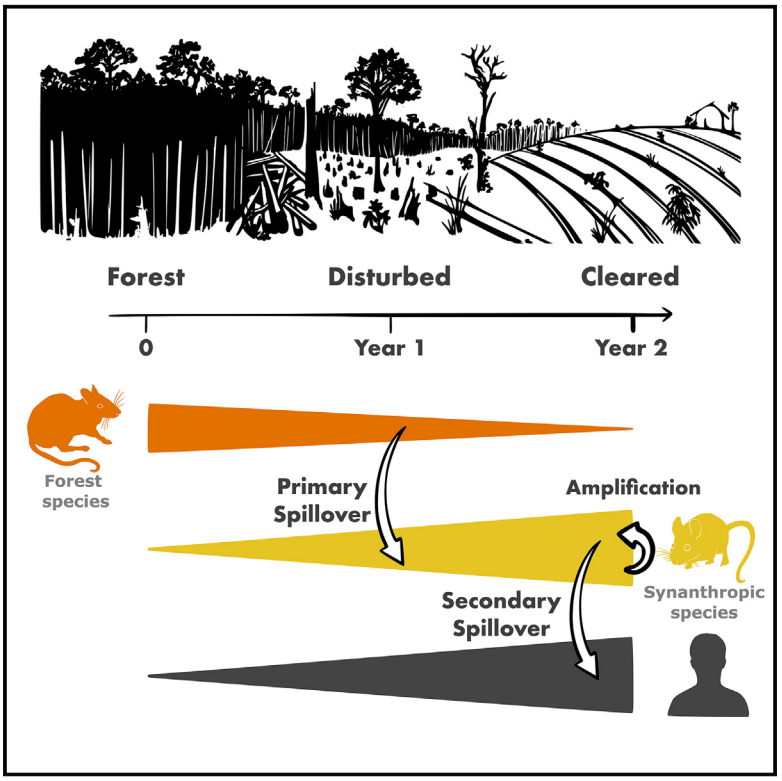
Small mammals at the edge of deforestation in Cambodia: Transient community dynamics and potential pathways to pathogen emergence

Graphical abstract



Highlights

- Deforestation results in rapid and complete turnover of rodent communities
- Disturbed zones transiently increase species diversity and contact opportunities
- Stable low-density forest species give way to fluctuating peri-domestic species
- Rapid host community changes may facilitate pathogen emergence during deforestation

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In brief

Our study investigated how deforestation affects rodent communities and their pathogens in nine sites in Cambodia. Across three zones—forest, disturbed, and cleared—representing the deforestation process in each site, we observed a complete turnover of rodent species. Disturbed forests had the highest species richness, and cleared land saw increased densities of peri-domestic species. These shifts create opportunities for disease transmission between forest and synanthropic species, which may act as bridge hosts with humans, potentially increasing risks of pathogen emergence.

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Small mammals at the edge of deforestation in Cambodia: Transient community dynamics and potential pathways to pathogen emergence

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SCIENCE FOR SOCIETY When a forest is cut down to make way for agriculture, animal communities face abrupt upheaval. As society grapples with the intertwined challenges of land-use change, biodiversity loss, and emerging infectious diseases, understanding these dynamics becomes crucial. We sampled small mammal communities in deforestation sites in Cambodia and found that the deforestation process results in a rapid and near-total turnover in small mammal species, new interaction between species in disturbed areas, and increased and fluctuating densities of rodents near agriculture. Why should we care? Because rodent community changes open new avenues for the transfer of pathogens between species that would not usually interact. These rodents can act as bridges for pathogens—once deep in the forest—to reach human settlements. As crop fields replace forests, we are not just losing trees and wildlife, we may also be unknowingly inviting new health risks into our communities.

SUMMARY

Conversion of forest to agricultural land results in rapid and profound changes in ecosystems and biodiversity loss and increases the risk of pathogen emergence. However, insights into the underlying ecological processes linking deforestation and pathogen spillover are required to anticipate and mitigate new pathogen spillovers.

Here, we studied small mammal communities and zoonotic pathogens in nine sites in Cambodia where the spatiotemporal deforestation edge was represented by three zones—forest, disturbed, and cleared—within each site.

Complete turnover of the small mammal community and species overlap in disturbed forest may provide opportunities for spillover on the spatiotemporal front of forest disturbance. Concurrently, boom-and-bust dynamics of synanthropic species in agricultural landscapes may support the amplification of pathogens in proximity to human settlements.

This combination of spillover and amplification may be a key mechanism involved in deforestation-induced pathogen spillovers, highlighting the global health threats of encroaching into natural areas.

INTRODUCTION

The recent emergence of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) and the subsequent devastating pandemic has highlighted the urgency to understand the factors and mechanisms involved in the emergence of new pathogens, specifically as they relate to human interactions with nature, and anthropogenic environmental changes.[1,2] Land-use/land-cover

(LULC) change and habitat degradation has, for a long time, been identified as a driver of disease emergence.[3–9] However, despite abundant literature conceptualizing, discussing, and reviewing this process, relatively little empirical evidence is available to describe specific spillover mechanisms[10] outside of a few better-described systems (e.g., Hantavirus,[11–13] *Borrelia burgdorferi*,[14,15] Hendra virus[16]). For instance, separate spillover events of Nipah virus in Malaysia and Bangladesh were linked to forest habitat fragmentation and degradation, and the creation of alternative anthropogenic habitat and food sources, bringing the pteropid bat reservoirs in closer proximity to susceptible domestic pigs and human populations.[17,18] In Malaysian Borneo, proximity to forest edge was associated with greater vector abundance and higher incidence of *Plasmodium knowlesi* infection.[19,20] In central Africa, Ebola outbreaks were associated with fine-scale measures of forest fragmentation, suggesting a transmission pathway from forest-dwelling bats to human communities living in forest-edges.[9,21,22]

Despite hypothesis-generating case studies and systems, evidence for the effects of LULC change on pathogen transmission has been mixed, and often pathogen- and scale-specific.[23–25] Paradoxically, one factor frequently ignored is the temporal dimension of LULC change. This presents two potential issues. First, the start and end stages of LULC change are not necessarily characteristic of the transition process associated with the system shift. This was aptly described by the concept of chronotone,[26] the temporal equivalent of ecotone describing an ecological transition between two states. Intuitively, differences between studies when sampling occurs along a chronotone may result in substantial difference in study outcomes and may partially account for the inconsistency in strength and direction of association between LULC and disease prevalence.[23,24,27,28] Second, the absence of a temporal component in LULC change studies may ignore important seasonal processes interacting with the habitat disturbance and contributing to pathogen emergence.[29–32] Previous studies in the context of forest degradation and fragmentation suggests a critical role for forest edge in increasing interspecies contacts and pathogen transmission.[33–36] Recent conceptual[30] and mathematical[37,38] models put forth hypotheses on causal pathways linking edge and boundary effects to pathogen spillover and emergence, and they highlight the need for empirical data to test these hypotheses.

