

Nationwide deadwood mapping reveals rising mountain forests vulnerability

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ABSTRACT

Forest mortality is increasing globally under climate change, making detailed, large-scale monitoring essential for understanding ecosystem responses and guiding adaptive forest management. Here, we present a spatio-temporal assessment of standing deadwood in Switzerland from 2018 to 2023, derived from centimeter-scale high-resolution aerial imagery. We reveal a consistent upslope concentration of standing deadwood, with highest shares occurring around mid to high elevations (~1,500 m), despite declining forest cover, and relative increases of up to 43% in overlapping survey areas following the 2018 drought. Maximum temperature anomalies and conifer dominance were the strongest predictors of standing deadwood. The consistent accumulation of standing deadwood at higher elevations suggests increasing vulnerability of mountain forests, with implications for carbon storage, biodiversity, and disturbance susceptibility under ongoing climate change. These patterns highlight the need to address rising forest mortality as a key component of climate-adaptive forest management. Furthermore, our results demonstrate the potential of high-resolution remote sensing for large-scale forest mortality monitoring. Our methods offer a reproducible and transferable framework for identifying vulnerability hotspots and supporting climate-adapted forest management.

1. Introduction

The increase in frequency and intensity of heatwaves (IPCC, 2023a) and droughts (Vicente-Serrano et al., 2020; Chen et al., 2025; Hao et al., 2018) is leading to an acceleration in global trends of forest mortality (Allen et al., 2015; Hartmann et al., 2022). In Europe alone, drought caused an estimated 500,000 ha of excess forest mortality in recent years (Senf et al., 2020). The extreme drought of 2018 had particularly severe impacts, affecting approximately 11,200 km² of forested area across Europe (Schuldt et al., 2020). Mortality impacts forest ecosystem functions, e.g., habitat provision, carbon storage, and water cycling, and thus also disrupts the wide range of ecosystem services that provide economic, ecological, cultural, and social benefits. Such services include timber production, carbon sequestration (Thürig and Kaufmann, 2010; Jandl et al., 2013), water provisioning (Winter et al., 2025), recreational and cultural value (de Groot et al., 2002; Häyhä et al., 2015), as well as

considerable potential for climate change mitigation and adaptation (IPCC, 2023b, 2023c). As climate extremes intensify, addressing forest mortality will be critical for sustaining ecosystem functions and the services they provide.

While our understanding of the drivers of tree mortality is still limited (Schweingruber and Wirth, 2009; Ammer et al., 2018), forest mortality often results from the interaction of multiple contributors, rather than from a single stressor (Franklin et al., 1987). Climatic stressors such as drought, elevated temperatures, and increased variability in precipitation have been associated with increased forest mortality rates (Hammond et al., 2022; Jääskeläinen et al., 2025; Neumann et al., 2017; Senf et al., 2020). Furthermore, these climatic stressors can also predispose tree species to other mortality agents such as bark beetle infestations (Hlásny et al., 2021; Schwarz et al., 2025). Forest composition modulates mortality responses, with drought- and heat-related mortality affecting both coniferous (e.g. Norway spruce,

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Scots pine) and deciduous forests (e.g. European beech), depending on species traits and disturbance interactions (Beloiu et al., 2022; Schuldt et al., 2020). However, studies investigating the physiology of tree mortality often cover limited sample sizes of tree species and environmental conditions (Mitchell et al., 2013). Switzerland provides a fitting example, with mortality tracked in 197 plots across Switzerland over 60 years (Hülsmann et al., 2018), and in 276 Swiss plots for more than a

century (Etzold et al., 2019). While these assessments can provide a valuable understanding of physiology and forest dynamics, the data are scarce and have coarse resolution. Studies over larger areas are usually based on standardized inventory data such as the ICP Forests network (Eichhorn and Roskams, 2013), which provides long-term but coarse and low-resolution data. Such existing monitoring networks are not suited to detect damage over continuous areas (Schuldt et al., 2020), and

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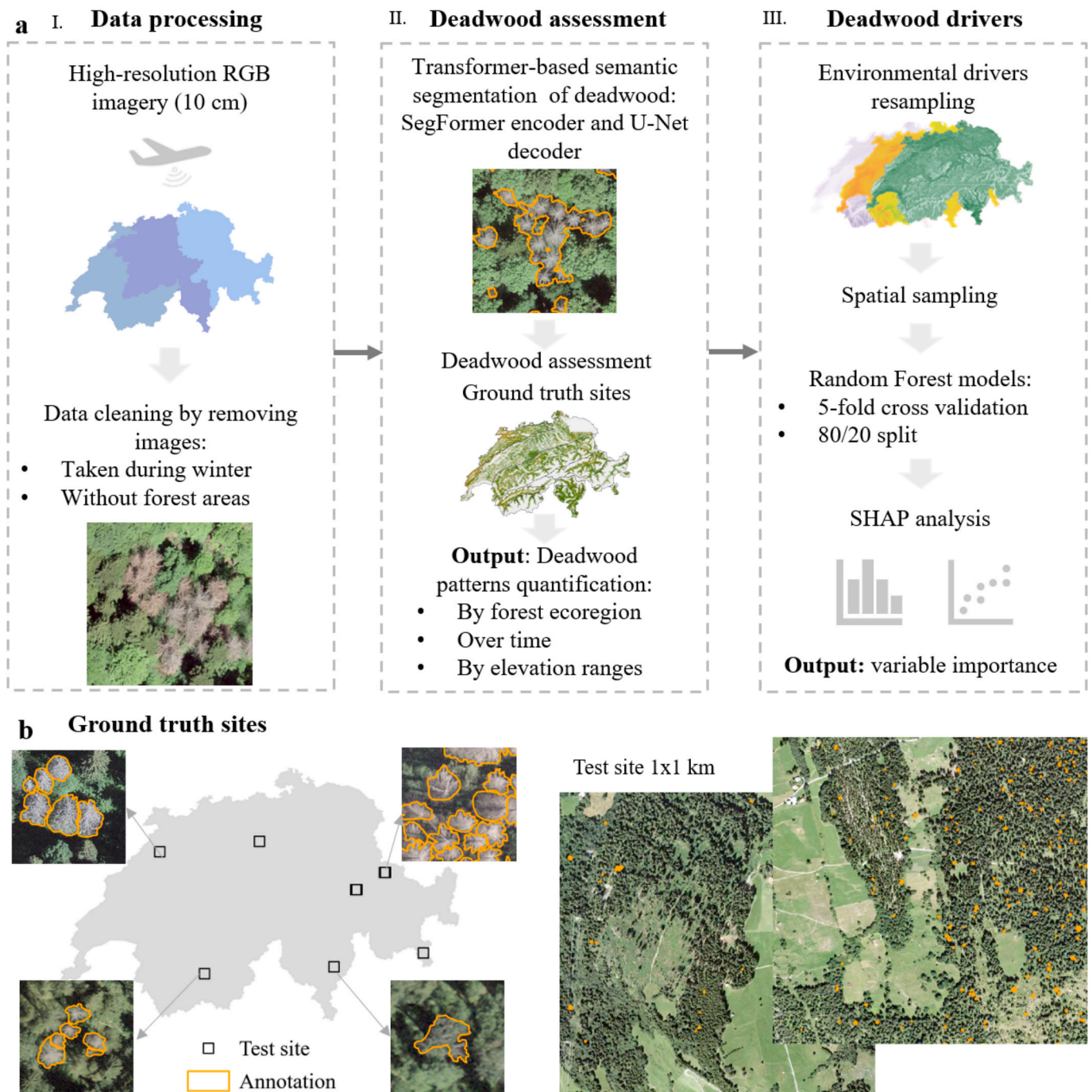


Fig. 1. A Workflow depicting the three steps of data processing, deadwood assessment, and deadwood drivers' quantification. **b** Location of the nine selected test orthophotos, examples of manual labels in four sample sites, and overview of two full, 1 km², test sites. In each panel, the orange shapes represent the manually delineated dead trees.

can lead to an underestimation of forest mortality (Cheng et al., 2024; Schiefer et al., 2024).

