forests

MDPI

Review

Microrefugia for Small Mammals in European Forests

Linas Balčiauskas [1,*] and Laima Balčiauskienė [1]

https://doi.org/10.3390/xxxxx

Supplements

Table S1. Search criteria and Boolean logic for retrieving studies on small mammals and forest microrefugia.

Chapter	Search string	N	n
1	("forest microclimate*" OR "forest microrefugia*" OR "sub-canopy temperature" OR "forest buffering") AND ("small mammal*" OR rodent* OR shrew*) AND (Europe OR "temperate forest" OR "boreal forest")	128	17
3.1	("small mammal*" OR rodent* OR shrew*) AND ("microclimate sensitivity" OR "thermal physiology" OR "water balance" OR "operative temperature" OR "vapor pressure deficit") AND ("boreal forest*" OR "temperate forest*" OR Europe)	3240	25
3.1.1.	("small mammal*" OR rodent* OR shrew*) AND ("heat stress" OR "evaporative water loss" OR "vapor pressure deficit" OR "energetic balance" OR "operative temperature") AND ("boreal forest*" OR "temperate forest*" OR Europe)	4660	9
3.1.2.	("small mammal*" OR rodent* OR shrew*) AND ("behavioural thermoregulation" OR torpor OR hibernation OR "sheltering" OR "subnivean zone" OR "snow insulation") AND ("boreal forest*" OR "temperate forest*" OR Europe)	9640	11
3.1.3.	("small mammal*" OR rodent* OR shrew*) AND ("microclimate" OR "thermal refugia") AND (survival OR reproduction OR demography OR dispersal OR movement) AND ("boreal forest*" OR "temperate forest*" OR Europe)	6250	11
3.2.1.	("forest canopy" OR "sub-canopy temperature" OR "thermal buffering") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	3320	13
3.2.2.	("forest litter" OR "coarse woody debris" OR "understory vegetation" OR "microhabitat humidity") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	4320	15
3.2.3.	("forest management" OR "microclimate buffering" OR "biodiversity resilience") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	6900	10
3.3.1.	("tree cavity" OR "coarse woody debris" OR "riparian bank" OR "rock crevice" OR "litter layer" OR "snow refugia") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	3450	13
3.3.2.	("thermal inertia" OR "humidity retention" OR "predator concealment") AND ("small mammal*" OR rodent* OR shrew*)	618	13
3.4.1.	("small mammal*" OR rodent* OR shrew*) AND (summer OR drought OR heatwave) AND ("forest microclimate*" OR "refugia") AND ("boreal forest*" OR "temperate forest*" OR Europe)	4250	6
3.4.2.	("snow depth" OR "subnivean" OR "winter survival" OR "insulation" OR "overwintering") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	13,700	11
4.1.	("operative temperature" OR "microclimate sensor*" OR "thermal model*" OR "biophysical model*") AND ("small mammal*" OR rodent* OR shrew*)	3090	16
4.2.	("microclimate" AND "demography" OR "survival" OR "reproduction") AND ("capture-mark-recapture" OR "occupancy model*" OR "BACI design")	1190	12
4.3.	("bio-logging" OR telemetry OR accelerometer* OR "behavioural monitoring") AND ("microclimate" OR "refugia") AND ("small mammal*" OR rodent* OR shrew*)	2470	10
5.1.	("microclimate model*" OR "downscaling" OR "LiDAR" OR "thermal mapping") AND ("forest" AND "small mammal*" OR rodent* OR shrew*)	3330	8
5.2.	("functional refugia" OR "thermal refugia" OR "hydric refugia") AND ("small mammal*" OR rodent* OR shrew*)	431	3
5.3.	("microclimate model validation") AND ("small mammal*)	5	4*
6.1.	("forest management" OR "coarse woody debris" OR "retention forestry" OR "habitat structure" OR "legacy trees" OR "microhabitat diversity") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	11,200	7

6.2.	("fuel reduction" OR "salvage logging" OR "biomass harvest" OR "biodiversity trade-off*" OR "retention forestry" OR "post-disturbance management") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	1360	11
6.3.1.	("refugia management" OR "deadwood retention" OR "variable retention forestry" OR "riparian buffer*" OR "adaptive silviculture") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	605	11
6.3.2.	("key performance indicator*" OR "biodiversity monitoring" OR "forest indicator species" OR "microclimate buffering metric*" OR "ecosystem resilience indicator*") AND ("small mammal*" OR rodent* OR shrew*) AND ("boreal forest*" OR "temperate forest*" OR Europe)	1	6 *
7	none, existing references analysed		26

* The initial systematic search did not yield sufficient coverage for 5.3 and 6.3.2 subsections, therefore, additional references were identified using the AI-assisted literature triage tool Undermind to complement the manual search. 5.3

Table S2. Eligibility criteria to reduce number of citable sources.

