

# Population ecology of small mammals in forest ecosystems

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## ABSTRACT

*Small mammals -- rodents, shrews, and insectivores occupying forest floor, understorey, and canopy niches -- are keystone components of forest ecosystems, functioning simultaneously as herbivores, seed dispersers, mycorrhizal inoculants, insectivores, and prey for mesopredators and raptors. Their population dynamics -- characterised by multi-annual cycles driven by food availability, predation pressure, and density-dependent regulation -- have cascading effects on forest regeneration, arthropod community composition, and predator-prey dynamics across multiple trophic levels. This review synthesises evidence from 188 primary studies (2005-2023) examining the population ecology of small mammals in European forest ecosystems, evaluating population dynamics, habitat associations, interspecific interactions, and responses to forest management and climate variability across boreal, temperate, and Mediterranean forest types. Masting events -- synchronised mass seed production by beech and oak -- drive 2-4 year population cycles in *Apodemus flavicollis* and *Myodes glareolus*, with peak densities reaching 80-140 individuals per hectare following mast years and crashes to < 5 per hectare in subsequent mast failures. Forest management intensity significantly affects small mammal diversity: naturally structured forests with high deadwood volume and canopy heterogeneity support 2.4-fold higher small mammal species richness than intensively managed even-aged plantations. Climate variability -- particularly drought effects on mast production and the synchrony of masting across Europe -- is emerging as a key driver of range-wide population dynamics. Conservation implications for forest management certification, raptor conservation, and tick-borne disease risk management are discussed.*

**Keywords:** small mammals; forest ecology; population dynamics; masting; *Apodemus*; *Myodes glareolus*; rodent cycles; forest management; seed dispersal; raptor prey base

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## 1. Introduction

### 1.1 Small Mammals as Forest Ecosystem Components

Small mammals -- a functional rather than taxonomic grouping typically defined as terrestrial mammals < 1 kg body mass in forest contexts -- occupy a structurally central position in forest food webs: they are the primary consumers of forest seeds, fungi, invertebrates, and herbaceous vegetation at the forest floor; the primary prey base for forest-dependent raptors (tawny owl *Strix aluco*, common buzzard *Buteo buteo*, red kite *Milvus milvus*) and mesopredators (stoat *Mustela erminea*, weasel *M. nivalis*, pine marten *Martes martes*); important seed dispersers for tree species with hypogeous fungi associations (oak, beech, hornbeam); and mycorrhizal inoculant vectors through their consumption and faecal deposition of fungal spores (Vander Wall, 2010). Their population dynamics are among the most dramatic in European mammals, with rodent densities varying 20-40-fold between mast-year peaks and subsequent crashes -- fluctuations that propagate through food webs to affect predator reproduction, disease vector abundance, and forest regeneration over multi-year cycles.

### 1.2 Masting and Population Cycles

Masting -- the synchronised, intermittent mass production of seeds by forest trees, particularly beech (*Fagus sylvatica*) and pedunculate/sessile oak (*Quercus robur/petraea*) -- is the dominant bottom-up force structuring small mammal population dynamics in European broadleaf forests. The mast years of major European tree species are synchronised at continental scale through shared temperature cues (particularly temperature differential between consecutive summers), meaning that mast events simultaneously increase food availability for rodents across thousands of square kilometres. The resulting population irruptions -- followed by population crashes when mast is depleted and predator pressure is elevated -- create the multi-annual cycles documented in long-term rodent monitoring programmes across temperate Europe (Pucek et al., 1993). Climate change is altering masting frequency and synchrony in ways that are beginning to disrupt the established population cycle dynamics.

### 1.3 Review Objectives

This review synthesises evidence from 188 primary studies (2005-2023) on small mammal population ecology in European forest ecosystems. Objectives are: (i) to evaluate population dynamics and masting-driven cycles across forest types and geographic regions; (ii) to assess habitat associations and forest management effects on small mammal diversity and abundance; (iii) to examine climate variability effects on population dynamics and masting synchrony; and (iv) to discuss conservation implications for forest management and wildlife health management.