To improve our understanding of mortality patterns and processes, we need spatially extensive mortality observations. However, systematic assessments and databases of forest health are scarce and challenging to obtain (Trumbore et al., 2015), especially spatially explicit data of observed mortality at the national level at high spatiotemporal resolution. In recent years, the adoption of remote sensing techniques in the field of ecology has accelerated, thanks to the increasing availability of data, artificial intelligence methods, and open-source, efficient software (Senf, 2022). The increasing availability of pre-processed, analysis-ready data (Dwyer et al., 2018; Frantz, 2019) allows for performing analysis over large areas with increasing temporal resolution. Large-scale assessments of forest mortality can be carried out with satellite observations (Campbell et al., 2020; Mosig et al., 2026a; Schiefer et al., 2023); however, they often rely on medium or coarse spatial resolution data, such as Sentinel-2 (10 m), Landsat (30 m), or MODIS (250 m). This does not enable the identification of mortality at the scale of individual trees, and can compromise the inferences on the underlying physiological processes (Hartmann et al., 2018). Recent studies highlight the potential of combining high-resolution remote sensing data, such as airborne and UAV imagery, with supervised deep learning to map standing deadwood (Cheng et al., 2024; Mosig et al., 2026; Schiefer et al., 2023). Deep learning and active-contour approaches have also been applied for instance segmentation of standing dead trees and fallen stems from aerial imagery (Polewski et al., 2024, 2021; Sani-Mohammed et al., 2022). However, despite the growing number of studies, spatially continuous assessments of forest mortality are lacking in most countries, including Switzerland. Improving the understanding of tree mortality requires large amounts of wall-to-wall data, covering wide gradients of climatic and environmental conditions, to allow the attribution of forest declines to human, climatic, and biotic drivers (Trumbore et al., 2015).

In this study, we utilize a globally calibrated semantic segmentation model (Möhrling et al., 2025) to identify standing deadwood in high-resolution aerial images (10–25 cm) throughout Switzerland and evaluate the biotic and abiotic factors contributing to tree mortality. Based on wall-to-wall aerial images from 2018 to 2023, we produced multi-year maps depicting standing deadwood, computed yearly percentages of deadwood in forested areas, and pinpointed spatial hotspots of tree mortality. Across the main Swiss forest ecoregions, standing deadwood accounted for 0.20–0.83% of forest cover, corresponding to 107–1,389 ha. Analyses within forest reserves further revealed how climatic, biotic, and abiotic conditions shape mortality in unmanaged forests. Together, these results provide the first nationwide, spatially explicit assessment of standing deadwood in Switzerland, demonstrating how high-resolution aerial imagery can be leveraged to track forest mortality and its drivers under ongoing climate change.

2. Methods

The overall workflow of the study is illustrated in Fig. 1a and consists of three main steps. Step I involves the data processing and cleaning. Step II focuses on the deadwood assessment. Step III covers the analysis of deadwood drivers. The study was carried out over the entire Switzerland. Within the study area, the elevation ranges from 193 to 4,628 m a.s.l., and the climate is temperate at low elevations, with areas in the cold and polar Köppen-Geiger climate classes at the highest elevations (Beck et al., 2018). Forests cover about 32 percent of Switzerland's land area, and canopy composition is dominated by Norway spruce (*Picea abies*, ~38%), European beech (*Fagus sylvatica*, ~18%), and silver fir (*Abies alba*, ~12%), which together contribute roughly 70% of canopy cover (NFI, n.d.).

2.1. Data

The aerial image dataset consists of RGB orthophotos from the SWISSIMAGE product, covering all of Switzerland with a ground resolution of 10 cm over plain areas and 25 cm over the Alps, provided by the Federal Office of Topography swisstopo (© swisstopo, n.d). The dataset is updated on a 3-year cycle, with yearly flights covering approximately one third of Switzerland (Fig. S1a). In this study, we used 86,774 images acquired between 2018 and 2023, to have two full cycles that allowed us to cover the entire Switzerland. Each orthophoto can be easily identified by the year and 8-digit ID included in the filename and based on the coordinates of the bottom left corner of the image. Because the orthophotos themselves do not have an explicit acquisition date, we determined the date of each image by checking its spatial overlap with the corresponding digital image strip footprints (© swisstopo, n.d). Each footprint represents the area covered by the acquisition flight and the corresponding date.

Forested areas in Switzerland have been determined based on the Forest Type NFI 2018 dataset (Waser and Ginzler, 2021), at a 10 m spatial resolution and canopy height > 5 m (Waser et al., 2017). The dataset represents the probability of broadleaf forest (0–100%). In this study, we used this dataset primarily to establish a baseline of vegetation areas taller than 5 m. Subsequently, we removed woodland patches smaller than 0.5 ha (FAO, 2020) to further refine our forest mask using ArcGIS. We grouped contiguous forest pixels and filtering patches by area by applying the functions “Region Group” and “Zonal Geometry”. The final forest mask includes all vegetation areas with canopy height > 5 m and areas > 0.5 ha.

The swissALTI3D digital terrain model (DTM) from swisstopo (© swisstopo, n.d) was used to determine the altitude of the RGB orthophotos in data cleaning. The DTM uses 0.5 m spatial resolution LiDAR data for areas below 2000 m a.s.l. and stereo-image-correlation for higher altitudes, with a spatial resolution of 2 m.

Orthophotos are acquired between March and November and thus show both leaf-on and leaf-off conditions. To distinguish standing dead trees from leafless deciduous trees, we defined the leaf-on period as April 1st to September 30th annually. We selected images based on strip footprint dates, forest presence by the forest mask, and visual checks. We excluded images not intersecting with the forest mask or overlapping leaf-off period strips. Images overlapping leaf-on period strips were kept. We flagged images overlapping strips with conflicting dates (leaf-on and leaf-off) as their exact acquisition date was indeterminable. Additionally, images from April to May were assessed due to delayed leaf-out in mountainous deciduous trees, affecting canopy coverage early in the season. Overall, we assessed 15,704 images across the six years to compose the dataset. Table S1 shows the number of images removed during data cleaning and the reasons for their removal. The data cleaning process resulted in a total of 44,129 orthophotos between the years 2018–2023 (Fig. S1b-c).