Here, we focused on the community and population changes in wild rodents, a taxon highlighted for its significance for zoonotic pathogen spillover and emergence,[39–41] and describe the change in small mammal community composition and abundance through the deforestation chronotone in Cambodia[42] as well as the occurrence of selected zoonotic pathogens. We particularly focused on the rapid transition from intact forest to first year of crop plantation and hypothesized that, if zones of degraded forest provided an opportunity for species mixing and pathogen spillover, we would (1) detect a mixed community of forest and synanthropic rodents in transition zones and (2) identify bridge host species[43] within this mixed community that support pathogen transmission across zones. We further hypothesized that, if changes in vegetation and microclimate conditions influenced demographic parameters, we would see distinct seasonal patterns of population size between zones. We found that complete turnover of the small-mammal community and species overlap in disturbed forest may provide opportunities for spillover on the spatiotemporal front of forest disturbance. Concurrently, boom-and-bust dynamics of synanthropic species in agricultural landscapes may support the amplification of pathogens in proximity to human settlements. This empirical study contributes to documenting the changes in host communities and potential mechanisms of spillover in the context of deforestation, addressing a critical gap in our understanding of the linkages between land-use change, pathogen emergence, and their local and global health impacts.

RESULTS

Study sites

Our study focused on the deforestation chronotone, which is the changes occurring during the transition from intact primary forest to agricultural fields. Within each site, sampling locations, hereafter zones, were selected in order to represent three stages of the deforestation process. Zones were defined as forest (primary forest, as undisturbed as possible), disturbed (on-going clearing), and cleared (recently converted to agriculture). As in all space-for-time designs, a critical assumption is that all three zones were in the same initial condition in the past and followed a comparable change process. The spatial clustering of zones within sites ensured these assumptions were met, and more generally ensured the comparability of zones within sites. This design was replicated in nine independent sites.

The nine sites were selected in areas of evergreen or semi-evergreen primary forest in the Mondulkiri, Kampong Thom, and Preah Vihear provinces of Cambodia (Figure S1). To be included, a site had to contain three clearly identifiable zones following the chronology of the deforestation process (Figures 1 and S1). The history of each site and zone, and the timing of each transition, was carefully checked with local community members (Table 1). To the extent possible, we ensured that the time of transition from intact to disturbed forest preceded the transition from disturbed to cleared forest and that the conversion to agricultural land had occurred within a maximum of 2 years prior to sampling (i.e., first-year plantation). In two sites, a disturbed zone was clearly identified but had not been fully converted, and was therefore ''older'' than the cleared zones. However, these were still within a maximum of 2 years past initial disturbance (site 3 and 6, Table 1) and were, therefore, considered to adequately represent the deforestation process. When candidate sites were close to each other, selection was made to respect a minimum distance of 3 km between sites, which we subsequently considered independent due to the expected range of targeted small mammal species. In addition, to explore the seasonal dynamics, sampling of each site/zone was repeated in dry (January–March) and rainy (June–August) seasons (Figure 1).

Sampling outcomes and community description

Sampling of the rodent community over nine sites, three zones along the deforestation chronotone, and two seasons (54 strata) resulted in a total of 20,214 trap nights and 1,817 capture events of 965 individuals, including 852 total recapture events of 425 individuals (44% of individuals recaptured across all sites/zone/seasons). This represented a total capture rate of 9.0 captures/100 trap-nights. Captured animals belonged to 14

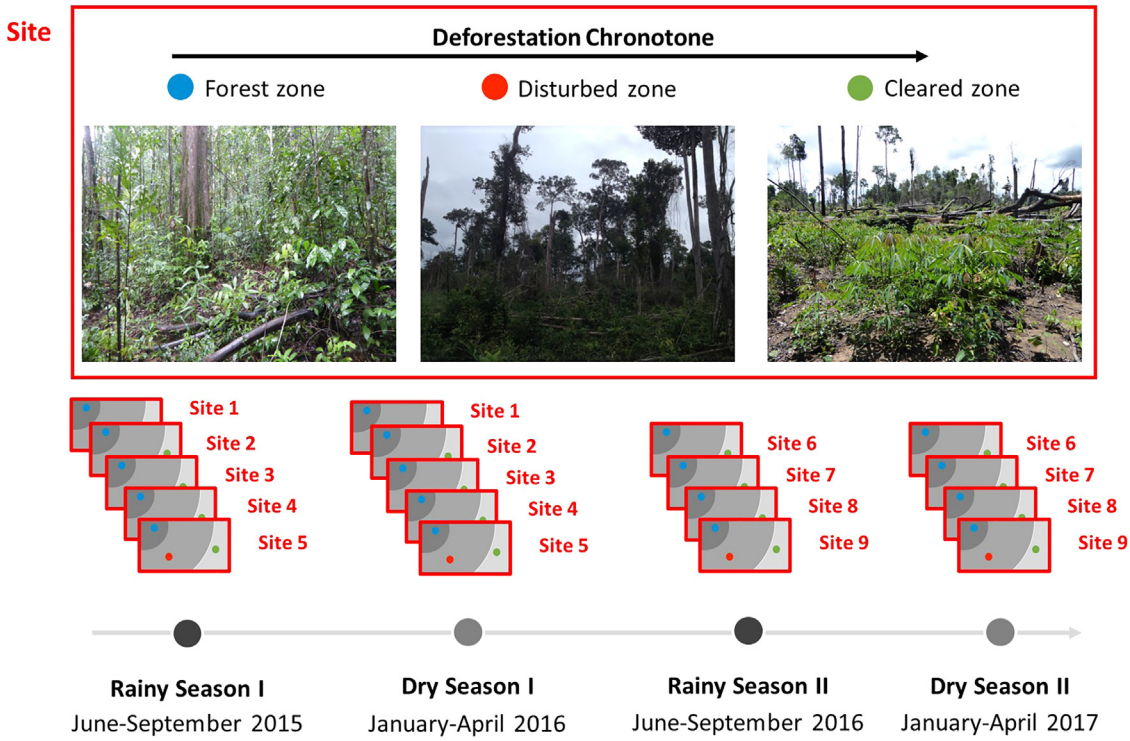

Figure 1. Study design overview

Each site was composed of three zones along a deforestation chronotone (top half of the figure).
A total of nine sites were sampled, five sites in year 1 and four sites in year 2.
Each site was sampled in both rainy and dry season (timeline in bottom half of the figure).

species, including 13 rodent species and one treeshrew species (Table 2). The most common species were *Mus cervicolor*, *Rattus* sp. R3 (sensu Aplin et al.[44]), and *Maxomys surifer*, representing 91% of captured animals. Among these, *M. surifer* was primarily captured in intact forest and occasionally in disturbed forest, *M. cervicolor* was primarily captured in recently converted land and occasionally in disturbed forest, and *Rattus* sp. R3 was captured in all three habitats (Table 2). Naive estimates of species richness (i.e., non-adjusted for detection probability) indicated an increase in species richness in disturbed zones compared to forest (Kruskal-Wallis test, $p = 0.01$) and recently cleared land ($p = 0.009$).

