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REVIEW

Treeline remote sensing: from tracking treeline shifts to multi-dimensional monitoring of ecotonal change

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Abstract

Remote sensing applications have a long history in treeline research. Recent reviews have examined the topic mainly from a methodological point of view. Here, we propose a question-oriented review of remote sensing in treeline ecology to relate remote sensing methodologies to key ecological metrics and identify knowledge gaps and promising areas for future research. We performed a meta-analysis to assess the role of remote sensing as a tool for measuring spatial patterns and dynamics of alpine and Arctic treeline ecotone globally. We assessed the geographic distribution, scale of analysis, and relationships between remote sensing techniques and treeline ecological metrics through co-occurrence mapping and multivariate statistics. Our analysis revealed that only 10% of treeline ecology studies applied remote sensing tools, often associated with the keyword 'climate change'. Monitoring studies adopted coarser spatial resolutions over longer temporal extents in comparison with other treeline studies. A multiscale and multi-sensor spatial approach was implemented in just 19% of papers. Long-term research commonly relied on aerial and oblique photography to measure treeline shifts through photointerpretation within a multidisciplinary framework. More recent treeline dynamics were often quantified using greenness trends derived from the pixel-based classification of satellite images. Many recent short-term studies focused on delineating tree scale metrics derived from the object-based classification of uncrewed aerial vehicle (UAV) images or LiDAR data. Over the past decade, high-resolution and low-cost UAV remote sensing has emerged as an interesting opportunity to fill the gap between local-scale ecological patterns and coarse-resolution satellite sensors. Additionally, treeline remote sensing applications would strongly benefit from multidisciplinary frameworks that integrate field studies in ecology and environmental science. The multi-dimensional structural complexity of treelines typically responds to environmental drivers over multiple scales and thus is best described with multiscale and multi-sensor approaches.

Introduction

Treelines have emerged as focal environments for ecological studies aimed at better understanding limits to tree establishment and growth, as influenced by climate change (Grace et al., 2002; Wang et al., 2019) and land use legacy (Batllori & Gutiérrez, 2008; Lu et al., 2021). The position of treeline defines the limit to forest extent, of critical importance to carbon accounting at regional to global scales. Climatic treelines are most strongly influenced by global and regional scale climatic patterns of minimum growing season length and average growing season temperature (Karger et al., 2019). At the landscape scale, other factors such as soil, meso-topography, and natural and anthropogenic disturbances interact with the broader scale drivers constraining vegetation processes (Butler et al., 2007). From a finer perspective, species competition and facilitation and micro-topographic heterogeneity are key factors for vegetation dynamics at the treeline (Batllori et al., 2009). However, treeline ecotones are challenging to study because they are dynamic, with processes acting at multiple spatial scales (e.g., Feuillet et al., 2020).

The utility of remote sensing (RS) for producing spatially contiguous, wall-to-wall classifications is fundamental for a comprehensive assessment of the spatial heterogeneity of treeline patterns and their changes over time (Guay et al., 2014). RS has a long and storied history in treeline studies, allowing processes observed at the local scale to be scaled up to landscape, regional, and global scales. To date, RS data sources in treeline ecology have consisted of ground-based repeated oblique photographs (Roush et al., 2007), images acquired using uncrewed aerial vehicles (UAVs, Mienna et al., 2022), aerial and terrestrial laser scanner data (Coops et al., 2013), historical aerial photos (Améztegui et al., 2016), multispectral satellite imagery (Morley et al., 2019), and Synthetic Aperture Radar (SAR) images (Antonova et al., 2019). Moreover, RS has often been combined with field vegetation sampling and dendroecological investigations to link patterns at different scales (Elliott & Kipfmueller, 2010). The importance of RS data for mapping treeline spatial and temporal patterns has been extensively recognized for years, although the geographical scope of treeline RS studies remains limited (Morley et al., 2018).

As researchers have learned more about treelines, we understand them as spatially heterogeneous ecotones; we are just beginning to understand what factors facilitate or slow their response to changing climates (Lu et al., 2021). With newer RS data sources and methodologies at our disposal, the application of RS for treeline studies has evolved over the years and continues to change rapidly. Recently, RS has generally improved in the availability of data, computational power, and spatial and temporal resolution (Senf, 2022). An important improvement RS offers to the traditional treeline ecology field survey is the extension of the spatial and temporal extent. RS can be adopted to measure treeline position (e.g., Wei et al., 2020; Zou et al., 2023) and its drivers at multiple scales, which is important because the socioeconomic, land use, and climatic drivers of treeline change are inherently scale-dependent (Weiss et al., 2015). A fundamental metric in treeline ecology is the spatial pattern (2D or 3D), often related to ecological mechanisms involved in the formation of treeline ecotones (Bader et al., 2021). Quantification of horizontal 2D structures of treeline mosaic and 3D structures (e.g., tree height) allows the reconstruction of forest dynamics driving the transition from krummholz to tree growth forms (Malanson et al., 2007). These local-scale attributes can be surveyed with high-resolution RS data, such as centimetric UAV-based RS (Mienna et al., 2022) and aerial or terrestrial LiDAR surveys (Maguire et al., 2019) to investigate the role of fine-scale drivers, including microclimate, microtopography, and species interactions.