Criterion	Inclusion	Exclusion
Ecosystem type	Forested or partially forested systems	Grasslands, tundra, urban habitats
Focal taxa	Small mammals (rodents, shrews)	Only plants, invertebrates, or microclimate without biotic relevance
Variables	Measured or modelled forest microclimate (T, RH/VPD, snow, soil moisture)	Only macroclimate or non-forested climate data
Scale	Plot to landscape (≤100 m resolution preferred)	Coarse (>1 km) gridded climate surfaces only
Region	Europe (broadly defined)	Non-European data unless in meta-comparison

Table S3. Parameters used for AI-assisted retrieval of studies on small mammals and forest microrefugia using Undermind in chapters with limited initial search results.

Chapter	Undermind parameters for the search
3.1	Studies in boreal forest ecosystems examining relationships between local vapor pressure deficit (measured or modeled microclimate VPD) and small mammals, encompassing any taxa and outcomes (e.g., abundance, behavior, habitat use, physiology), across observational or experimental designs
3.1–3.3	Review-type syntheses on fine-scale microhabitat and microclimatic refugia supporting resilience of European forest vertebrates—with emphasis on small mammals—under combined climate change and land-use/forestry change, covering structural elements (e.g., tree cavities, deadwood, understory/canopy structure, rock features) and microrefugia processes (e.g., cold-air pooling, aspect, topography) across European forest biomes.
3.1.3 & 3.3	Empirical studies on wild rodents and shrews in European forest habitats linking specific microhabitat or refugia features (e.g., structural cover, belowground refugia, microclimate patches) to variation in survival, reproduction, and movement (including dispersal) across seasonal and interannual contexts.
3.2.1–3.2.2	Studies examining how forest canopy density and vertical structure (e.g., LAI, gap fraction, LiDAR-derived complexity) modulate buffering of temperature and humidity extremes at 0–30 cm height across European forests (including leaf-on vs. leaf-off conditions), and how that buffering translates into thermal exposure and activity or occurrence patterns of rodents and shrews.
3.2 & 3.3	Studies assessing how canopy structure, understory density, and detrital layers (litter and coarse woody debris) modify near-ground operative temperature and vapor pressure deficit experienced by small mammals across diel and seasonal cycles, including mechanistic pathways (radiation, wind, humidity) and implications for thermal and hydration risk in surface and within-litter or woody microhabitats.
3.4	Studies examining how summer heat and drought interact with winter and subnivean conditions to influence small mammals in boreal forests.
4	Methodological best practices for temperate forest small mammals (rodents and shrews) to measure operative thermal environments and link microclimate exposure to demography, including sensor selection, placement, and shielding; standardized reporting metrics (ΔT at organism height, VPD safe-hours, shelter thermal inertia); QA/QC and data archiving; study designs (BACI, paired refugia vs. non-refugia, manipulative retention); monitoring approaches (CMR, occupancy, survival, reproduction); analytical methods linking exposure time to vital rates (time-varying covariates, joint models); and use of animal-borne sensors (temperature, accelerometry, GPS/VHF) for behavioral validation with ethical and sample-size guidance.
5.1–5.3	Studies on mapping and modeling small-mammal climate refugia in European boreal forests by downscaling climate to organism height using LiDAR-informed canopy and understory structure and hydrologic modifiers; incorporating relevant microclimate and biophysical variables; defining refugia using species-specific safe-hours or exposure thresholds and shelter availability indices; and validating predictions with independent telemetry and capture datasets.
6	Europe-wide forest management, silviculture, and landscape design approaches for creating and maintaining small-mammal refugia, including quantitative operational targets (deadwood volume and attributes, retention patch size and density, riparian buffers), documented trade-offs with fuel reduction and timber production within decision frameworks, and examples of adaptive monitoring KPIs.

Table S4. Context-dependent magnitudes or typical ranges of near-ground microclimate buffering reported across forest types, structures, seasons, and regions. Values are synthesized from the cited literature and presented as conditional, context-dependent ranges rather than fixed targets. The evidence source is indicated where relevant. Reported values reflect the differences in conditions between forests and open or edge-influenced areas. These values vary depending on canopy structure, soil moisture, season, and measurement height.