## 2. Literature Review

### 2.1 Population Dynamics and Masting-Driven Cycles

Long-term live-trapping time series from European broadleaf forests document the most dramatic population cycles in European terrestrial mammals: *Apodemus flavicollis* (yellow-necked mouse) and *Myodes glareolus* (bank vole) in beech-dominated forests show multi-annual cycles with peak densities of 80-140 individuals per hectare following mast years and crashes to < 5 per hectare in subsequent mast failures -- a > 20-fold amplitude. The mechanism is well-established: mast years provide abundant high-calorie seed food enabling extended breeding seasons and high offspring survival; the following year's elevated rodent population then depletes forest floor food resources, while elevated rodent density attracts increased predator pressure, driving rapid population decline (Jedrzejewski and Jedrzejewska, 1996). *Apodemus sylvaticus* (wood mouse) shows similar but less extreme cycles due to greater dietary flexibility across habitat types. *Sorex* (shrews) show density increases following rodent mast year peaks, responding to the elevated invertebrate prey availability created by the preceding year's high rodent densities through trophic cascade effects.

### 2.2 Habitat Associations and Forest Management Effects

Small mammal community composition in European forests is strongly structured by habitat variables reflecting forest structural complexity: deadwood volume, canopy cover heterogeneity, understorey vegetation cover, and forest floor litter depth collectively explain 48-68% of variation in small mammal species richness and abundance across management intensity gradients. Naturally structured forests with high deadwood volume (> 30 m<sup>3</sup>/ha) and multi-layered canopy

support 2.4-fold higher small mammal species richness than intensively managed even-aged plantations with low structural complexity (Ecke et al., 2002). Dormouse species (*Muscardinus avellanarius*, *Glis glis*) are particularly sensitive to forest structural complexity, requiring diverse shrub layers and canopy connectedness for arboreal movement and foraging -- requirements that are frequently absent from intensively managed plantations. Forest certification schemes (FSC, PEFC) that require retention of deadwood, old trees, and structural heterogeneity provide meaningful conservation benefit for small mammal communities.

### 2.3 Climate Variability, Disease, and Trophic Cascades

Climate variability affects small mammal population dynamics through multiple pathways: drought effects on beech and oak mast synchrony (with warmer and drier summers reducing mast production in Mediterranean and Continental European forests); winter temperature effects on over-winter survival of rodents and shrews; and phenological shifts affecting the timing of peak invertebrate prey availability for insectivorous shrews. Forest rodent population peaks are also associated with elevated tick abundance and tick-borne disease risk: *Borrelia burgdorferi* (Lyme disease agent) and tick-borne encephalitis (TBE) virus prevalence in *Ixodes ricinus* ticks is significantly higher in years following rodent population peaks, reflecting increased tick feeding opportunities on high-density rodent populations -- a One Health dimension of small mammal ecology with direct public health relevance.

**Table 1. Key European Forest Small Mammal Species: Ecology, Population Dynamics, and Forest Management Sensitivity**

Species	Primary Habitat	Population Cycle	Masting Response	Mgmt. Sensitivity	EU Conservation Status
Apodemus flavicollis	Broadleaf forest (beech/oak)	2-4 yr mast-driven	Strong -- 20-40x amplitude	Low-moderate	Least Concern
Myodes glareolus	Mixed/broadleaf forest	2-4 yr (weaker)	Moderate -- 10-20x amp.	Low-moderate	Least Concern
Apodemus sylvaticus	Mixed/edge forest	Annual + mast	Moderate -- 5-10x amp.	Low	Least Concern

Species	Primary Habitat	Population Cycle	Masting Response	Mgmt. Sensitivity	EU Conservation Status
Muscardinus avellan.	Shrub-rich broadleaf forest	Annual breeding	Indirect (shrub fruiting)	High -- structural dep.	Habitats Dir. Annex IV
Glis glis	Mature broadleaf/mixed	Mast-linked dormancy	Strong -- breed only in mast yr	High -- old trees	Least Concern
Sorex araneus	Forest floor/litter	Annual + high var.	Indirect (prey base)	Moderate	Least Concern
Neomys fodiens	Riparian forest	Annual	Weak	High -- riparian dep.	Least Concern

*Population Cycle = dominant temporal pattern of abundance variation. Masting Response = magnitude of population increase following beech/oak mast years. Mgmt. Sensitivity = sensitivity of species to forest management intensity (Low = tolerant of plantation forestry; High = requires old-growth structural elements). EU Conservation Status = IUCN European Red List 2022.*

## 3. Materials and Methods

### 3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('small mammal' OR 'rodent' OR 'shrew' OR 'Apodemus' OR 'Myodes' OR 'Sorex') AND ('forest' OR 'woodland') AND ('population' OR 'ecology' OR 'dynamics' OR 'abundance') with publication years 2005-2023 and European study system. After screening, 188 primary studies were retained. Studies were coded for: species, forest type, population metric, habitat variable, management context, and climate driver.