Previous reviews of RS for treeline research have been framed mainly around technical and methodological features of RS data and approaches (e.g., Chhetri & Thai, 2019; Morley et al., 2018). However, a more question-oriented discussion of RS applications for treeline ecology would help to inform the use of RS to better detect and quantify global change effects on the multidimensional structure of treeline ecotones. Therefore, we systematically reviewed the role of RS using a question-oriented approach. Through a synthesis of available information, we shed light on potential improvements and limitations arising from the combined use of RS data and data from relevant field-based disciplines. In our review, we treat RS as one component of an integrated and multiscale geospatial analysis approach. In summarizing current knowledge and developing suggestions for future research, we address the following questions:

1. **How is the multi-dimensional structural complexity of treeline measured through RS?**
2. **How are different RS tools employed to calculate key ecological metrics?**
3. **How can the use of RS be improved to fill gaps of knowledge in treeline ecology?**

Methods

Systematic review

We systematically reviewed the role of RS as a tool to measure spatial patterns and dynamics of treeline ecotones. We surveyed and compiled the international literature using two comprehensive databases: Scopus and Web of Science Core Collection. The final search string, reported here as applied in Web of Science, included the following key terms: ALL = ((treeline OR 'tree line' OR timberline OR 'timber line' OR forestline OR 'forest line' OR 'treeline ecotone' OR 'alpine treeline') AND ('remote sensing' OR satellite OR aerial OR LiDAR OR UAV* OR UAV OR image* OR photog*)). The rationale underlying the adopted query was the simultaneous presence of the terms 'remote sensing' and 'treeline,' together with their synonyms and the categories of RS approaches within the topic words (title, abstract, and keywords) of published literature. The query was limited to published articles, reviews, proceedings, book chapters, and books, for the entire period of record (1987–2022) available in the databases (Fig. 1).

Dataset creation

We downloaded metadata of selected publications on June 17, 2022 from Scopus and Web of Science to create

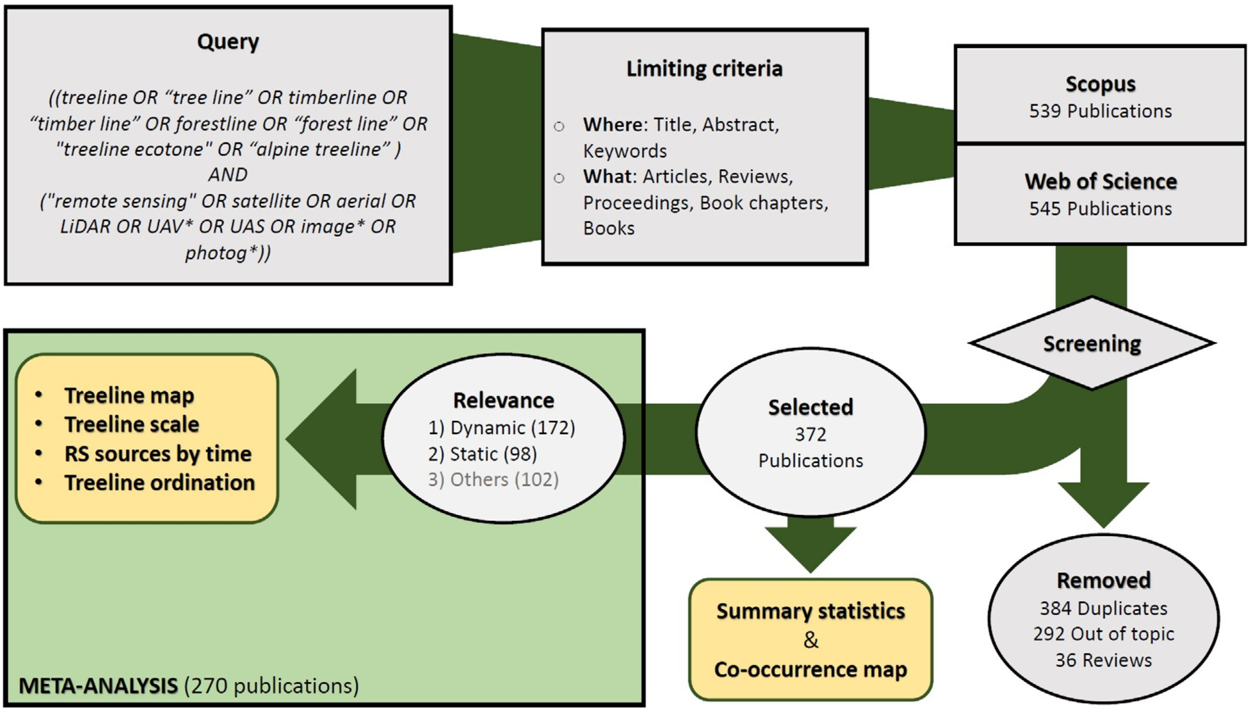

Figure 1. Framework of systematic review and meta-analysis: gray boxes = literature selection; yellow boxes = statistical analyses.

a unique database that was screened for duplicates. After a careful reading, we performed a meta-analysis on the collected metadata and topic-related variables obtained from the selected publications. The final dataset included the following categories: bibliographic (authors, title, journal, keywords, abstract, publication year, DOI); geographic (mountain range, country, continent); treeline type (latitudinal or elevational, upper or lower); spatial and temporal scale (resolution and extent); RS data sources (aerial and oblique photography, satellite imagery, aerial and terrestrial laser scanner, UAV); sensors (type and number); analytical tools (e.g., GIS and GNSS); data analysis techniques (e.g., pixel-based, object-based); RS-derived treeline metrics (e.g., canopy cover, tree height, greening and vegetation indices (VIs), spatial patterns, drivers, forecast); data collection other than RS (e.g., dendroecology, paleoecology, field surveys, ecophysiology). The final dataset incorporated both Boolean variables, such as image classification methods, and quantitative variables, such as scale attributes.