2.2. The semantic segmentation model

In this study, we applied a transformer-based semantic segmentation model to detect standing deadwood from aerial images across a wide range of resolutions (Möhrling et al., 2025). The model was trained on 434 drone images of varying spatial resolutions obtained from the deadtrees.earth (Mosig et al., 2026). The model architecture consists of a SegFormer encoder and a U-Net decoder. As input, it takes RGB image tiles and outputs masks, converted to a probability distribution by applying a sigmoid layer. To obtain binary masks of presence/absence of standing deadwood, the model classifies pixels with probability $p > 0.5$ as standing deadwood. A comprehensive description of the model's architecture, hyperparameters, and performance is available at Möhrling et al., (2025). We assessed standing deadwood in Switzerland by applying the segmentation model to the entirely cleaned aerial orthophoto dataset and filtered the results with our forest mask to retain

predictions within forested areas.

To independently assess the performance of the semantic segmentation model on Swiss aerial imagery, we employed tree mortality datasets that include 48,368 delineated tree crowns (Berger, 2024). Their crowns were primarily identified using RGB orthophotos and subsequently matched to corresponding RGBI images acquired simultaneously during the same aerial flights. The trees in the dataset are categorized into four health classes. For our purposes, we extracted the 15,587 trees classified as dead. Since the validation process requires fully labeled images for a reliable calculation of performance metrics, we complemented this dataset by manually delineating 1,497 additional dead trees. Finally, we selected a subset of 2,366 dead trees for model validation. These trees appear in nine aerial 10 cm orthophotos that cover 9 km² of fully labeled forest area across all the forest ecoregions included in this study (Fig. 1b).

We validated our approach by applying the segmentation model to selected subsets of aerial orthophotos, which resulted in the generation of relevant segmentation masks. Subsequently, we utilized the tree mortality reference data to generate equivalent binary masks. We then applied the forest mask to both the model outputs and the reference masks to ensure that performance metrics were assessed exclusively within forested areas. Although the model identifies standing deadwood throughout the entire orthophotos, the reference labels are restricted to forest areas. Consequently, this masking step was essential for calculating comparable performance metrics. In the end, we assessed the filtered masks by computing Precision, Recall, and F1-score (Table S2).

As described above, the segmentation model classifies deadwood pixels with probability $p > 0.5$. The initial training of the model does not optimize such a threshold. However, since the results of all subsequent analyses depend on the deadwood segmentation output, we carried out a sensitivity analysis to evaluate how sensitive the model is to the probability threshold used for deadwood classification. We performed the analysis using the previously described tree mortality reference data, which covers nine fully labelled orthophotos over 9 km² of forest, validating the model outputs produced by varying the threshold from 0.1 to 0.9 (Table S3). Since the F1 score varied by only approximately 0.002 relative to the default threshold, we retained the default probability threshold of 0.5 for the semantic segmentation model.

2.3. Swiss forest ecoregions and forest reserves

We assessed standing deadwood in seven main Swiss forest ecoregions, dividing Switzerland into units based on climate, forest vegetation, and altitude (FOEN, F.O. of the E., 2019). Lowland and low mountain environments are represented by the Swiss Central Plateau (mean elevation 572 m a.s.l., ranging from 244 m to 1,548 m a.s.l.) and the Jura (803 m a.s.l., from 266 to 1,679 m a.s.l.), while the remaining regions span the Alps from montane to alpine conditions, including the Southern Pre-Alps (1,124 m a.s.l., from 193 m to 2,951 m a.s.l.), the Northern Intermediate Alps (1,755 m a.s.l., from 435 m to 3,929 m a.s.l.), the Southern Intermediate Alps (1,936 m a.s.l., from 311 m to 3,898 m a.s.l.), and the Continental Alps (2,426 m a.s.l., from 992 m to 4,628 m a.s.l.), capturing strong climatic and forest structural gradients across the country. The Northern Intermediate Alps, initially divided by beech presence, were merged and renamed. Similarly, the Southern Pre-Alps categories were combined into “Southern Alps”. Lastly, Mendrisiotto was merged into the Southern Pre-Alps due to its small size and limited data, only available from 2018 swisstopo orthophotos.

For the identification of the main predictors of standing deadwood in Switzerland in forest reserves and unmanaged areas, we used the forest reserves dataset (BAFU, B. für U.B. | O., 2022). These 2,564 units cover 7.3% of the Swiss forests and identify areas where no management takes place, as well as areas where targeted action is taken to promote endangered species. The spatial distribution of the forest ecoregions and the location of the forest reserves is shown in Fig. S3.

2.4. Deadwood drivers

To identify the drivers of deadwood we fitted regression models using the shares of standing deadwood per pixel in the previously described forest reserves areas as a response variable. Since standing deadwood was originally segmented at 10 cm on the image orthophotos, we aggregated the data to a 10 m grid to match the resolution of the forest mask applied to filter standing deadwood within forested areas. For each available forest reserve, we extracted the corresponding deadwood pixels for every available year between 2018 and 2023. Due to repeated aerial surveys in swisstopo's 3-year cycle, standing deadwood in several forest reserves was quantified twice with a 3-year interval. To prevent duplication and ensure unique representation per pixel, only the first deadwood occurrence for each reserve was retained, focusing on post-drought conditions of 2018.

As predictor variables we considered both abiotic and biotic factors. Detailed information on their spatial resolution is available in Table S4. Elevation, from the swissALTI3D DEM, was included to represent site topographic conditions. To represent edaphic site conditions, we included the Topographic Wetness Index (Sørensen et al., 2006), available water content (Meusbürger et al., 2022), as well as the proportions of sand, clay, and organic carbon (Baltensweiler et al., 2021). Biotic variables include the probability of broadleaf, (Forest Type NFI (2018)), canopy height, (vegetation height model NFI (Ginzler, 2021)), and basal area (unpublished Swiss NFI data based on the vegetation height model NFI). For consistency, the environmental predictors were also resampled to the same 10 m grid, ensuring that all variables were aligned to a common spatial framework.

Additionally, we included precipitation, mean, minimum, and maximum temperature (Table S5), provided by the Land Change Science Group, WSL. Daily observations from all available weather stations of the Federal Office of Meteorology and Climatology MeteoSwiss have been interpolated (Thornton et al., 1997) at 100 m spatial resolution. Furthermore, we used precipitation, minimum, mean, and maximum temperature to calculate the corresponding climatic water balance (Hargreaves and Samani, 1985). From these data, we derived yearly standardized anomalies of minimum and maximum temperature, as well as precipitation and climatic water balance, relative to the norm of 1981–2010:

$$\text{Standardized anomaly}_i = \frac{X_i - \mu_{1981-2010}}{SD_{1981-2010}}$$

Where i is the reference year, X_i the mean for the reference year, and $\mu_{1981-2010}$ and $SD_{1981-2010}$ the mean and standard deviation for the 1981–2010 period, respectively.

For each deadwood pixel, anomalies were computed for the year of deadwood occurrence, as well as the preceding five years, as climate extremes can show delayed effects on tree mortality (Klap et al., 2000; Knapp et al., 2024). Anomalies are reported in Fig. 4a, and from Fig. S4 to Fig. S7. To avoid multicollinearity among the predictors, we excluded the variables with Pearson correlation higher than 0.8 (Table S6).

We first quantified spatial dependence in the response variable to obtain a minimum deadwood sampling distance to avoid spatial autocorrelation by computing an empirical variogram of standing deadwood with the Matheron estimator (Matheron, 1962), and fitting a Gaussian (Chilès and Delfiner, 2012) theoretical variogram model, whose characteristic inflection and steeper rise near the origin capture the expected short-range continuity within forest reserves and the rapid loss of similarity across larger gaps between different forest reserves. The model estimated deadwood values become uncorrelated beyond a spatial range shown in Fig. S8. Both empirical and fitted variograms indicated 95% of the sill was reached at 50 m. The operation was conducted in Python using the SciKit GStat package (Mälicke et al., 2021).