Table 1. Site characteristics and sampling dates

Year	Site ID	Province	Village	Dates rainy season	Randomized dry season order	Dates dry season	Time since forest stage (months)	
							Disturbed	Cleared
1	S1	Mondulkiri	Orona	15–26 June 2015	4	21 March to 1 April 2016	6	6
1	S2	Mondulkiri	Pouy Doem Svay	6–17 July 2015	5	18–29 April 2016	6	18
1	S3	Kampong Thom	Sro Lov Sroung	27 July to 7 August 2015	2	8–19 February 2016	12	8
1	S4	Mondulkiri	Ochra	17–28 August 2015	1	18–29 January 2016	1	9
1	S5	Kampong Thom	Rom Chek	8–17 September 2015	3	1–12 March 2016	7	24
2	S6	Phreah Vihear	Chrab Poy Rong Roueng	13–24 June 2016	1	16–27 January 2017	24	9
2	S7	Mondulkiri	Gati	3–14 July 2016	4	20–31 March 2017	9	18
2	S8	Kampong Thom	Tra Peing Pdov	28 July to 8 August 2016	3	27 February to 10 March 2017	6	20
2	S9	Kampong Thom	NA	15–26 August 2016	2	6–17 February 2017	6	13

See Table S1 for additional site information.

Table 2. Composition of small-mammal community across sites, zones, and seasons

	Total	Rainy season				Dry season			
Species	N = 965[a]	Forest N = 68[b]	Disturbed N = 136[b]	Cleared N = 387[b]	Total rainy[a]	Forest N = 91[b]	Disturbed N = 125[b]	Cleared N = 158[b]	Total dry[a]
M. cervicolor	522 (54%)	0	38	316	354 (60%)	0	32	136	168 (45%)
Rattus sp. *R3*	201 (21%)	8	63	60	131 (22%)	13	43	14	70 (19%)
M. surifer	157 (16%)	55	22	0	77 (13%)	60	20	0	80 (21%)
N. fulvescens	24 (2.5%)	1	4	0	5 (0.8%)	8	9	2	19 (5.1%)
T. belangeri	22 (2.3%)	2	5	0	7 (1.2%)	7	8	0	15 (4.0%)
Bandicota savilei	10 (1.0%)	0	0	3	3 (0.5%)	0	4	3	7 (1.9%)
B. berdmorei	9 (0.9%)	1	3	0	4 (0.7%)	0	5	0	5 (1.3%)
Mus caroli	5 (0.5%)	0	0	5	5 (0.8%)	–	–	–	–
Vandeleuria oleracea	5 (0.5%)	–	–	–	–	0	2	3	5 (1.3%)
R. exulans	4 (0.4%)	0	1	3	4 (0.7%)	–	–	–	–
Berylmys bowersi	2 (0.2%)	–	–	–	–	2	0	0	2 (0.5%)
Leopoldamys sabanus	2 (0.2%)	–	–	–	–	1	1	0	2 (0.5%)
Chiropodomys gliroides	1 (0.1%)	–	–	–	–	0	1	0	1 (0.3%)
Rattus andamanensis	1 (0.1%)	1	0	0	1 (0.2%)	–	–	–	–

[a]n (%).
[b]n.

Change in density across zones and seasons

Small mammal density across all species was greatly influenced by the deforestation zone and season. Specifically, areas recently converted to agriculture had higher rodent densities than intact and disturbed forest in the rainy season (Table 2; and Figure 2A). In contrast with intact forest ($\beta_{RainySeason} = -0.254$, p = 0.1), there was a significant difference in rodent density between rainy and dry season in disturbed ($\beta_{Disturbed*RainySeason} = 0.43$, p = 0.03) and cleared zones ($\beta_{Cleared*RainySeason} = 1.3$, p < 0.001) (Figure 2A; and Table S7). When focusing on the three predominant species, *M. surifer* density decreased from forest to disturbed and was absent from cleared areas (Figure 2B). *Rattus* sp. R3 was the most generalist of the three species, and one of the only two species captured in all three zones (Figure 2C). *M. cervicolor* was never captured in forest and increased in density from disturbed to recently cleared land. *M. cervicolor* reached the highest densities among the predominant species and displayed the same marked seasonal variations in cleared land as seen in the all-rodent model (Figure 2D).

Change in diversity across zone and season

Species richness estimates through the deforestation process indicated an initial increase in species richness in disturbed forest compared to intact forest ($\beta_{Disturbed} = 1.038$, 95% credible interval [CrI] = [0.009, 2.058], p = 0.024), followed by a simplification of the rodent community in recently converted zones ($\beta_{Cleared} = -1.261$, 95% CrI = [−2.249, −0.252], p = 0.008). This pattern was similar in wet and dry seasons ($\beta_{RainySeason} = -0.654$, 95% CrI = [−1.672, 0.408], p = 0.105) (Figure 3). The increased diversity of small mammal species in disturbed areas was related to the co-occurrence of both intact forest species (e.g., *M. surifer*, *Niviventer fulvescens*, *Berylmys berdmorei*) and synanthropic species found in converted zones (e.g., *M. cervicolor*, *Rattus exulans*) (Table 2).

Change in vegetation and microclimate

Vegetation surveys confirmed multiple microhabitat gradients reflecting the shift in vegetation type. Canopy cover decreased from 72.7% (95% confidence interval [CI], 71.9%–73.6%) in intact forest to 36.5% (95% CI, 34.7%–38.3%) in disturbed forest, to 4.0% (95% CI, 3.3%–4.8) in recently cleared zones (Kruskal-Wallis test, p < 0.001; Figure S1D). Similarly, overall vegetation density decreased from forest (median = 43.7%; interquartile range [IQR]:, 10.1–80.7) to disturbed forest (median = 29.2; IQR, 2.1–79.0) and to converted land (median = 8.6, IQR:0–56.6) (Kruskal-Wallis test, p < 0.001; Figure S1A). In contrast, crop cover increased from 0% in intact and disturbed forest to 11.6% (95% CI, 10.1%–13.0%) of vegetation transect length in recently converted areas (Kruskal-Wallis test, p < 0.001; Figure S1C). While vegetation density and canopy cover remained high in forest in both rainy and dry seasons, significant changes in crop cover were observed in agricultural zones (8.4% [6.9%–10.0%] in dry season compared to 14.7% [12.3%–17.1%] in rainy season, p = 0.03). Microclimate data showed similar variations across zones and seasons, with an increase in average temperature, diurnal temperature fluctuations, and frequency of temperature extremes (>40°C) from intact to converted zones (Figure 4). For instance, over 6 days, the cumulative time above 40°C was 10 min (mean = 1.14, SD = 3.36 min) in intact forest zones, compared to 11 h (mean = 1.3, SD = 2.6 h) in disturbed zones and 46 h (mean = 5.2, SD = 6.0 h) in cleared zones (F = 4.53, p = 0.02).