Data analysis

From an initial list of 700 papers that met our search criteria, we excluded 292 papers that did not squarely address at least one of the two main topics (RS or treelines), as well as 36 review articles that did not include original data. We summarized key characteristics of treeline RS papers (n = 372) and classified the selected papers into three categories based on their relevance to the general goal of the review: (1) treeline dynamics, (2) static vegetation mapping, (3) others (Fig. 1). Since our study is framed around ecological questions, the latter category was a residual one including studies located at the treeline that used RS data to investigate processes not directly related to vegetation ecology. We performed summary statistics and created a distance-based map of keyword co-occurrences through VOS VIEWER v. 1.6.18 (Van Eck & Waltman, 2010). Nodes of these maps are grouped using modularity-based clustering and the smart local moving algorithm (Waltman & Van Eck, 2013). In these maps, the frequency of occurrence defines node size and connection lines indicate bibliographic links of co-occurrence.

We assessed the geographic distribution, scale of analysis, and relationships between RS techniques and treeline ecology metrics only for the most relevant papers (categories 1 and 2, n = 270). We obtained a map of research sites in QGIS v. 3.22.5 by collecting geographic coordinates of latitudinal and elevational treelines among mountain ranges of the world (GMBA Mountain Inventory v.2, Snethlage et al., 2022). We used a Mann–Whitney test to compare spatiotemporal resolution and extent for papers with different research goals (treeline dynamics vs. static vegetation mapping). We assessed RS data sources over time through a stacked curve graph to describe technological advances and emergent topics in treeline ecology. We explored the relationships between RS approaches and treeline ecology metrics by using a multivariate statistical approach. First, we obtained groups of studies characterized by similar data sources and tools through a Cluster Analysis (CA with Gower distance and Flexible Beta value = −0.25) on a matrix of RS attributes. The resulting groups were defined through descriptive statistics. Then Nonmetric Multidimensional Scaling (NMS with Gower distance) was used as a non-parametric ordination technique to explore the relationships between a main matrix of RS approaches against a secondary matrix of treeline metrics. All multivariate statistical analyses were performed with PcOrd v.7 software (McCune & Mefford, 2016). Univariate statistical analyses were performed using R v4.2.2 and all graphs were created within the 'ggplot2' R package (Wickham, 2016).

Results

Our systematic review of the treeline RS literature yielded 372 papers, of which 94% were research articles, 5% conference papers and 1% book chapters (a list of the data sources is found in Table S1). RS applications on the study of treeline ecotones began in 1987 and showed an increasing net trend of published papers described by the general keyword 'treeline'. The proportion of RS papers addressing treeline dynamics or change has also increased. However, the use of RS techniques to describe and measure treeline ecotones is a small fraction (10%) of the overall scientific production on the treeline ecology topic (548 treeline RS papers from 5453 treeline papers that do not mention RS).

The majority of papers (23%) were published in RS-related journals such as *Remote Sensing* and *Remote Sensing of Environment*, followed by general ecology and forest ecology journals, 13% and 8%, respectively (Table S2). Seventeen disciplines were represented in our systematic review, demonstrating the high interdisciplinarity of the treeline ecology topic. After removing the terms 'treeline' and 'remote sensing' and merging similar keywords such as 'climate change' and 'climate-change,' we observed that the words climate change, LiDAR, NDVI, and Landsat were the most frequent keywords used in the selected papers. Climate change, Landsat, aerial imagery, LiDAR, and NDVI were the most important nodes in our co-occurrence map. The phrase 'climate change' was, by a large margin, the most connected keyword in the entire dataset (Fig. 2).

Treeline types and geographic distribution

Elevational treeline studies were more abundant than latitudinal ones (76% and 21%, respectively), and only a minority of papers (3%) assessed both types of treelines (Fig. 3). Within the elevational treeline group, upper ecotones were studied far more frequently (96%) than lower ones (1%), with a small percentage of studies (3%) analyzing both upper and lower treelines. A large majority of elevational treeline remote sensing studies were located in the northern hemisphere, especially in the Rockies (13.3%), European Alps (12.6%), Scandes (11.9%), and Himalayas (10.8%) mountain ranges. We found just 21 altitudinal studies located in the southern hemisphere, where the Andes emerged as the most studied (61.9%) mountain range below the Equator.