However, to ensure spatial independence between sampled observations relative to the 100 m climate grid, we set a range of 142 m (the

diagonal of a 100 m squared cell) to ensure that no more than one sampled pixel fell within a single grid cell of the climatic predictors. This distance avoids pseudoreplication of predictor values, while also exceeding the distance required to minimize spatial autocorrelation. We then sampled pixels from ten mortality strata to preserve the overall distribution. Pixels were drawn within each stratum using a Generalized Random Tessellation Stratified (Stevens and Olsen, 2004). If a stratum's tessellation failed, we used a random sampling as a fallback. Last, we applied an iterative filter using a KD-tree algorithm (Maneewongvatana and Mount, 1999) that enforces a minimum spacing of 142 m while prioritizing points from higher mortality strata, resulting in a final dataset of 24,113 pixels. The resulting sampled deadwood distribution at the 10 m scale is shown in Fig. S9, which reports the full dataset and the dataset split by forest ecoregion. The distribution of the other environmental predictors is presented in the same format in the subsequent figures, from Fig. S10 to Fig. S18.

2.5. The random forest models

We compared regression models from different model families to assess whether performance was primarily dependent on the choice of modelling approach. We tested random forest regressions (Breiman, 2001), extreme gradient boosting regressors (XGBoost) (Chen and Guestrin, 2016), generalized linear models (GLMs) (Nelder and Wedderburn, 1972) with a Tweedie distribution, and spatial error regression models (Arraiz et al., 2010). Details on model architectures, hyperparameter tuning, and comparative performance are provided in Table S7–S10.

Among the tested approaches, including random forests, XGBoost, Tweedie GLMs, and spatial error regression models, random forests achieved the best performance and were therefore retained for the main analysis of deadwood drivers. The spatial error models verified spatial dependence, but they did not improve model performance; therefore, we retained non-spatial random forests for the subsequent analyses. We fitted eight random forest regression models: one on the full dataset, and one for each Swiss forest ecoregion. We applied an 80/20 train-test split of each dataset, and we optimized the hyperparameters of each random forest through a 5-fold cross validated grid search on the training dataset. The grid search found the optimal number of trees (100, 300, 600, 1000) and the minimum leaf size (1, 3, 5, 10, 15, 20, 30, 50) to minimize the root mean squared error.

Upon identification of the optimal parameters, each random forest model has been fitted on each corresponding full training dataset with a minimum squared error criterion. Since the deadwood distribution is heavily right-skewed (Fig. S9), for each ecoregion we applied a train-test split based on an adaptive stratification. We binned the response variables into up to 10 quantile-based bins, defined to guarantee that each bin contained at least two data points, one for the training and one for the test dataset. Since sample sizes varied substantially among forest ecoregions, we performed a leave-one-ecoregion-out sensitivity analysis to assess whether the full-dataset model was disproportionately influenced by data-rich ecoregions. We iteratively excluded each ecoregion from the training dataset and fitted a random forest model on the remaining data using the same modelling workflow as for the full-dataset model. We then compared the performance of each leave-one-ecoregion-out model with that of the full-dataset model to evaluate how sensitive model performance was to the removal of individual ecoregions. The hyperparameters and performance of the random forest models are reported in Table S9, the results of the sensitivity analysis in Table S11.

We determined the main environmental drivers of standing deadwood by computing SHAP (SHapley Additive exPlanations) (Lundberg and Lee, 2017) values for each random forest model. SHAP values quantify the marginal contribution of each predictor to the model's output for individual observations, allowing an interpretation of each predictor's influence. As a complementary interpretation, we

additionally calculated permutation importance for each model. This quantifies error increase after permuting a single variable expressed as the change in root mean squared error (Δ RMSE). Each variable was permuted 100 times per model, and the permutation importance was averaged. The random forest models and the computation of the permutation importance values were implemented in Python, using the Scikit-learn package (Pedregosa et al., 2011), while the SHAP values were computed using the SHAP package (Lundberg et al., 2020).

3. Results

3.1. Uneven distribution of standing deadwood across Swiss forests

We mapped a cumulative total of 4,434 ha (0.47%) of standing deadwood out of 940,131 ha of monitored forested area across Switzerland. The quantification was based on the most recent annual observation available for each location, providing a spatially continuous assessment of standing deadwood despite differences in acquisition year across regions (Fig. S1f). The highest standing deadwood was identified in the northern and central parts of Switzerland, while the lowest was in the southern part. The Jura region, characterized by low mountains (803 m mean elevation), contained the highest amount (1,389 ha; 0.83% of forest area), followed by the Northern Pre-Alps (1,048 ha; 0.43%), while the Continental Alps record the lowest values (107 ha; 0.20%) (Fig. 2a–b, Table S12).

Cumulative deadwood also varied across Swiss cantons (Fig. 2c). The highest proportions were found in the Jura (1.21%), Vaud (0.86%), and Schaffhausen (0.79%), while the lowest proportions were observed in Zug (0.3%), Uri, and Nidwalden (both at 0.29%). The amount of standing deadwood detected in each ecoregion and canton is strongly constrained by the extent of forest captured in the available leaf-on aerial images. Coverage varies across years and regions (Fig. S1f), ranging from only 0.2% of the forest in the Continental Alps (2018/2021) to 87% in the Southern Pre-Alps (2018) (Table S13, Table S14).

Yearly shares of standing deadwood per ecoregion ranged between 0.14% and 1.13% (Fig. 2d, Table S13). The highest values were observed in the Jura, reaching 1.13% in 2020 and 1.03% in 2023, followed by the Swiss Central Plateau with 1.10% in 2020 and 0.51–0.58% in 2019 and 2022–2023. The Northern Pre-Alps showed rates from 0.24% in 2018 to 0.57% in 2023, while the Northern Intermediate Alps ranged from 0.20% in 2018 to 0.68% in 2020. When aggregating across all regions surveyed per year (Fig. S1a–c), yearly totals of standing deadwood ranged from 751 to 1,313 ha between 2018 and 2023, corresponding to 0.25% to 0.65% of the mapped forest area (Table S15).

3.2. Standing deadwood increases over time and peaks at higher elevations

Across the overlapping survey areas, deadwood was mapped independently in each set of high-resolution aerial images, yielding paired estimates for the first and second survey years within each observation cycle (Fig. 3a, Table S16). Within these shared observation zones, the second survey consistently showed a larger deadwood extent than the first. For Switzerland as a whole, the mapped deadwood area was 514 and 733 ha in the 2018–2021 pair (+42.7%), 590 and 629 ha in the 2019–2022 pair (+6.5%), and 347 and 452 ha in the 2020–2023 pair (+30.4%). In protected areas, the corresponding paired values were 44 and 61 ha (+40.2%), 70 and 87 ha (+24.4%), and 20.9 and 21.3 ha (+1.8%).