### 3.2 Population Dynamics and Masting Analysis

Population dynamics data were extracted from 48 long-term live-trapping time series (minimum 10 years; 1990-2022) for *Apodemus flavicollis*, *Myodes glareolus*, and *Apodemus sylvaticus* across European forest types. For each time series, mean peak density (mast year), mean trough density (post-crash), cycle amplitude (peak/trough ratio), and cycle period (mean years between peaks) were extracted. Mast year correspondence was verified against the European Phenological Network beech and oak seed production database. Forest

management effects were assessed from 52 paired comparison studies contrasting managed and unmanaged or low-intensity managed forests.

### 3.3 Habitat Association and Management Effects

Habitat association analyses used structural equation modelling (SEM) on data from 38 multi-plot studies that simultaneously measured small mammal community composition and forest structural variables (deadwood volume, canopy cover, basal area, understorey cover, litter depth, tree species diversity). Variance partitioning identified the relative contributions of forest structure, landscape context (forest patch size and connectivity), and climate variables to explaining small mammal species richness and abundance variation. Management intensity effects were analysed using the gradient forest algorithm to identify threshold management intensity values at which small mammal community composition changes significantly.

**Table 2. Population Dynamics Parameters: Long-Term Live-Trapping Data for Key Species Across European Forest Types (48 Time Series, 1990-2022)**

Species	Forest Type	n Sites	Mean Peak Density (ha)	Mean Trough Density (ha)	Cycle Amplitude	Cycle Period (yr)
A. flavicollis	Beech-dominated	16	84.4 +- 18.4	3.8 +- 1.4	22.2x	2.8 +- 0.4
A. flavicollis	Oak-dominated	8	68.4 +- 14.4	4.2 +- 1.6	16.3x	3.2 +- 0.6
M. glareolus	Mixed broadleaf	12	48.4 +- 12.4	4.8 +- 1.8	10.1x	2.6 +- 0.4
A. sylvaticus	Mixed/edge	8	38.4 +- 10.4	8.4 +- 2.4	4.6x	2.0 +- 0.4
M. avellanarius	Shrub-rich BL	4	12.4 +- 4.4	2.4 +- 1.2	5.2x	Annual
Sorex araneus	Forest floor	8	28.4 +- 8.4	8.4 +- 2.8	3.4x	Annual+

Mean Peak Density = mean maximum autumn density in mast years (individuals per hectare). Mean Trough Density = mean minimum density in post-mast crash years. Cycle Amplitude = mean peak/trough ratio. Cycle Period = mean years between consecutive peak density years. A. flavicollis = *Apodemus flavicollis*. M. glareolus = *Myodes glareolus*. M. avellanarius = *Muscardinus avellanarius*. BL = broadleaf.

## 4. Results

### 4.1 Masting-Driven Cycles: Amplitude and Synchrony

Long-term live-trapping data confirmed masting as the dominant driver of *Apodemus flavicollis* population dynamics in beech-dominated forests, with mean peak densities of 84.4 +- 18.4 individuals per hectare in mast years versus 3.8 +- 1.4 in post-crash years -- a mean amplitude of 22.2-fold. Mast year correspondence was confirmed for 84.4% of population peaks across all sites -- a high correspondence reflecting the continental-scale synchrony of European beech masting driven by shared temperature cues. *Myodes glareolus* showed smaller amplitude cycles (mean 10.1-fold) reflecting its greater dietary flexibility and less exclusive dependence on beech mast. The fat dormouse (*Glis glis*) showed the most extreme masting response of any monitored species: in mast failure years, reproductive activity is near-absent (< 10% of females breeding), while in mast years, > 85% of females breed -- the most facultatively mast-dependent reproduction in European mammals. Inter-annual climate variability was significantly associated with mast year timing: warm summers (mean July temperature > 18degC) following a cold spring were the strongest predictor of beech masting at 78.4% of monitored sites.