Treeline spatiotemporal scale

Based on our goal-oriented classification of papers, we retrieved 172 studies measuring treeline dynamics ('Dynamic' = 46%), 98 mapping treeline vegetation without any change assessment ('Static' = 28%), and 102 addressing other research goals ('Others' = 26%) but located at the treeline. Temporal and spatial scales varied between studies that monitored temporal changes and those that only mapped treeline ecotone vegetation (Table S3). 'Dynamic' treeline papers adopted broader spatial resolutions (186.3 vs. 44.1 m) over longer temporal extents (48.9 vs. 1 year) than those in the 'Static' and 'Other' categories. We did not observe a strong difference in spatial extent between treeline categories; however, only 54% of the selected papers reported the spatial extent of their analysis. Only 19% of studies adopted a multiscale spatial approach (maximum of four scales), of which 65% measured treeline dynamics and 35% mapped treeline vegetation at a single point in time.

A large majority of papers adopted a temporal resolution ranging from 1- to 5-time steps (average = 5.7), but many studies used a yearly time-series approach. Temporal extent varied from 1 to 130 years (average = 26.9), with a higher frequency of studies analyzing less than 10 years. Research studies embracing temporal extents longer than 100 years combined historical vegetation maps with RS data. The spatial resolution was strictly determined by the RS data source, resulting in a higher frequency of fine scale (few cm to 10 m) studies followed by many studies adopting satellite imagery with medium resolution (10 to 30 m) and few studies using coarse resolution data (250 m to 1 km). Studies of treeline dynamics or change adopted larger spatiotemporal extents and coarser spatiotemporal resolutions.

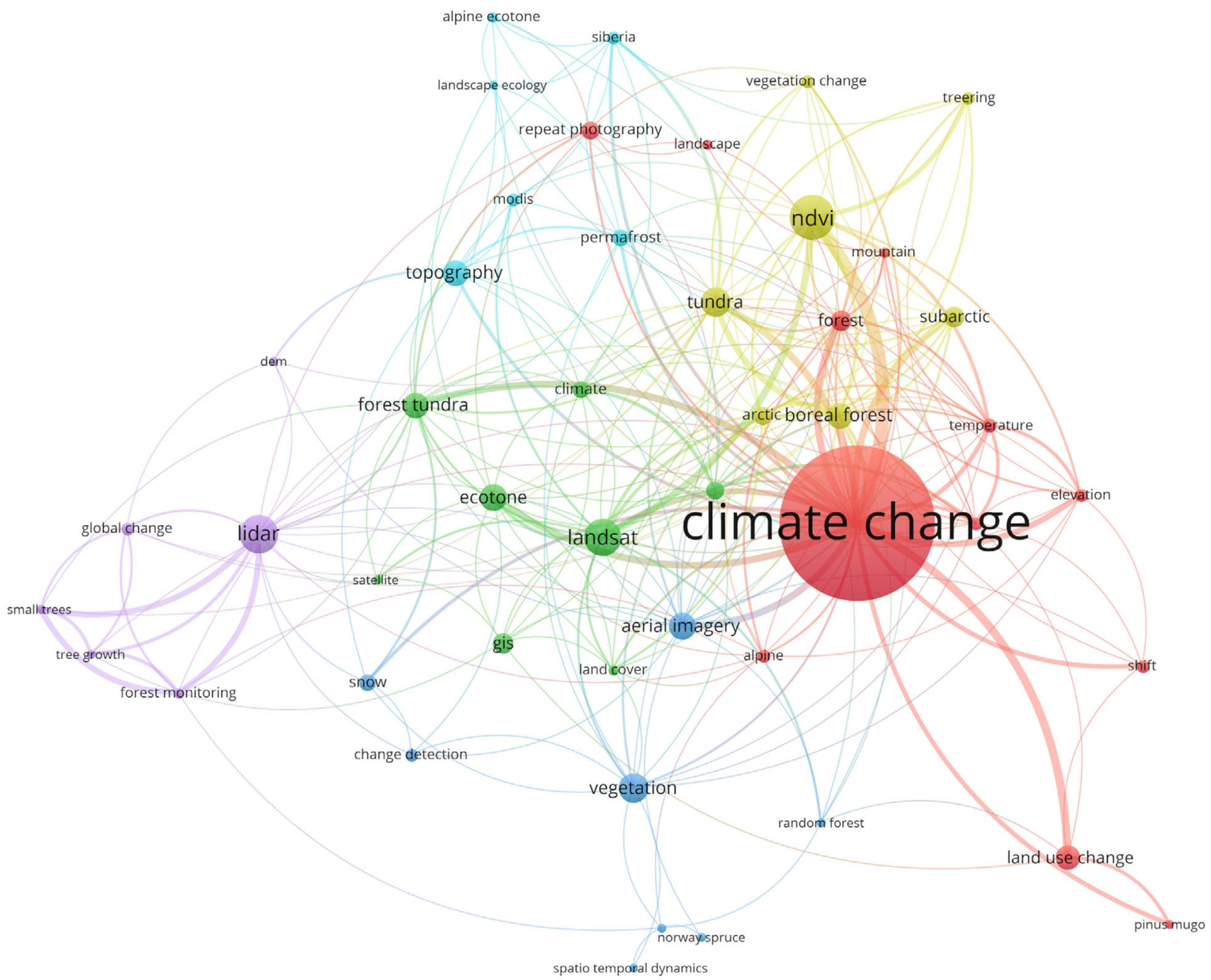

Figure 2. Co-occurrence map based on keywords (minimum appearance 5 times) of selected 372 papers. Six clusters are indicated with different colors: (1) red (12 items) = climate change and land use change; (2) green (8 items) = Landsat and ecotone; (3) blue (8 items) = aerial imagery and vegetation; (4) yellow (7 items) = NDVI and tundra; (5) purple (6 items) = LiDAR and forest monitoring; (6) cyan (6 items) = topography and alpine ecotone. Lines indicate connections between co-occurrent keywords.