Along the elevation gradient, deadwood percentage across the overlapping survey areas peaked at 1550 m a.s.l., despite declining forest area (Fig. 3b). In these shared observation zones, largely located in the Alpine regions, deadwood area increased upslope and reached its maximum at 1400–1600 m a.s.l., whereas forest area peaked earlier (~1100–1300 m a.s.l.). The peak in deadwood percentage was dominated by the deadwood shares in 2023. In previous years the deadwood

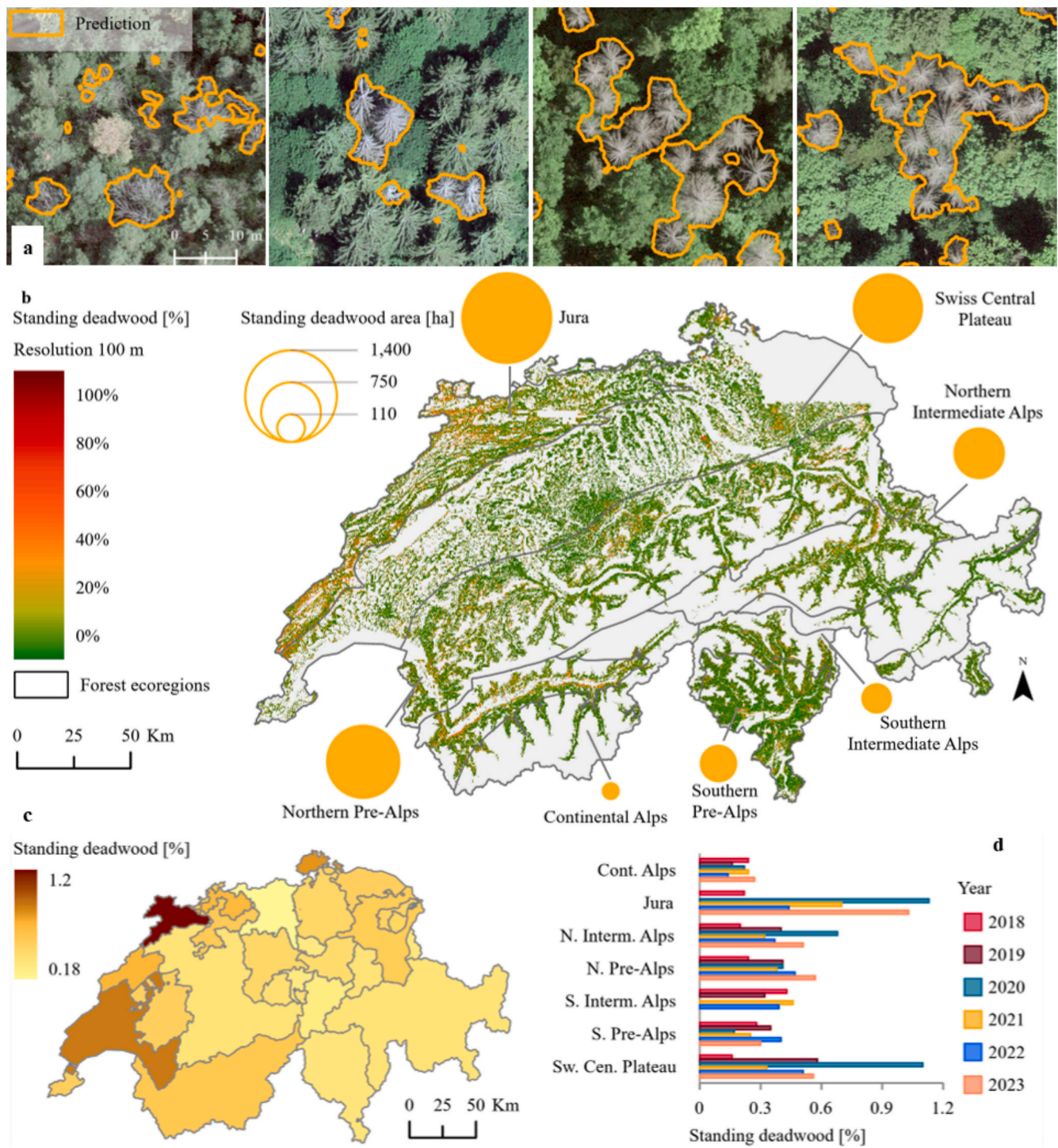


Fig. 2. Standing deadwood segmentation, mapping, and summary statistics across Swiss forest ecoregions and Cantons (2018 – 2023). **a** Examples of dead trees segmentation. In each panel, the orange shapes represent the standing deadwood predictions of the segmentation model. **b** Composite map of standing deadwood from 2018 to 2023 for the main forest ecoregions in Switzerland. The segmentation outputs have been aggregated at 100 m spatial resolution for visualization purposes. The fraction of standing deadwood has been calculated as the ratio between the deadwood area, and the forest area in each pixel. For each location, the most recent annual share of deadwood is displayed, ensuring continuous spatial coverage despite regional differences in acquisition year. The orange circles denote the total area of standing deadwood per ecoregion from 2018 to 2023. **c** Share of cumulative deadwood at the cantonal level, relative to the cantonal forest area. **d** Histogram of share of standing deadwood in forested areas per ecoregion, per year.

percentages peaked between 1450 and 1650 m a.s.l. across most survey years, with only a few years showing maximum at lower elevations (Fig. S19a). Across the slope gradient, the deadwood peaked at 55°, after which it decreased. Deadwood and forest area showed largely similar distributions, both concentrated on mid-slopes of 35° (Fig. 3c). All

patterns refer to the cumulative deadwood for the exact spatial overlap of the six survey years (2018–2023).

Along the elevation gradient, standing deadwood share across the non-overlapping survey areas also peaked at ~ 1,550 m a.s.l., despite declining forest area at higher elevations (Fig. 3b). Forest area