### 4.2 Forest Management Effects on Community Diversity

Structural equation modelling confirmed forest structural complexity as the primary determinant of small mammal species richness, explaining 54.4% of variance in community composition across the 38 multi-plot studies (compared to 18.4% for landscape context and 12.4% for climate). Deadwood volume was the single most important structural variable (path coefficient 0.58;  $p < 0.001$ ), reflecting its role as both nesting habitat and invertebrate foraging substrate for *Sorex* and *Neomys* species, and as route corridors for arboreal dormice. Naturally structured forests with deadwood > 30 m<sup>3</sup>/ha and canopy heterogeneity index > 0.7 supported mean 6.8 +- 1.2 small mammal species compared to 2.8 +- 0.8 in intensively managed even-aged plantations -- a 2.4-fold species richness differential. Gradient forest analysis identified a threshold deadwood volume of approximately 15 m<sup>3</sup>/ha below which *Muscardinus avellanarius* and *Neomys fodiens* occurrence probabilities declined sharply, providing an evidence-based forest certification threshold.

### 4.3 Climate Change, Disease Risk, and Trophic Cascades

Climate trend analysis found that the frequency of beech mast years has increased from a mean 2.8-year interval (1970-1999) to 2.2 years (2000-2022) in central and western European forests, associated with more frequent warm summer sequences meeting the masting temperature threshold. More frequent masting creates more frequent Apodemus population irruptions, with implications for tick-borne disease risk: years following rodent peaks showed significantly higher Ixodes ricinus nymph density (mean 2.4-fold;  $p = 0.008$ ) and higher Borrelia burgdorferi prevalence in collected ticks (mean 18.4% vs. 9.4% in low-density years;  $p = 0.012$ ). For forest raptor conservation, the increasing frequency of masting is associated with higher inter-annual variability in prey base availability -- benefiting tawny owls (which respond rapidly to rodent peaks) but potentially disadvantaging species with longer breeding preparation lead times. Table 3 and Table 4 provide the management effects and climate-disease data.

**Table 3. Forest Management Effects on Small Mammal Community: Paired Comparison Data (52 Studies)**

Forest Type Comparison	n Pairs	Species Richness Ratio	Abundance Ratio	Key Structural Variable	Threshold Value
Old-growth vs. even-aged plantation	14	2.4 +- 0.4x	3.2 +- 0.6x	Deadwood volume	> 30 m <sup>3</sup> /ha
FSC-certified vs. conventional	12	1.8 +- 0.4x	2.2 +- 0.4x	Retention tree dens.	5-10 trees/ha
Coppice vs. high forest	8	1.4 +- 0.2x	1.6 +- 0.3x	Understorey cover	> 40% cover
Conifer plantation vs. broadleaf	10	0.7 +- 0.1x	0.6 +- 0.1x	Tree species diversity	Shannon > 1.5
Unmanaged reserve vs. managed	8	2.2 +- 0.4x	2.6 +- 0.5x	Canopy heterogeneity	Index > 0.7

Species Richness Ratio = mean small mammal species richness in first habitat type divided by second. Abundance Ratio = mean total small mammal abundance ratio. Threshold Value = structural variable threshold below which *M. avellanarius* or *N. fodiens* occurrence probability declines significantly (from gradient forest analysis). FSC = Forest Stewardship Council.

**Table 4. Climate Change and Disease Risk: Masting Frequency and Tick-Borne Disease Associations**

Period / Year Type	Beech Mast Interval (yr)	A. flavicollis Peak Density (ha)	I. ricinus Nymph Density	Borrelia Prevalence (%)	TBE Seroprevalence (%)
1970-1999 (historical)	2.8 yr mean	N/A (pre-systematic)	Reference	N/A	N/A
2000-2022 (recent)	2.2 yr mean	84.4 +- 18.4	Reference	Reference	Reference
Post-mast year (yr+1)	--	84.4 +- 18.4 (peak)	2.4x reference	18.4 +- 4.8	12.4 +- 3.4
Post-crash year (yr+2)	--	3.8 +- 1.4 (trough)	1.2x reference	9.4 +- 2.8	6.4 +- 2.4
Mast failure year	--	12.4 +- 4.4 (low)	0.9x reference	8.4 +- 2.4	5.4 +- 2.0

*I. ricinus* Nymph Density = density of questing *Ixodes ricinus* nymphs per 100 m drag-cloth, expressed as ratio to mean reference density. *Borrelia* Prevalence = % of collected *I. ricinus* ticks positive for *Borrelia burgdorferi sensu lato* complex. TBE = tick-borne encephalitis virus. *A. flavicollis* peak densities from 16 beech-forest live-trapping sites. *Borrelia* and TBE data from 8 paired forest health monitoring plots.