Remote sensing data and approaches

The selected papers adopted different RS approaches, tools, and data sources. Most used only one source of data (77%), but some used two data sources (19%), and a minority (1%) used three data sources. Satellite imagery was the most frequent (55%) data source, followed by aerial photography (40%), oblique photography (11%), aerial and terrestrial laser scanner (10%), and uncrewed aerial systems (3%). RS approaches have changed over time following technological advances and the availability of novel analytical tools (Fig. 4).

Oblique photography was likely the first descriptive RS approach for measuring treeline shift, but interestingly has been widely used also during the last two decades. We observed a consistent and stable use of aerial photography over time, with a significant increase during the last 15 years. Satellite multispectral RS shows a similar trend with a positive peak in the last 10 years. Laser scanner techniques, both aerial and terrestrial, have only been used for treeline RS since 2006 and uncrewed aerial systems since 2016. More than 20 sensors and platforms appeared in the selected papers, with Landsat being the most common (45%), followed by Quickbird, MODIS, SPOT, and Worldview satellite missions that together accounted for 27% of the dataset (Table S4). Pixel-based classification was the most frequently used RS processing approach (51% of studies), followed by visual photointerpretation (36%) and object-based classification (11%). Only 1% of studies adopted a sub-pixel

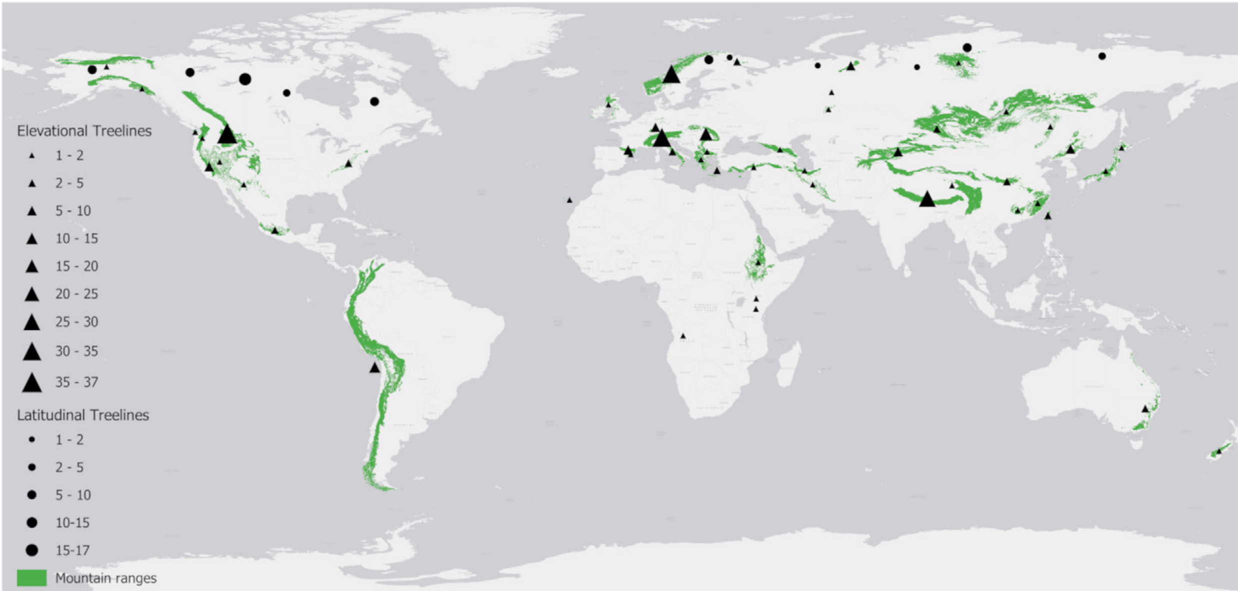

Figure 3. Geographical locations of published papers including latitudinal treelines (black dots) and elevational treelines (black triangles), superimposed on the world's mountain ranges mapped according to the GMBA Mountain Inventory v.2 (Snethlage et al., 2022).