Pathogen findings

Among the priority zoonotic pathogens from the group Arenavirus, Hantavirus, *Orientia*, *Rickettsia*, and *Leptospira* that we tested for, all were detected in the sample of small mammals (Table 3 and S8; Figure 5;). Overall, among the three predominant species, prevalence of infection with at least one tested zoonotic pathogen was 1.9% in *M. surifer*, 1.0% in *Rattus* sp. R3, and

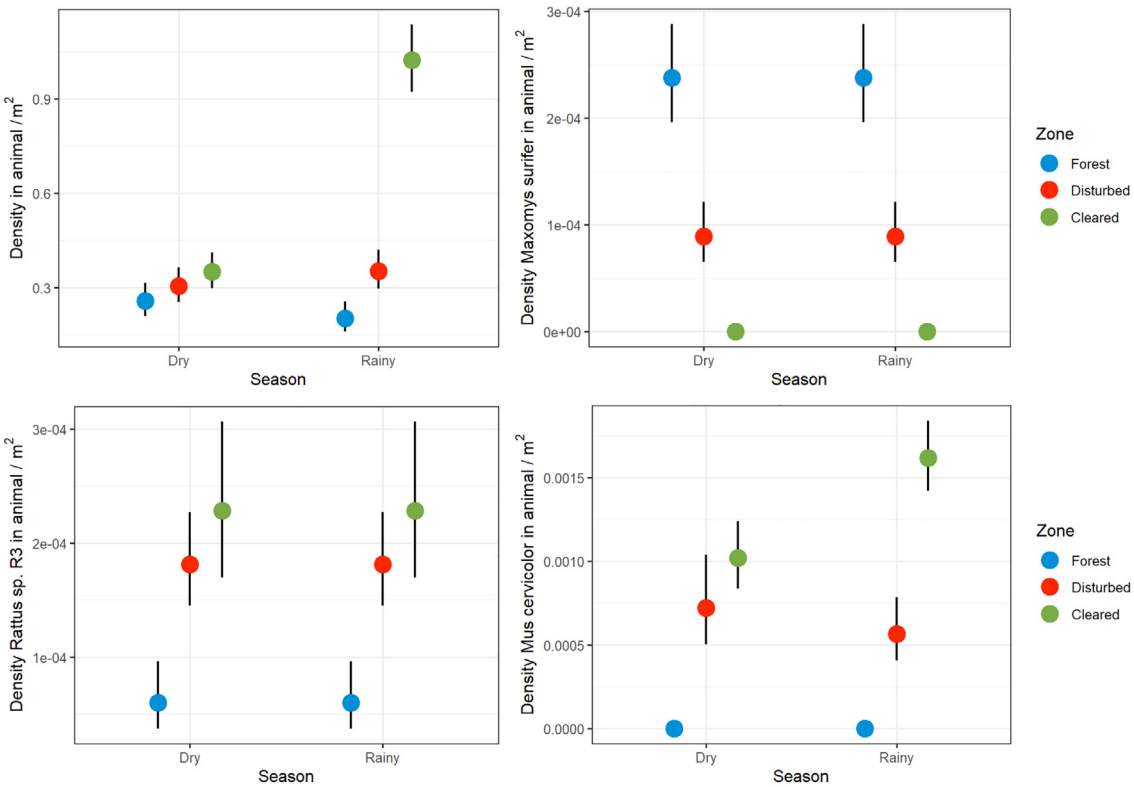

Figure 2. Small mammal density estimates across zones and seasons

Density estimates across zones and seasons for (A) all small mammals, (B) *M. surifer*, (C) *Rattus* sp. R3, and (D) *M. cervicolor*.

Error bars show the 95% credible intervals around the density estimates.

3.5% in *M. cervicolor* (Fisher's exact test, p = 0.2). There was no significant difference between seasons. In forest and disturbed zones, each small mammal species was host for one or two pathogens, whereas *M. cervicolor* in cleared zones was host for four pathogens, although limited sample size prevented statistical testing of difference in pathogen diversity among host species. Arenavirus occurred in two individuals of two species, *Tupaia belangeri* and *N. fulvescens*, that were captured in intact forest and disturbed forest. *Orientia* was only found in cleared zones. *Leptospira* spp. infections were found in all zones and only found in *M. cervicolor* in the cleared zone. *Rickettsia* was present in all three zones and carried by species that are typically found in more than one zone, such as *N. fulvescens* in forest, *M. cervicolor* in disturbed and cleared zones, and *Rattus* sp.

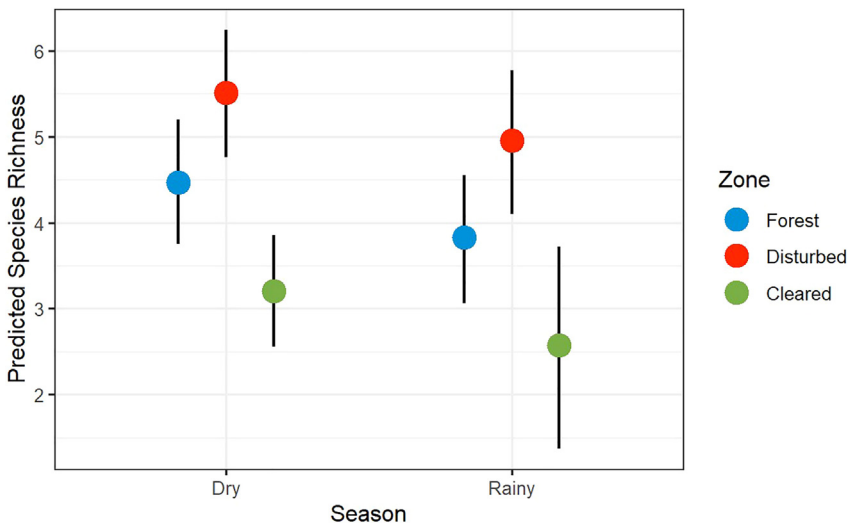

Figure 3. Predicted species richness in the small mammal communities across zones and seasons

Error bars show the 95% credible intervals around the species richness estimates.