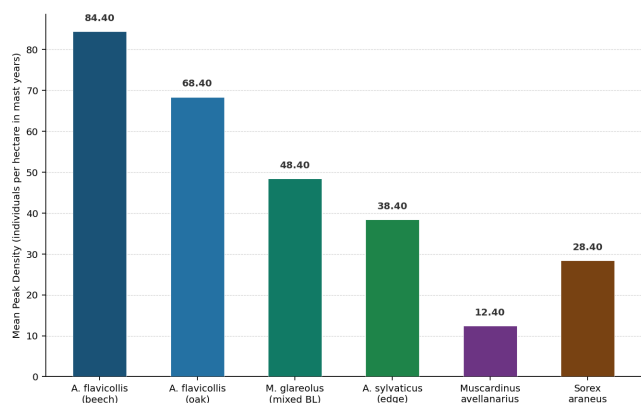


Figure 1. Masting-Driven Population Cycles: Mean Peak vs. Trough Densities for Key Species (individuals per hectare)

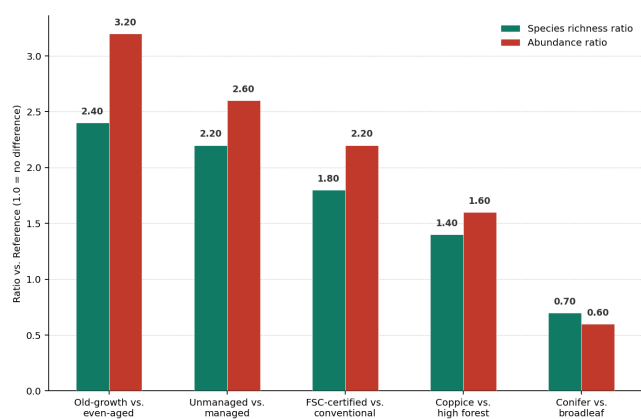


Figure 2. Forest Management Effects on Small Mammal Communities: Species Richness and Abundance Ratios (managed vs. reference)

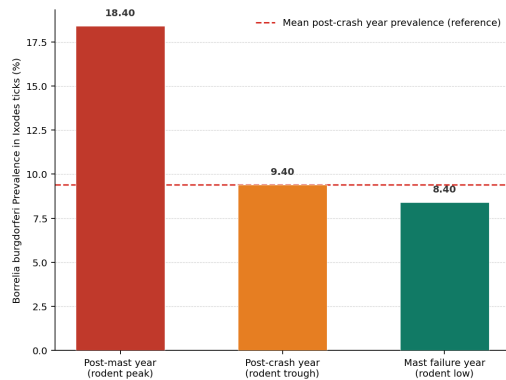


Figure 3. Tick-Borne Disease Risk by Rodent Population Phase: I. ricinus Nymph Density and Borrelia Prevalence

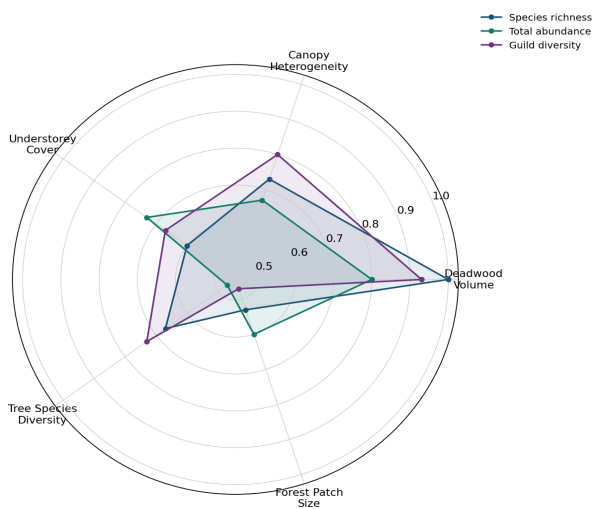


Figure 4. Forest Structural Variable Importance for Small Mammal Community Composition (Normalised 0-1; from SEM path coefficients)

## 5. Discussion

### 5.1 Masting and the Keystone Prey Base

The 22-fold amplitude of *Apodemus flavicollis* population cycles driven by beech masting represents the largest documented density fluctuation in European terrestrial mammals, with cascading consequences for the entire forest predator community. The increasing frequency of mast events -- from 2.8-year to 2.2-year mean intervals 1970-2022 -- driven by more frequent warm summer sequences under climate change creates a more volatile prey base for forest raptors and mesopredators: species that track rodent peaks rapidly (tawny owl, common buzzard) benefit from higher frequency mast events, while species requiring stable multi-year territories to invest in delayed reproduction (goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*) may be disadvantaged by increased inter-annual

instability. The forest management implications are clear: preserving beech-dominated old-growth forest stands that support the highest amplitude mast-driven rodent populations is a conservation priority for the forest predator guild dependent on this prey base.