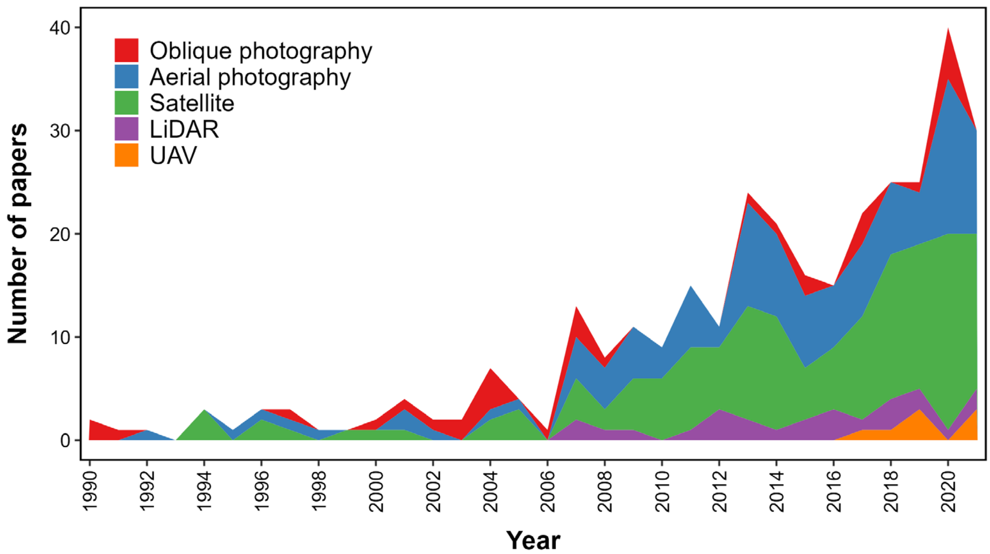

Figure 4. Frequency of treeline studies (number of papers) adopting different RS approaches from 1990 to 2021. Aerial and terrestrial laser scanner approaches were merged together in a single category (LiDAR). Studies performed in the period 1987–1989 were merged in 1990 and the first semester of 2022 was merged to 2021.

approach, and 10% of studies adopted multiple approaches to image classification, generally combining pixel-based classification of satellite imagery and photo-interpretation of aerial/oblique photos. Surprisingly, only half of the studies reported accuracy metrics for image registration, classification accuracy, and model performance.

Remote sensing tools for measuring treeline features

From the cluster analysis performed on 270 papers, we obtained four clusters described by their RS characteristics (Table 1). The 'Long-Term Aerial' cluster mainly consisted of long-term studies (averaging 43.6 years) using

Table 1. RS data sources, tools, and classification approaches reported as a proportion of papers for each of the four clusters obtained from the cluster analysis. Temporal resolution (ResTe) and extent (ExtTe) are instead reported as the average number of steps and years, respectively.

Cluster	N	AERIAL	SATEL	LiDAR	UAV	OBLIQ	GIS	GNSS	PixBa	ObjBa	PhoInt	MulDi	Accur	TeRes	TeExt
Long-term aerial	72	0.99	0.17	0.08	0.00	0.08	0.85	0.28	0.46	0.04	0.65	0.49	0.56	3.36	43.56
Long-term oblique	24	0.08	0.08	0.00	0.00	1.00	0.42	0.08	0.04	0.00	0.88	0.67	0.00	3.46	75.29
Satellite time-series	132	0.14	0.99	0.02	0.02	0.00	0.77	0.27	0.81	0.03	0.22	0.60	0.49	8.24	20.58
High-resolution mapping	42	0.40	0.12	0.45	0.14	0.02	0.57	0.52	0.14	0.57	0.05	0.43	0.76	1.64	19.10

GIS (85%) and photointerpretation (65%) to classify historical and recent aerial photographs (99%). Similarly, the 'Long-Term Oblique' cluster was comprised of long-term studies (averaging 75.3 years) involving the use of oblique photography (100%) as a component of multidisciplinary research (67%). Shorter-term studies (19–20 years) were split into two different clusters: 'Satellite Time-Series' was mainly composed of time-series satellite datasets (99%) that were analyzed using a pixel-based classification approach. Finally, the 'High-Resolution Mapping' cluster grouped all papers adopting a high spatial resolution approach using LiDAR (45%), UAV (14%), and very high-resolution (VHR) images (aerial 40% and satellite 12%). This latter cluster was often related to object-based image analysis (57%) and field data collection (GNSS 52%) to measure geometric accuracy (76%).

Long-term discrete monitoring of treeline shift through oblique photography was the only RS approach showing a decreasing trend over time, whereas aerial photography showed a fairly constant temporal pattern (Fig. 5). The open availability of satellite images of coarse (MODIS) and medium (Landsat) resolution in 2001 and 2007, respectively, favored the increasing use of these products to measure treeline ecotones. The use of High-Resolution Mapping has been concentrated in the last 15 years with the increased availability of LiDAR and UAV systems.

The ordination of selected papers through NMS described multivariate relationships among RS data, approaches, and tools, as these, in turn, were related to treeline attributes and metrics (see Fig. 6; Table S5). Treeline dynamics expressed by greenness trends (Greening) were often measured yearly (TeRes) using satellite images (Satellite Time-Series, cluster #3) with pixel-based (PixBa) classification techniques. Short-term studies were mostly based on High-Resolution Mapping (cluster #4) of single tree attributes such as height (Height) and crown dimensions (Crown) that were obtained by adopting an object-based classification approach using drone (UAV) images or LiDAR data. These studies often measured treeline