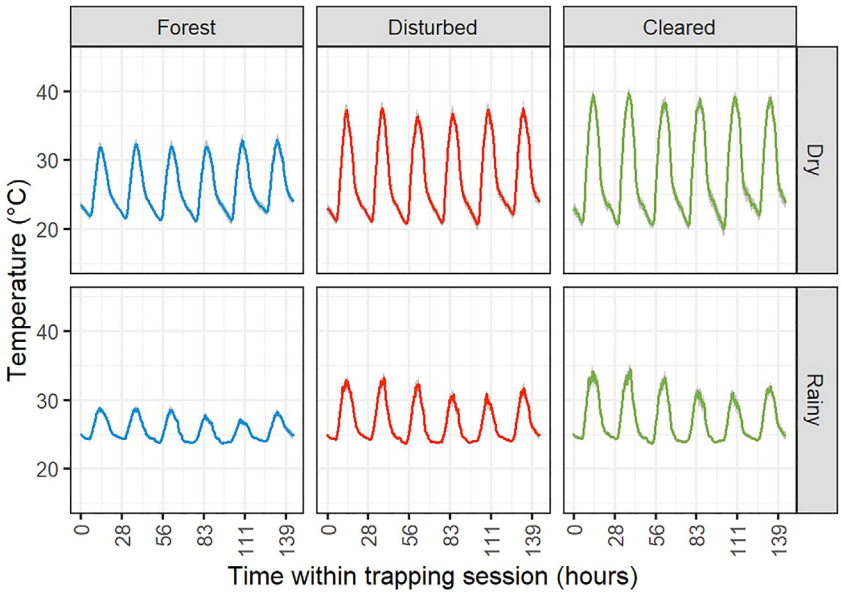

Figure 4. Average temperature fluctuations over 6 days across zones and seasons

R3 in cleared zones. Hantavirus was present in the forest in *T. belangeri* and *M. surifer*, in the three predominant species in disturbed zones (*M. surifer*, *Rattus* sp. R3, and *M. cervicolor*) and persisted in *M. cervicolor* in cleared zones. For these pathogens, there was no significant difference in apparent prevalence between zones, although the higher absolute number of captures in zone 3 (i.e., higher density in cleared zones) resulted in a greater absolute number of pathogen detections in this zone.

DISCUSSION

Rapid shifts in small-mammal community

The use of this space-for-time design to study the transition period between intact forest to converted land (i.e., deforestation chronotone) gave us a rare look into the transient dynamics of small mammal communities through the process of deforestation. Specifically, we identified spatio-temporal edge effects on rodent species diversity and density, along with seasonal interactions.

We documented a near-total turnover of the small mammal community over an average 14-month period from initial disturbance of intact forest through selective logging followed by progressive clearing until complete conversion and plantation of first crop. Among the 14 species of small mammals, 12 were found in either intact forest or agricultural zone, but never in both, and only two species, *Rattus* sp. R3 and *N. fulvescens*, were found in all three zones. Higher species diversity in the zone of disturbed forest was the result of persistence of some of the most resilient or adaptable species (e.g., *M. surifer*, *N. fulvescens*, *Rattus* sp. R3), and very early invasion by synanthropic species (e.g., *M. cervicolor*). Similar patterns of forest species loss, progressive turnover, and dominance by agrophilic or exotic species have been observed in deforestation gradients,[45–48] often resulting in a gradual loss of diversity as a function of proximity to forest.[49,50] Early emergence of human-associated rodent species in disturbed forest has also been documented in other tropical forest in Southeast Asia.[51] The focus on the deforestation chronotone and the related small spatio-temporal scale of sampling may have helped to identify transient processes that are more difficult to observe at larger scale. For instance, the observed higher species richness in the intermediate stage of deforestation provided empirical support for an increased species mixing along edges,[52,53] driven by patterns of persistence of forest specialists and influx of disturbance-adapted species.[54,55] However, caution is required when comparing our result to studies sampling along land-use gradients at much larger spatial scales. For instance, the forest patches that were considered intact forest in this study were embedded in a larger-scale fragmented landscape of forest and agricultural land, which may influence the baseline diversity of our forest zones.

We found an overall increase in rodent density in recently planted zones and marked seasonal differences in rodent density in recently planted cleared zones compared to stable densities in intact forest. Effectively, over the rapid transition from intact forest to crop plantations, the small mammal community dynamic shifts from a stable low-density community to seasonal boom-and-bust dynamics. This was mainly driven by the shift of the community to generalist synanthropes in recently cleared zones, predominantly *M. cervicolor* and *Rattus* sp. R3. Higher primary productivity in managed habitat supports higher densities of these agrophilic and disturbance-adapted species.[56] The onset of resource pulse related to crop cycles and the predominance of smaller and short-lived rodent species (i.e., *M. cervicolor*) explains the transition from fairly stable low-density rodent community in forest to a boom-bust dynamic in cleared land.[57–59] While there seem to be apparent seasonal fluctuations in *Rattus* sp. R3 (Table 2), the spatially explicit capture-recapture (SECR) analysis did not allow us to differentiate between a seasonal change in density and a seasonal change in detection probability, as the Akaike Information Criteria (AIC) of these models were not substantially different (Table S5).

Vegetation and microclimate data documented significant change in environmental conditions during the deforestation process, which likely contributed to the drastic shift in small mammal community. We confirmed the anthropogenic shift in vegetation composition, with gradual loss of canopy cover and overall vegetation density. This was accompanied by a loss of microclimatic buffering effect, as shown by an increased average temperature and decreased relative humidity from forest to agricultural land, and an increase in diurnal fluctuations. The loss of buffering effect of fragmented or degraded tropical forest[60] and the resulting loss of thermal niche is likely to contribute to a pattern of species loss and persistence in response the human disturbance and, in our case, the overall simplification of the small-mammal community.[61,62] This loss

Table 3. Summary of pathogen detection in small mammals across different zones

Pathogen	Forest, N = 159[a]	Disturbed, N = 261[a]	Cleared, N = 545[a]	p value[b]
Arenavirus	1/158 (0.6%)	1/261 (0.4%)	0/538 (0%)	0.2
Hantavirus	2/158 (1.3%)	3/261 (1.1%)	3/538 (0.6%)	0.4
Leptospira spp.	1/157 (0.6%)	1/261 (0.4%)	9/538 (1.7%)	0.3
Rickettsia spp.	1/159 (0.6%)	1/261 (0.4%)	3/545 (0.6%)	>0.9
Orientia tsutsugamushi	0/159 (0%)	0/261 (0%)	4/545 (0.7%)	0.4

[a]n/N (%).
[b]Fisher's exact test.

of buffering effect also amplified seasonal differences in temperatures between forest and cleared zones, with cleared zones much more frequently reaching temperatures above 40°C, which would challenge the thermoregulation capacity of most rodent species.[63] We hypothesize that the amplification of seasonal temperature extremes could contribute to the onset of the boom-bust dynamic of *M. cervicolor* in cleared zones.[64]

Hypothesized pathways for pathogen emergence

These rapid shifts in small-mammal communities observed on the front of deforestation provide important clues to the potential processes involved in land-use change-induced pathogen emergence. From a pathogen transmission perspective, the species mixing documented in disturbed zones provides opportunities for pathogen spillover between species that would otherwise not co-occur. Higher species interactions often characterize ecotones and habitat edges[53,65] and was identified as a factor facilitating pathogen spillover.[30,36] Following initial spillover, onward transmission within the new host is critical to pathogen amplification and eventual emergence.[66–69] The overall increase in small mammal density, driven by *M. cervicolor* and *Rattus* sp. R3, may support the amplification of pathogens. In a study of rodents and their pathogens across Southeast Asia, Morand et al.[70] also found that *Rattus* sp. R3 and *M. cervicolor* were associated with agricultural areas, and Bordes et al.[71] highlighted the high pathogen richness in *Rattus* sp. R3., including zoonotic pathogens. The density fluctuations of synanthropic species in recently cleared land, with seasonal recruitment of naive individuals into the population, may increase this potential for amplification of pathogens by these species, as described in other systems such as Hantavirus, cowpox virus, and *Yersinia pestis*.[72–74] Population fluctuation and synanthropy were indeed found to increase zoonotic transmission risk in a global dataset of rodent species.[75]

In sum, we hypothesize that the rapid change in small-mammal communities between forest and first-year plantation may provide opportunities for spillover at the front of forest disturbance, while the shift in the population dynamics of synanthropic species provides opportunities for amplification of pathogens in proximity to human settlements, which may result in secondary spillovers into humans (Figure 6). In this proposed model, synanthropes would effectively act as bridge hosts between sylvatic reservoirs and human-dominated landscapes.[43] This combination of spillover and amplification may be key elements explaining pathogen emergence in areas of land conversion. There is no reason to presume that these newly created interfaces would be unidirectional, and spillover from synanthropes to forest species may occur, with potential conservation impacts compounding the direct effects of habitat loss.