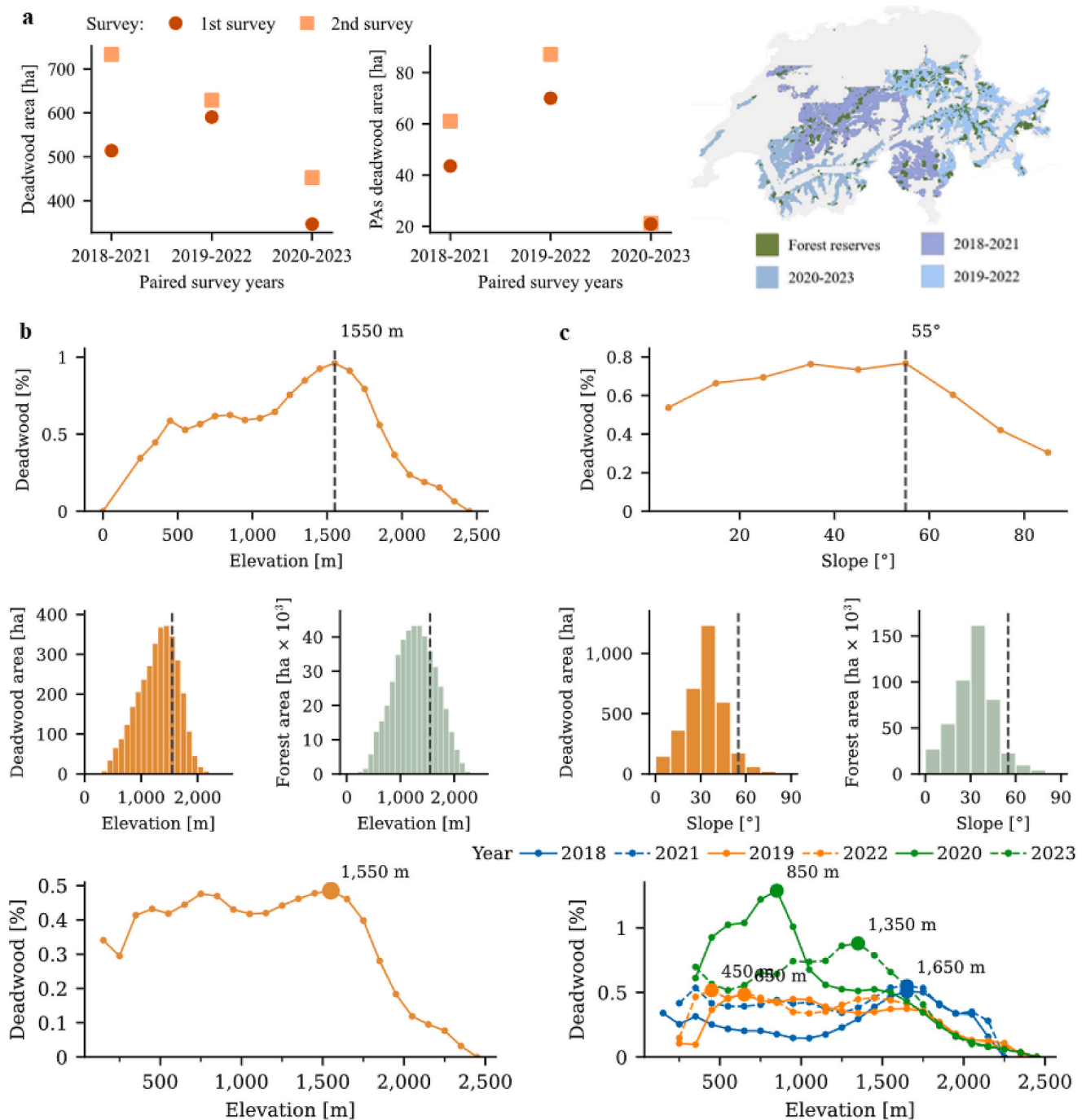


Fig. 3. Standing deadwood patterns across repeated surveys and topographic gradients. **a** Standing deadwood mapped in paired survey years for the 2018–2021, 2019–2022, and 2020–2023 acquisition cycles for the overlapping forest areas and for protected areas, together with the map of the shared survey region. **b** Percentage of deadwood per elevation class for the overlapping forest areas, deadwood and forest area distributions along elevation gradients, and overall percentage of deadwood per elevation class aggregated across 2018–2023 over the entire study area. **c** Percentage of deadwood per slope class, deadwood and forest area distributions along slope gradients, and yearly percentage of deadwood per elevation class over the entire study area (solid lines: 2018–2020; dashed lines: 2021–2023, paired by color).

consistently peaked at lower elevations (~550–1,150 m a.s.l.) and declined sharply above ~1,800 m, whereas standing deadwood share and area were systematically concentrated at higher elevations (Fig. 3b–c, Fig. S20c). As a result, deadwood area maxima was displaced 200–400 m upslope relative to forest area maxima. In contrast, standing deadwood share peaked at even higher elevations, indicating an increasing proportion of standing deadwood at higher elevation where overall forest cover is reduced. The probability of broadleaf followed a similar elevational trend: lower broadleaf probabilities, indicating

forests more dominated by conifers, peaked at 1,750 m a.s.l. (Fig. S21).

3.3. Temperature anomalies and forest composition shape deadwood patterns

Standing deadwood variability in Swiss forest reserves was partly explained by the selected environmental and forest-related variables, with the full model accounting for 17% of the observed variability and ecoregion-specific models explaining between 4% and 21% (Table S9).

Model performance was highest in the Northern Intermediate Alps (21%) and Swiss Central Plateau (18%) and lowest in the Southern Intermediate Alps (4%), with intermediate values in the Southern Pre-Alps (17%), Jura (16%), Continental Alps (15%), and Northern Pre-Alps (8%). The leave-one-ecoregion-out sensitivity analysis indicated that excluding any single ecoregion from the training dataset had only minor effects on model performance when evaluated on the remaining test data (Table S11).

Across the full dataset, probability of broadleaf and lagged temperature anomalies were the most influential among the selected predictors within the fitted models, followed by canopy height, basal area, and soil properties (Fig. 4b, Table S18–19). As probability of broadleaf represents the probability of broadleaf forest, the SHAP dependence plot indicates that the model linked higher predicted proportions of standing deadwood to low broadleaf probability, and therefore to forest dominated more by conifers (Fig. 4d). Long-lag maximum temperature anomalies showed a consistently positive association with standing deadwood, whereas long-lag minimum temperature anomalies showed the opposite tendency, and short-lag anomalies contributed comparatively little to the fitted model. In particular, probability of broadleaf showed reduced importance in the Continental Alps and Northern Intermediate Alps, while long-lag maximum temperature anomalies contributed less in several ecoregion-specific models despite their high relevance in the model fitted on the full dataset, indicating possible region-dependent differences in how the selected variables relate to standing deadwood patterns.

Ecoregion-specific analyses broadly mirrored the global patterns but revealed regional contrasts in the relative importance of drivers (Fig. S22). The models assigned temperature anomalies the highest relative importance in both high-elevation regions such as the Continental Alps and lowland regions such as the Swiss Central Plateau whereas precipitation anomalies were most influential in mid-elevation mountain regions such as the Northern Intermediate Alps. Forest composition and structure, particularly probability of broadleaf, had higher relative importance in lower mountain regions including the Jura and the Southern Pre-Alps. Despite the limited explanatory power of the models, these results suggest that forest structure and climate variability consistently emerged as the most important among the selected deadwood variables, with their relative contribution varying across ecoregions.

SHAP dependence plots indicated non-linear responses across climatic, structural, and site-related predictors (Fig. 4d). Associations with lagged temperature, precipitation, and climatic water balance effects were visible but generally weak (Fig. S23 and S24), with precipitation anomalies and the 1-year lag climatic water balance showing slight positive trends at higher values, and minimum temperature anomalies associated with reduced deadwood shares at the lower end of their ranges (Fig. S23f–k, 24b, d–h). Structural variables showed clearer contrasts, with basal area positively associated with standing deadwood and canopy height exhibiting elevated deadwood shares at intermediate values followed by declines in taller stands (Fig. 4d). Soil and site-related variables, including clay content, soil carbon, and topographic wetness index, displayed non-monotonic responses with minimum deadwood shares at intermediate levels, while available water content showed a U-shaped relationship and elevation of a consistent negative association (Fig. S24c, i–j).

4. Discussion and conclusions

This study provided the first spatially explicit, nationwide assessment of standing deadwood dynamics, revealing systematic variation across elevation, forest composition, and climate gradients. Across forest ecoregions, standing deadwood shares ranged from 0.20 to 0.83% of forest area, with pronounced spatial heterogeneity. We showed that forest composition and climate jointly shape these patterns (up to 17%): standing deadwood was most strongly associated with conifer-

dominated forests and positive temperature anomalies, whereas forest structural attributes showed secondary influence and edaphic factors contributed little explanatory power. Together, these results point to climate-sensitive forest composition as a primary determinant of contemporary standing deadwood distribution at the national scale.