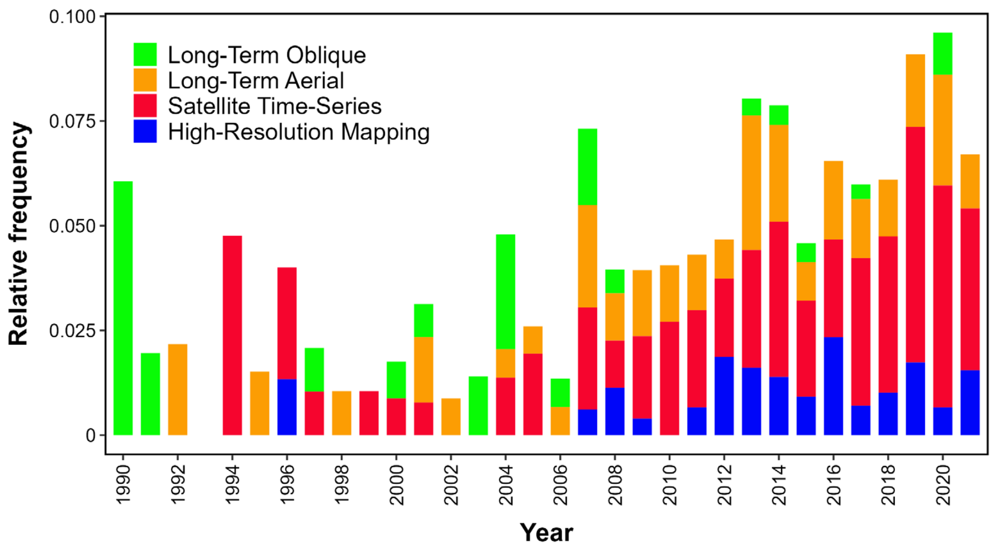

Figure 5. Temporal trend of the frequency of published treeline papers that used RS as relativized by the frequency of all treeline papers published in the same year. Papers are grouped based on Cluster Analysis performed on a matrix of RS attributes. Studies performed in the period 1987–1989 were merged in 1990 and the first 3 months of 2022 were merged with 2021.

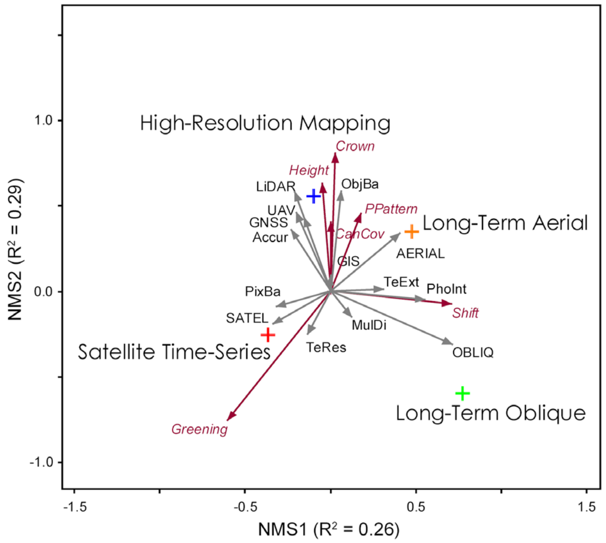

Figure 6. Multivariate ordination (Nonmetric Multidimensional Scaling) of 270 papers based on RS attributes (gray vectors – main matrix) and treeline metrics (purple vectors – secondary matrix). Clusters of papers (CA) are indicated by crosses representing group centroids. A biplot reporting NMS1 and NM3 (third factor) is shown as (Fig. S1). Treeline metrics variables were: Crown = tree crown; Height = tree height; PPattern = point pattern analysis; CanCov = canopy cover; Shift = altitudinal or latitudinal shift; Greening = greening trends. Rs attributes were: SATEL = satellite imagery; OBLIQ = oblique photography; AERIAL = aerial images; UAV = uncrewed aerial vehicles; LiDAR = terrestrial and aerial laser scanner; GIS = geographic information systems; GNSS = global navigation satellite systems; Accur = accuracy assessment; TeExt = temporal extent; TeRes = temporal resolution; PixBa = pixel-based; ObjBa = object-based; PhoInt = photointerpretation; MulDi = multidisciplinary.

canopy cover (CaCov), adopted point pattern analysis (PPattern), and mostly consisted of pure RS studies with neither a sound ecological component nor links to other disciplines. Long-term research used aerial photographs (Long-Term Aerial, cluster #1) and oblique photography (Long-Term Oblique, cluster #2) to measure treeline shifts by adopting a photointerpretation classification approach often associated with other survey techniques or disciplines (MulDi).

Discussion

Relating the spatiotemporal dynamics of treelines to processes of global environmental change is an important research topic for ecologists worldwide. The ability of RS to extract cross-scale wall-to-wall information, for both vegetation patterns and the physical processes that interact with vegetation, is key to infer causal influences underlying ecotonal dynamics and structure (Holtmeier & Broll, 2017). We observed that RS investigations have mainly focused on climate change as their primary target of analysis, using vegetation indices derived from medium-resolution satellite imagery, particularly in latitudinal treeline ecotones.

Multi-dimensional treeline structure through RS approaches

RS data can be used to measure treeline in several dimensions, from a one-dimensional line to a three-dimensional space changing over time. The increase in the availability of RS data and the improvement in resolution is pushing treeline research toward a finer spatiotemporal scale and a greater multi-dimensional focus.