Initial evidence and future directions

Four of the five targeted zoonotic pathogens were found across the three zones, showing their ability to persist across the deforestation chronotone despite the almost complete species turnover. Patterns of Hantavirus infection across the communities provide insights into potential spillover mechanisms. Detection of Hantavirus in intact forest suggests endemic circulation in forest-dwelling species (*T. belangeri* and *M. surifer*). *M. surifer* was also found infected in disturbed zones, along with synanthropic species found in both disturbed and cleared zones (*Rattus* sp. R3 and *M. cervicolor*). Finally, Hantavirus infections persisted in *M. cervicolor* in cleared areas. This provides support to the hypothesis that interspecies transmission allows pathogen persistence along the deforestation chronotone, facilitated by primary pathogen spillover between disturbance-tolerant forest species (e.g., *M. surifer*) and disturbance-adapted synanthropic species (e.g., *Rattus* sp. R3 and *M. cervicolor*).

This research may shed new light on the disease-diversity relationship debate[76–79] by suggesting that transient increase in species richness and subsequent loss of diversity may both be involved in the spillover and emergence processes. Indeed, while the negative diversity-disease relationship is consistent across scales and ecological contexts,[78–80] this focus on chronotone (at fine temporal scale) highlighted transient increase in diversity that may result in temporary but possibly significant increase in pathogen transmission and spillover.

Based on the limited number of pathogens tested, data were too sparse to infer a change in pathogen diversity across the deforestation chronotone, but it is noteworthy that the predominant synanthropic species, *M. cervicolor*, had the highest pathogen diversity of all species. It is well established that generalist and synanthropic rodent species, which are able to cope with habitat disturbance and persist in anthropogenic landscapes, are linked to higher reservoir competence for zoonotic pathogens.[40,70,81] Future work leveraging the samples collected with next-generation sequencing and metagenomic approaches will elucidate the changes in pathogen diversity. If the spatio-temporal edge indeed acts as a contact and transmission zone, we would expect an increasing pathogen diversity despite the community simplification. In our study, there was no detected effect of the zone or season on pathogen prevalence but it is noteworthy that the higher rodent density in recently cleared zones resulted in a higher absolute number of pathogen detections than in other zones. Assuming some level of density dependence on the risk

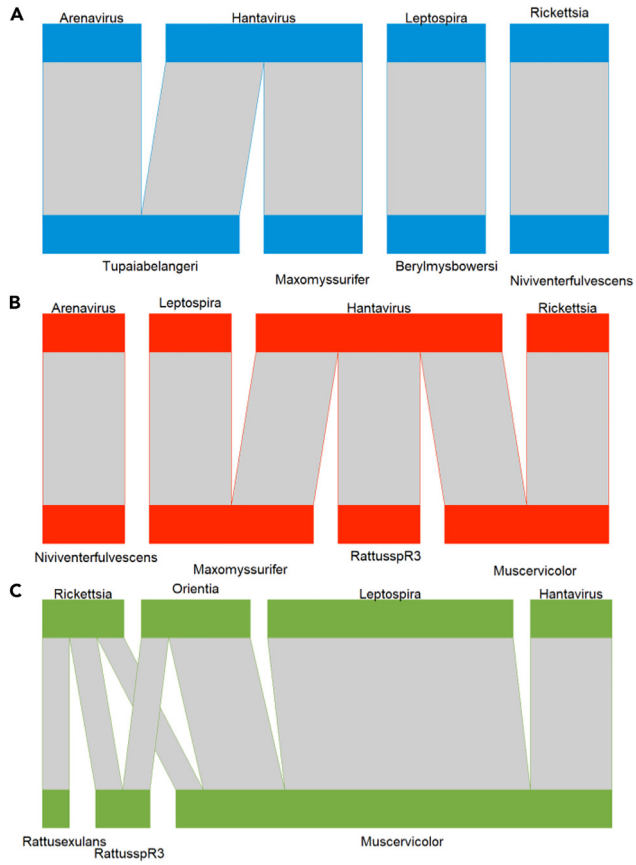

Figure 5. Bipartite networks showing host-pathogen associations in (A) forest, (B) disturbed, and (C) cleared zones

Link thickness is proportional to the number of occurrences of each pathogen within each rodent species across sites.

of transmission from rodent reservoir to humans, this preliminary evidence is consistent with a higher risk of secondary spillover to humans in areas recently converted to agriculture.

Previous systematic reviews have not found a consistent direction in prevalence change following land-use change.[23–25] However, most previous studies have focused on static cross-sectional comparisons of different LULC types, ignoring the dynamic nature of spillover and emergence processes. In contrast, detailed studies from multiple systems support a link between habitat degradation and pathogen spillover.[9,19,21,82,83] Reviews and meta-analyses that have focused on habitat degradation confirm a more consistent link between habitat degradation, species loss, and pathogen emergence.[40,80,84] Beyond comparisons of prevalence in different LULC, the focus on the transition period between LULCs using a fine-scale space-for-time design (with only minor deviations from a strict temporal sequence) was critical in understanding the rapid shifts in the small mammal community that may provide causal pathways for pathogen spillover. While the design was very demanding in field resources, we encourage others to replicate this approach to test the generalizability of these observations in forested biomes and to study dynamic changes in other biomes. Seasonal dynamics have previously been highlighted as a critical component of pathogen dynamics[29] and should continue to be integrated in the study of LULC change as this study demonstrates significant interaction effects between LULC change and seasonality that are critical to our understanding of the change in host communities.[30]

Other processes operating at the individual level in the context of environmental changes, such as physiological and immunological processes, likely play important roles in mediating the downstream effects on health outcomes (e.g., survival, reproduction) and eventually population dynamics.[66,85] Similarly, nutritional status likely is a component of the mechanisms linking LULC change to pathogen dynamics via the effects on immune competence.[86] While we were not able to include these dimensions in this study, we encourage future replications of this work to include eco-physiological and eco-immunological measurements to further elaborate on the causal pathways linking LULC change and individual and population health and the dynamics of pathogens. Finally, while we focused on the ecological processes involved in initial pathogen amplification within the host community, initial land conversion, secondary spillover, and subsequent spread within human populations are driven by additional socio-economic and cultural factors that are central to future pandemic-prevention interventions.[10] Integrative and participatory approaches to understanding these socio-ecological edges are critical to understanding and preventing future spillover events and disease emergence.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Mathieu Pruvot (mpruvot@ucalgary.ca).