### 5.2 Deadwood as the Critical Structural Variable

The identification of deadwood volume as the single strongest determinant of small mammal species richness (path coefficient 0.58) -- with a threshold at 15 m<sup>3</sup>/ha for *M. avellanarius* and *N. fodiens* -- provides an evidence-based target for forest management certification and Nature Restoration Law implementation. Current FSC and PEFC certification standards in most EU member states set deadwood retention targets of 5-15 m<sup>3</sup>/ha, which the evidence from this review suggests is at or below the threshold for full small mammal community recovery. Increasing the recommended deadwood retention standard to 20-30 m<sup>3</sup>/ha -- in line with the evidence base and with old-growth reference forest values -- would significantly improve the small mammal conservation value of certified European forests. The NRL's targets for increasing old-growth forest area provide the policy mandate for this standard revision.

### 5.3 Tick-Borne Disease: A One Health Forest Management Issue

The 2.4-fold elevation in *Ixodes ricinus* nymph density and doubling of *Borrelia* prevalence in years following *Apodemus* population peaks -- combined with the increasing frequency of mast years -- represents a One Health dimension of forest rodent ecology that links wildlife population dynamics directly to public health risk. Forest management interventions that reduce rodent peak densities -- including reducing beech monoculture area and increasing tree species diversity to distribute masting events across species -- would simultaneously benefit small mammal community diversity (through structural heterogeneity) and reduce the amplitude of disease risk peaks. Public health communicators should incorporate mast year forecasts -- based on summer temperature patterns -- into Lyme disease and TBE risk warnings to forest users, providing a practical linkage between wildlife ecology knowledge and public health communication.

## 6. Conclusion

### 6.1 Summary

This review of 188 studies on small mammal population ecology in European forests confirms beech masting as the dominant driver of *Apodemus flavicollis* cycles (mean 22-fold amplitude; 2.8-year period), with masting frequency increasing from 2.8 to 2.2 years under recent climate trends. Naturally structured forests support 2.4-fold higher small mammal species richness than intensively managed plantations, with deadwood volume the strongest structural predictor (threshold 15 m<sup>3</sup>/ha for sensitive species). Post-rodent-peak years show 2.4-fold higher tick density and doubling of *Borrelia* prevalence, linking forest rodent dynamics to tick-borne disease public health risk.

### 6.2 Recommendations

Four recommendations follow. First, forest management certification standards (FSC, PEFC) should increase recommended deadwood retention targets to 20-30 m<sup>3</sup>/ha, consistent with the evidence threshold for full small mammal community recovery and with NRL old-growth forest area targets. Second, beech monoculture area should be progressively diversified towards mixed-species stands in NRL forest restoration programmes, reducing masting event amplitude and tick-borne disease risk peaks while improving small mammal guild diversity. Third, forest raptor conservation plans should incorporate mast year forecasts into territory density planning, acknowledging the increased inter-annual prey base variability associated with more frequent masting. Fourth, public health authorities should integrate mast year predictions based on summer temperature patterns into annual Lyme disease and TBE risk communications for forest users.

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### Declarations

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#### Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, modelling, interpretation, or the decision to publish.

#### Data Availability Statement

The systematic review database (188 studies with coding attributes), long-term population dynamics extraction data, SEM model scripts, and all R analysis code are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741832>.

#### Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary field data collection or animal handling was conducted. Ethical approval was not required.

## **Appendix A**

### **Forest Structural Variable Thresholds and Small Mammal Community Assessment Protocol**

This appendix provides the evidence-based forest structural variable thresholds for small mammal community conservation and the minimum field assessment protocol for monitoring small mammal community response to forest management change under NRL restoration programmes.

#### **Part I -- Evidence-Based Forest Structural Thresholds for Small Mammal Conservation**

#### **Part II -- Minimum Monitoring Protocol for NRL Forest Restoration**