The yearly deadwood rates across forest ecoregions (0.14–1.13%) of the leaf-on forest area were consistent with plot-based mortality estimates from Switzerland, i.e. 0.3 (Rigling et al., 2013) and 1.5% (Etzold et al., 2019) and for European forests, i.e. 0.5 and 2% (Idoate-Lacasia et al., 2025; Nagel et al., 2021; Woods et al., 2021). While comparable in magnitude, monitoring networks estimate mortality from discrete sample plots, whereas our analysis maps standing deadwood continuously across entire forest areas, enabling the identification of spatial patterns, gradients, and regional hotspots of forest mortality at the national scale.

Consistent with the widespread increase in forest mortality reported following the 2018 drought (Obladen et al., 2021; Schiefer et al., 2024; Thonfeld et al., 2022), including within Switzerland (Braun et al., 2021; Frei et al., 2022), standing deadwood increased systematically in areas covered by repeated aerial surveys. At the national scale, deadwood extent increased by 42.7%, 6.5%, and 30.4% between the 2018–2021, 2019–2022, and 2020–2023 survey pairs, respectively, with comparable increases observed within forest reserves (40.2%, 24.4%, and 1.8%). This increase was evident both at the national scale and within forest reserves, indicating a general rise in standing deadwood between successive survey years. However, because image coverage varied widely across years and regions (0.2–87% of forest area), temporal trends could only be assessed in areas surveyed more than once. Continuous, country-level acquisitions of high-resolution aerial imagery would therefore be required to enable consistent spatial and temporal assessments of changes in standing deadwood.

Standing deadwood accumulated disproportionately at higher elevations (~1,550 m) and on steeper slopes (55°), indicating that recent forest deadwood is structured by topographic gradients rather than forest availability alone (~550–1,150 m). The upslope displacement of deadwood share relative to forest area suggests increasing vulnerability of montane and subalpine forests, where warming temperatures reduce historical cold limitations while episodic drought and heat extremes impose novel stress combinations (Pepin et al., 2015). Similarly, elevated deadwood shares on steep slopes may reflect enhanced water limitation, shallow soils, and reduced buffering capacity against drought stress under warming climates (Anderegg et al., 2020; McDowell et al., 2008). The elevation pattern also overlapped with forest composition, as conifer-dominated forests peaked at 1,750 m, consistent with the higher vulnerability of conifer species in montane forests (Spînu et al., 2026). Together, these patterns support the interpretation that climate change is reshaping spatial gradients of forest mortality, with topography modulating exposure and sensitivity to climatic extremes.

Among the selected predictors, forest composition, climate anomalies, and stand structure were identified as the variables most strongly linked to standing deadwood patterns in Swiss forest reserves. Probability of broadleaf emerged as the most important predictor within the fitted model, with SHAP dependence plots linking higher deadwood shares to conifer-dominated stands. This pattern reflects the heightened vulnerability of coniferous species, particularly Norway spruce, to drought and heat stress (Idoate-Lacasia et al., 2025; Schiefer et al., 2024). Temperature anomalies, especially multi-year maximum temperature anomalies, were also associated with higher deadwood occurrence, consistent with lagged drought effects on tree mortality reported across Europe (Klap et al., 2000; Knapp et al., 2024). Structural attributes were also relevant in the fitted models: deadwood shares increased with canopy height up to intermediate stand heights and with higher basal area, which may reflect the combined influence of stand development, competition, and exposure to climatic stress (Etzold et al., 2019; Ma et al., 2023). In contrast, edaphic factors had a lower relative importance in the fitted model, with lower deadwood shares on clay-rich