Materials availability

Biological materials generated in this study by small-mammal sampling have been archived at the Institut Pasteur du Cambodge and may be made available for further collaboration with the co-authors of this study.

Data and code availability

All original data and code have been deposited at Zenodo under the https://doi.org/10.5281/zenodo.10042694 and are publicly available as of the date of publication. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Rodent capture-mark-recapture

Zones within a site were sampled concurrently, and sites were sampled following a random sequence within each season. In each zone of a given site, 50 locally made Havahart-type traps were deployed on a square or rectangular grid with traps spaced by 20 m. Traps were covered with a plastic trap cover indicating the trap number and protecting from excessive sun exposure or rain. The grids in forested and converted land were always set about 200 m away from the edge of the patch, based on expected maximum home range among rodent species. The location of grids in disturbed land was often more constrained by the topography, but grids were always set up as far as possible from habitat edges. All traps were baited with sweet potato dipped in peanut butter in the evening of each trapping day, and checked the next morning at dawn. Trapping occurred on eight consecutive nights. Traps with new captures were placed in a light cotton bag to be brought to the mobile field laboratory located on a strategic location between zones. Traps that closed with no animal capture or showed other evidence of trap malfunction were recorded. Field team staff were trained for consistency and randomly assigned to trapping grids and trap lines each day to avoid systematic errors.

Animals were processed immediately after being brought to the field laboratory. Animals were first weighed and transferred to a mobile safety cabinet where they were briefly anesthetized with isoflurane using the microdrop technique.[87]

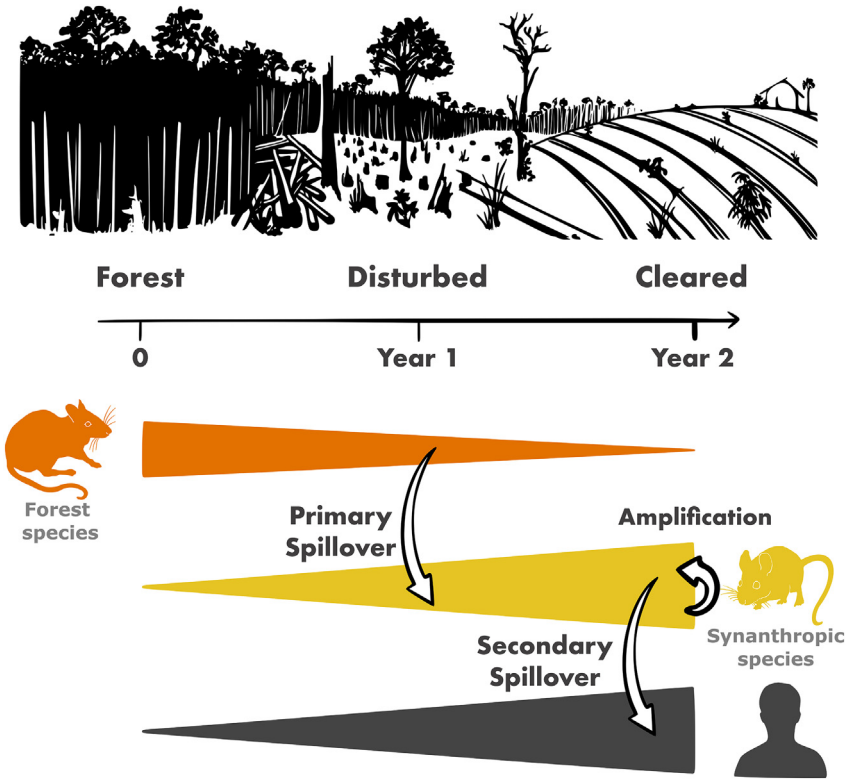

Figure 6. Hypothesized mechanisms linking deforestation and pathogen emergence

Animals were marked with a unique aluminum ear tag on the left ear and with a 1-mm ear punch on the other ear. The ear punch was placed in 95% alcohol for genetic species identification. Oral swabs, feces or rectal swabs, and urine or uro- swabs were collected in duplicate and stored in RNAlater Stabilization Solution (Invitrogen, Carlsbad, CA, USA) and viral transport medium (VTM; containing tryptose phosphate broth 2.95%, 145 mM NaCl, 5% gelatin, 54 mM Amphotericin B, 106 U of penicillin-streptomycin per liter, and 80 mg of gentamicin per liter [Sigma-Aldrich, Steinheim, Germany]). Finally, a blood sample was obtained by saphenous vein puncture on larger rodents and from the retro-orbital sinus on species of the *Mus* genus. A dry blood spot on Whatman FTA cards (Qiagen, Valencia, CA, USA) was prepared from the extracted blood. When volume was sufficient, the rest of the blood was centrifuged for 20 min, and serum was separated from the clot. The blood clot was split into tubes with RNAlater and VTM. When blood volume was insufficient, the whole blood was placed in an empty cryovial. All samples were stored in liquid nitrogen immediately after sampling until transfer to a −80°C freezer at the Institut Pasteur du Cambodge. Additionally, data were recorded on sex, age (juvenile or adult), lactation status (teat score: invisible, raised, lactating), sexual maturity (open or closed vagina; testicles fully descended, partially descended, or not descended), number of injuries, and various body measurements (head and body, skull, hind foot, tail, ear, ano- distance). Following these procedures, rodents were released at their respective capture locations. Recaptured animals were released immediately at the capture location after recording their ear tag number. Small mammal community descriptive statistics were produced from the capture data and the site/species matrix using the R package vegan.[88] All animal procedures were reviewed by the Wildlife Conservation Society's Institutional Animal Care and Use Committee and approved under permit #15:04. Prior to starting the research, we organized community meetings with the nearest village or communities to inform about the purpose of the research and request permission to establish our sites in the area.