Forest context (evidence source) [1]	Structural feature	Metric	Indicative magnitude	Season	Notes	References
Mediterranean (EU-emp)	Closed, continuous canopy	Near-ground air temperature (ΔT)	~2–4 °C average reduction in summer maximum temperatures under dense canopy	Summer	Event-based extremes and surface temperatures may show larger local offsets; heatwave-specific near-ground air temperature data remain scarce	[110,131]
Temperate (EU-emp)	Dense canopy cover	Near-ground air temperature (ΔT)	~2–4 °C average summer buffering; locally stronger cooling during hot, high-radiation periods	Summer	Magnitude increases nonlinearly with canopy closure; extreme-event maxima are poorly constrained	[45,109,131]
Temperate (EU-emp)	High canopy cover + moist soils	Understory maximum temperature	~1–3 °C buffering on average, increasing with soil moisture and canopy closure	Summer	Soil moisture strongly modulates buffering; disentangling canopy vs hydrology remains challenging	[45]
Boreal (EU-emp)	Closed canopy	Near-ground air temperature (ΔT)	~1–4 °C typical summer buffering; substantial local variation	Summer & shoulder seasons	Near-ground (<15 cm) and microhabitat measurements remain sparse; winter and subnivean effects better documented than summer extremes	[63,111,131]
Forest vs. open (MR-emp)	Dense canopy	Vapor pressure deficit (VPD)	Consistent reduction relative to open sites; strongest under dry, high-radiation conditions	Summer	Quantitative VPD offsets vary with wind and soil moisture; European near-ground VPD data limited	[63,109,111]
Managed (MR-syn)	Coarse woody debris (CWD)	Microhabitat thermal stability	Structural proxy: ~30–50 m^3 ha^{-1} commonly associated with increased microhabitat buffering	Year-round	Threshold derived from synthesis; direct European microhabitat temperature data inside CWD are scarce	[18,117]
Managed (MR-syn)	Retention patches	Canopy & microhabitat buffering	Structural proxy: ~10–20 % basal area retention frequently linked to buffering functions	Year-round	Effects depend on spatial configuration and surrounding matrix; few direct microclimate measurements	[18,117]
Riparian (MR-emp)	Unharvested buffers	Near-ground microclimate	Partial buffering typically observed at ≥30 m buffer width; outcomes variable	Summer	Effectiveness depends on stream size, aspect, and matrix; not all buffers achieve interior conditions	[61,117]
Riparian (MR-syn)	Unharvested buffers	Interior-like microclimate conditions	Interior-equivalent conditions require wider buffers (≈ ≥50 m)	Summer	Limited Europe-specific microclimate validation; guidance precautionary	[61,131]

[1] EU-emp, Europe-specific empirical evidence; MR-emp, mixed-region empirical evidence; MR-syn, mixed-region synthesis.

Table S5. Operationalization of organism-relevant microclimate metrics for small mammals.

Component	Operational definition	Implementation guidance	Key references
Sensor placement and preprocessing	Near-ground microclimate measured at biologically relevant height for small mammals	Deploy sensors at 0–10 cm above or below ground (litter, CWD, burrows). Sensors must be radiation-shielded and ventilated; unshielded sensors can overestimate temperature by >25 °C under direct radiation. Record at hourly or finer resolution; apply quality control to remove spikes, burial, or flooding artifacts.	[19, 91, 92]
Operative temperature (T_e)	Integrated thermal environment experienced by an organism	Where physical models are unavailable, near-ground air temperature at organism height may be used as a proxy for comparative analyses. T_e integrates radiative, convective, and conductive heat exchange and is more biologically meaningful than ambient air temperature.	[19, 20, 90]
Temperature offset (ΔT)	Difference between organism-scale and reference temperature	$\Delta T = T_{\text{organism height}} - T_{\text{reference}}$, where $T_{\text{reference}}$ is typically measured at 1.5–2 m height or derived from macroclimate grids. ΔT quantifies local microclimate buffering or amplification.	[43, 47, 52]
VPD safe-hours (definition)	Duration for which vapor pressure deficit at organism height remains below a dehydration-risk threshold	Compute as the number of hourly observations where VPD < threshold within a defined time window. Thresholds must be explicitly stated and justified.	[14, 19, 25]
VPD threshold selection	Physiologically or ecologically justified VPD limit	Thresholds may be defined at the species level (laboratory dehydration limits), functional guild level (e.g., insectivores vs. rodents), or inferred from field-based occupancy or activity patterns along moisture gradients when physiological data are unavailable.	[22, 24, 25]
Temporal aggregation of VPD safe-hours	Method for summarizing exposure through time	Cumulative safe-hours reflect chronic hydric stress (demographic or seasonal inference). Consecutive safe-hours reflect acute stress exposure (behavioral constraints). Hourly resolution is suited to behavior; daily or seasonal aggregation is suited to demographic analyses.	[25, 27, 96]
Thermal inertia of microhabitats	Resistance of a microhabitat to temperature change	Approximated as dampening of diel temperature amplitude or lag between external and internal temperature peaks. High thermal inertia indicates strong buffering (e.g., litter, coarse woody debris, soil, subnivean spaces).	[53, 56, 57]
Implementation frameworks	Standardized computation and reporting	Frameworks such as myClim automate calculation of ΔT, VPD safe-hours, and related metrics from time-series data. Studies should report sensor height, shielding, temporal resolution, thresholds, and aggregation choices to ensure reproducibility.	[47, 96]