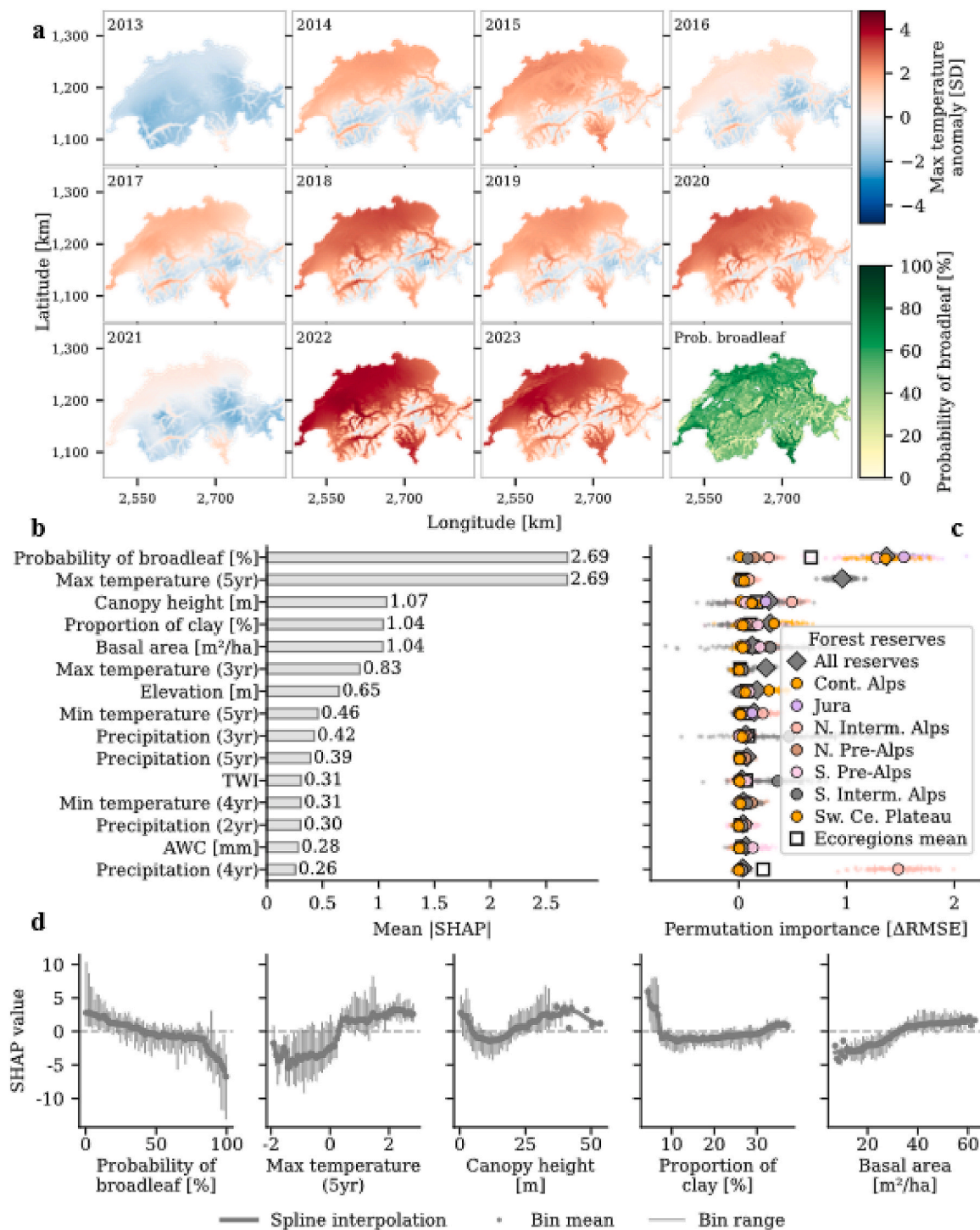


Fig. 4. Maximum temperature anomalies, probability of broadleaf, SHAP values, permutation importance, and SHAP dependence plots of standing deadwood drivers derived from random forest models. **a** Yearly maximum temperature anomalies for 2013–2023 relative to the norm of 1981–2010, and country-level probability of broadleaf forest. Anomalies are calculated from the yearly mean maximum temperature and expressed as departures from the 1981–2010 mean in units of that baseline's standard deviation. **b** Absolute mean SHAP values of the fifteen most relevant variables from the random forest model fitted on the full dataset. SHAP values have been calculated on the entire test dataset. Abbreviations: TWI, Topographic Wetness Index; AWC, Available Water Content. **c** variable permutation importance of the ten most relevant variables of the random forest models on the full and ecoregion-specific datasets, expressed as the change in RMSE when that feature is randomly permuted. Positive values indicate that shuffling the feature makes the model perform worse, and larger positive values correspond to higher importance. Jittered dots show all permutation repeats; diamond and larger circles with horizontal error bars mark the mean and standard deviation across repeats for the full dataset and ecoregion-specific datasets, respectively. Hollow black squares represent the average across ecoregions for each feature. **d** SHAP dependence plots for the full dataset model showing the marginal effects of the five most important predictors on standing deadwood. SHAP values for each predictor were binned in 70 bins, and a cubic spline was used to interpolate the average SHAP values for each bin. The solid grey lines show the spline interpolation, the grey dots indicate the mean SHAP value within each bin, and the vertical grey lines depict the range of SHAP values for each bin.

soils, consistent with reduced drought sensitivity due to higher soil water-holding capacity (de Toledo et al., 2012, 2011). The interpretation relies mainly on the SHAP values from the random forest model trained on the full dataset. Since SHAP values and permutation importance quantify different aspects of model behavior, differences among the lower-ranking predictors are to be expected (Orlenko and Moore, 2021).

Despite identifying ecologically meaningful associations among the selected predictors, the modest explanatory power of the models is consistent with other large-scale forest mortality studies (Ma et al., 2023; Trugman et al., 2021) and reflects the inherent complexity of mortality processes rather than methodological shortcomings. In addition, the leave-one-ecoregion-out sensitivity analysis revealed that removing any single ecoregion did not disproportionately affect the full-dataset model, suggesting that the model reflects patterns that are broadly consistent among ecoregions. Tree mortality is stochastic and threshold-driven, shaped by interacting climatic stress, biotic agents, and disturbance events operating across multiple spatial and temporal scales, many of which are not captured by available predictors. Unobserved disturbances such as insect outbreaks, pathogens, windthrow, and legacy effects of past management, along with the spatial aggregation of deadwood metrics, are likely major sources of unexplained variability and restrict how well static environmental covariates by themselves can explain standing deadwood patterns. To the best of our knowledge, however, there are currently no nationally consistent, wall-to-wall, high-resolution datasets for these disturbance processes that can be directly incorporated into our assessment workflow. By focusing on forest reserves, where management interventions are absent or minimal, we reduced management-related biases, strengthening the interpretation of climate and structural drivers despite limited predictability. The model comparison presented here is also restricted to non-spatial regression approaches. The only exception is a spatial error model used to verify the presence of spatial dependence. Explicitly spatial modelling frameworks could yield different estimates of predictive performance and variable importance and we cannot exclude this possibility.

Mapping standing deadwood using semantic segmentation of high-resolution aerial imagery enables spatially explicit, large-scale assessments, but several data-related constraints should be considered. The approach captures only mortality visible in the upper canopy and does not detect understory deadwood, leading to a likely underestimation of total standing deadwood. Alternative approaches such as airborne laser scanning and full-waveform LiDAR offer complementary three-dimensional information to support the detection of deadwood components that are difficult to identify using only optical imagery, including fallen trees (Polewski et al., 2018, 2015) and small understory trees (Yao et al., 2012). Detection accuracy depends on model performance (Möhrling et al., 2025), and partial canopy dieback may occasionally be misclassified as standing deadwood. Annual orthophoto acquisitions also vary in spatial coverage and represent single temporal snapshots, which may miss recent mortality or deadwood removal. Despite these limitations, the spatial consistency of deadwood patterns across independent survey years, overlapping and non-overlapping areas, and multiple analytical scales supports the robustness of the main conclusions and highlights the value of repeated high-resolution imagery for national-scale forest monitoring and climate-adaptive management.

The observed spatial concentration of standing deadwood at higher elevations suggests that montane and subalpine forests may represent emerging hotspots of elevated mortality under climate stress, challenging the long-held assumption that these systems are buffered from drought and heat stress (Idoate-Lacasia et al., 2025; Klap et al., 2000; Schiefer et al., 2024). Increasing deadwood accumulation has important implications for carbon storage, habitat availability, and disturbance regimes, influencing biodiversity, fuel continuity, and the likelihood of secondary disturbances such as insect outbreaks and windthrow (Etzold

et al., 2019; Ma et al., 2023).

By providing spatially explicit, wall-to-wall deadwood maps, this study moves beyond descriptive reporting and provides information that can support prioritization of monitoring efforts, identification of vulnerable forest areas, and evaluation of management strategies under changing climatic conditions. More broadly, the reproducible and transferable framework presented here demonstrates how high-resolution remote sensing can be integrated into climate-adaptive forest management, enabling consistent national-scale assessments and supporting proactive decision-making in forests increasingly exposed to climate extremes (Waser et al., 2025).

5. Data and code availability

Aerial orthophotos at 10 cm are freely available on the swisstopo website (<https://www.swisstopo.admin.ch/en/orthoimage-swiss-image-10>). The standing deadwood segmentations and derived products, i.e., aggregations at 10 m and 100 m, deadwood shares for forest ecoregions and Swiss Cantons, are available on Zenodo at <https://doi.org/10.5281/zenodo.17985499>. The sources of the environmental variables are listed in Table S4. The Topographic Wetness Index and basal area data are available from Lars T. Waser. The climate data are available from the Land Change Science Group, WSL. A visualization of the deadwood maps is integrated in <https://www.treeai.earth/>.

The code for the aerial orthophotos downloading, data processing, deadwood assessment, and random forest modelling is available on Zenodo at <https://doi.org/10.5281/zenodo.17985499>. The code to run the semantic segmentation model is publicly available at <https://github.com/cmosig/deadtreesmodels>.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used ChatGPT and Grammarly, both AI-assisted tools, to correct and improve the clarity of sentences, as well as ChatGPT and GitHub Copilot for programming assistance. After using this tool or service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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CRediT authorship contribution statement

Luca Ferrari: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Lars T. Waser:** Writing – review & editing, Methodology, Data curation. **Achilleas Psomas:** Writing – review & editing, Methodology, Data curation. **Clemens Mosig:** Writing – review & editing, Software. **Teja Kattenborn:** Writing – review & editing, Software. **Christian Ginzler:** Methodology, Data curation. **Verena C. Griess:** Writing – review & editing, Supervision, Funding acquisition. **Mirela Beloiu:** Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.isprsjprs.2026.09.041>. The supplementary material report: the yearly coverage of the leaf-on orthophotos and the summary of the data cleaning process, the metrics of the segmentation model validation, the spatial distribution of the Swiss forest reserves, the summary and references of the random forest input variables.

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