Laboratory procedures

Laboratory procedures are more extensively described in supplemental notes. Briefly, all swab samples were extracted using QIAamp Viral RNA kits (Qiagen, Valencia, CA, USA); a few tissue samples obtained on animals that died during trapping or handling were extracted with RNeasy Mini Kit (Qiagen, Valencia, CA, USA), and blood samples were extracted by DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. RNA extracted from feces/rectal swab, oral swab, uro-/urine, kidney, liver, lung, and spleen were used to produce cDNA using SuperScript III First-Strand Synthesis Super-Mix (Invitrogen, San Diego, CA, USA) according to the manufacturer's instructions. Broadly reactive consensus nested PCRs were used to target the L gene of Old World Mammarenavirus using primer pairs that were previously described in Vieth et al.,[89] and Blasdell et al.[90] A similar approach was used to target the L gene of Hantavirus.[91] DNA extracted from feces/rectal swab, oral swab, uro- swab/urine, and kidney samples were selected to screen for common pathogenic *Leptospira* spp. using TaqMan real-time PCRs targeting the *lipL32* gene[92] and *rrs* genes.[93] Animals were deemed positive when at least one sample tested positive for at least one of the two targets. DNA extracted from whole blood or dry blood spot were used in a multiplex real-time PCR to detect spotted fever group (SFG) and typhus group (TG) rickettsials targeting citrate synthase gene[94] and scrub typhus group targeting 16S rRNA gene.[95] DNA extracted from skin samples was processed to confirm animal species using previous published DNA barcoding protocols targeting vertebrate mitochondrial cytochrome oxidase subunit 1 (COI).[96] PCR products were characterized by Sanger sequencing using an ABI 3700 Genetic Analyzer sequencer using both forward and reverse direction primers at a commercial provider (Macrogen, Seoul, Republic of Korea). Species confirmation was done by comparing COI sequence with homologous sequence contained in GenBank (https://blast.ncbi.nlm.nih.gov/), Barcode of Life Database (https://www.boldsystems.org/), and the CERoPath database (www.ceropath.org/virtual_museum/rodent_information_center).

Vegetation assessment

At each trap location, a vegetation assessment consisted of general vegetation measurements and 5-m transects starting from the trap in two random directions. Vegetation assessments were conducted by a separate team to allow consistency in the way assessments were conducted. General vegetation assessment variables used in this study included canopy cover as determined by the average of two readings of a spherical crown densiometer (Forestry Suppliers, USA) and vegetation density as determined by image analysis of a digital photograph (GNU Image Manipulation Program, gimp.org) of a 1 × 2-m^2 white sheet from a 5-m distance. On line intercept vegetation transects,[97] vegetation intersecting the path of the measuring tape was classified at the functional type level, including grass, tree stump, fallen tree, live tree, live branch, dead branch, shrub, vascular plant, woody vine, bamboo, dead bamboo, soil litter, bare ground, and rock. The length of intersection along the tape of a particular vegetation type was recorded along the two 5-m transects (total 10 m per trap). For each functional type, the overall proportion of the transect distance covered was calculated.

Microclimate data

Six weather stations were deployed in each zone of each site during the eight nights of capture. Weather stations were placed in proximity to a trap location and to optimize the coverage of the zone. Each weather station consisted of a temperature and relative humidity data logger (Hobo U23 Pro v2) with sensor mounted on a solar radiation shield (RS1 Solar Radiation Shield, Onset, USA),

recording every 10 min, and a rain gauge (Tru-Chek Direct-Reading Rain Gauge, Forestry Suppliers, USA), which was recorded daily.

Stratified SECR analysis

Change in small mammal density through the deforestation process, and across season, was assessed using the extensively documented oSCR package[98] developed for multi-session (i.e., stratified) SECR analysis. This allowed testing the effect of environmental variables that vary across sessions (in our case, zone of deforestation and season) within a single statistical model. In this application, data were organized in 54 sessions representing combinations of nine sites, three zones, and two seasons. Zone and season were added as session-specific covariates that could then be used to model the spatial point process model (density surface of individual activity centers), the baseline encounter model (detection probability of individuals at their activity center), and the spatial decay model (rate of decrease in detection probability as distance from activity center increases).[98] Models were run across all small mammal species (to model an overall small mammal density) or for the three predominant rodent species. For all models, and for both the encounter and point process sub-models, we tested the effect of season and zone separately, additively, and their interaction. For the small mammal model, we allowed the spatial decays to vary by zone to account for variation in average home range size across the small mammal communities, and we allowed for an additive effect of zone and season in the species-specific models. After excluding models that did not converge, all models were ranked according to their AIC to identify best-fit models (code and data available at https://github.com/mathieurrpruvot/LUCpub).

Bayesian community occupancy analysis

Change in rodent community composition and species richness was assessed using a Bayesian hierarchical community occupancy model following model formulations previously described by Kery et al.[99] In this model, species-specific effects are drawn from a common community distribution with hyperparameters that are estimated. Specifically, the probability of occurrence for species k (psi_k) was modeled as a function of a species random intercept, a random site intercept (to account for clustering of zones within sites), species-specific random slopes for the effect of disturbed zone and cleared zone (in comparison to forest zone), and a species-specific random slope for the effect of season (used as binary variable where season = 1 in rainy season). Code and data are available at https://github.com/mathieurrpruvot/LUCpub. Models were built in JAGS and run in R 4.2.0 (R Core Team, 2022) using the rjags[100] and jagsUI[101] packages. This community occupancy model was fitted using Markov chain Monte Carlo (MCMC) method with three Markov chains for 200,000 iterations each with 45,000 burn-in iterations discarded and chains thinned every third iteration. Mixing of Markov chains was visually confirmed, and convergence was assessed by ensuring that all Gelman-Rubin statistic ($\widehat{R}$) values were below 1.1.

A significant advantage of the Bayesian approach is access to the matrices of the z[i] latent occurrence variable (which appropriately account for the probability of detection), from which species richness can be computed. The multiple iterations give access to the uncertainty around this z matrix, and, therefore, around species richness. Following estimation of species richness, the effect of environmental conditions can be estimated with full propagation of uncertainties. We estimated species richness for each zone of each site at each season and assessed the effect of zone and season on this index using a model akin to a meta-analysis as previously described in Kery et al.[99] Species richness estimates were modeled following a simple linear regression with zone, season, and their interactions as fixed effects and two error terms, one accounting for the propagated uncertainty around richness estimates and one representing residual variance (code and data available at https://github.com/mathieurrpruvot/LUCpub). These models were also run with three Markov chains for 10,000 iterations with 1,000 burn-in iterations.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2023.11.003.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.P., S.C., A.F., P.D., V.D., P.F.H., and S.H.O.; methodology, M.P. and S.H.O.; investigation, M.P., S.C., V.H., S.I., V.B., J.-L.R., C.F., S. Sek, R.S., S.R., S.N., S. San, Y.T., M.C., S.K., S. Sours, S.T., U.C., U.H., S.T., S.Y., S.P., and L.K.; data curation, M.P., S.C., V.B., J.-L.R., C.F., and S. Sours; formal analysis, M.P., J.-L.R., and C.F.; writing – original draft, M.P.; writing – review & editing, M.P., S.C., V.H., A.F., P.D., V.D., P.F.H., and S.H.O.; supervision, M.P., S.C., A.F., P.F.H., and S.H.O.; funding acquisition, P.D., V.D., A.F., and S.H.O.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

This project was a very close collaboration between international and Cambodian researchers and early career researchers. We ensured fair representation of all participants in this research in regard to origin and career stage. In the recruitment of field staff, we worked diligently to prevent any gender bias, maintained gender neutrality throughout the research (e.g., randomized task assignment), and paid close attention to maintain a safe working environment for all staff regardless of gender and origin. Finally, in all sites where we worked, we actively engaged with the local communities prior to and following the project to ensure that the research did not have any negative impact on these communities and that they benefited from the research results.

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