Treeline position detection (i.e., unidimensional feature) is an important first step for monitoring future changes in treeline elevation or latitude caused by climate, topography, and disturbances (e.g., Van Bogaert et al., 2011). Treeline position had already been measured more than 200 years ago by early biogeographers such as Alexander von Humboldt to describe vegetation patterns across elevation and latitude (von Humboldt & Bonpland, 1807). Over the past half-century, the availability of RS data has facilitated a consistent spatiotemporal quantification of trends over larger areas. For doing so, oblique and aerial photography have traditionally been the most common RS data sources. In our review, 97% of studies employed oblique photography, followed by aerial (56%) and satellite (50%) imagery. The strength of oblique and aerial photography consists in the long temporal extent that makes these unique and indispensable data sources for historical landscape analysis of treeline (Roush et al., 2007).

The treeline ecotone patch mosaic, described by the two-dimensional spatial pattern of tree cover, is an important measure of tree density variability along the slope, which is directly influenced by demographic processes of establishment and mortality. Moreover, infilling or densification processes may be decoupled from treeline shift, because species interactions and anthropogenic factors such as agropastoral pressure drive them at finer scales (Feuillet et al., 2020; Vitali et al., 2019). Therefore, object-based classification of aerial photographs is a natural RS approach for developing landscape scale patch-matrix models of treeline heterogeneity. For this reason, a large proportion of studies utilizing aerial photography (41%), oblique photography (34%), and satellite imagery (34%) have developed a land cover mosaic using a patch-matrix representation based on variable tree cover densities (Améztegui et al., 2016; Batllori & Gutiérrez, 2008; Garbarino et al., 2020).

Individual tree attributes such as crown dimensions and height push treeline analysis into a 3D space, allowing quantification of growth patterns and local scale canopy processes caused by disturbance and dieback mechanisms (Bader et al., 2021). VHR data sources such as LiDAR and UAV-based stereophotography are powerful approaches to obtain single tree attributes at the treeline (Coops et al., 2013); however, limited information is available on estimation errors for tree height and crown dimensions. Our meta-analysis shows that airborne LiDAR has been the primary approach to measure tree heights and tree crowns for mapping at the local scale (70% and 38% of cases, respectively), although 11 studies (36% of cases) adopted UAVs to map treeline attributes.

RS data and techniques to achieve key ecological metrics

Satellite time series have been widely used to assess the relationship between treeline dynamics and climatic changes due to the comparable temporal extent and resolution of these datasets (e.g., Wang et al., 2022). Satellite datasets are long-term continuous archives with a detailed temporal progression of change from a RS perspective (e.g., band ratios such as vegetation indices). Their sufficiently high temporal resolution (i.e., days to weeks) allows the detection of trends or inflection points for an ecologically meaningful quantification of change at the global and regional scale (Kennedy et al., 2014). Indeed, several treeline applications have been developed to identify ecological processes through vegetation indices. A recent study used a composite index based on NDVI gradients and elevation to detect alpine treeline ecotones in the northwestern USA (Wei et al., 2020). Satellite-derived NDVI time series are useful for assessing trends in greening, biomass productivity, and drivers of change such as increased temperature and growing season length at a regional scale (Choler et al., 2021). Spatial patterns of the taiga, sub-taiga, and forest-steppe ecotones were detected through NDVI in inner Asia, resulting in a strong positive correlation between higher greenness patterns and increasing precipitation and temperature (Klinge et al., 2018). Temporal trends in greenness have shown a stronger ecotone shift in Arctic treelines, compared to temperate ones (Lu et al., 2021), although some studies have demonstrated relative stability of the boreal forest border in the last century (Masek, 2001). NDVI anomalies in latitudinal treelines of Northern Canada have been found to be particularly correlated with global warming (Olthof & Latifovic, 2007), but a direct link between climate change and reduction in tundra due to shrub and tree encroachment has been observed in the Arctic region (Wang & Overland, 2004).

Historical spatial patterns of forest alpine environments have been widely investigated through object-based classification of aerial images from the 20th Century (Garbarino et al., 2020). Alongside historical photography, integration of historical land cover maps, or military maps (e.g., of the Austro-Hungarian Empire; Shandra et al., 2013) lengthens the temporal extent of analysis. Diachronic analyses of aerial photographs have been applied in human-dominated landscapes of Europe to disentangle the role of land use and climate change on the treeline ecotone at a landscape scale (Treml et al., 2016; Vitali et al., 2018). In treelines affected by land use legacies, upward elevational shifts can be faster than those experienced by climatic treelines, highlighting the combined role of topography and land use legacy on forest expansion (Améztegui et al., 2016). Landscape and local scale drivers can be measured and derived from digital elevation models, climate data, and distance to the historical position of trees by using aerial photos and satellite imagery (Stueve et al., 2009). Such historical information has often been compared to recent orthoimages or satellite imagery. Nevertheless, multiple data sources can be integrated to reduce the uncertainty associated with the historical ecological approach (Mietkiewicz et al., 2017). For example, field data on vegetation structure were combined with multispectral images acquired by four satellite missions (GeoEye, SPOT-7, Sentinel-2, and Landsat-8) to correlate spectral features and vegetation structural changes at the treeline of the Central Mountain Range, Taiwan (Morley et al., 2019). Treeline position and shift measured through aerial photography have been used to explain the mismatch between tree densification and elevational upward shift (Feuillet et al., 2020). Treeline position can be automatically detected through open-source geographic datasets and tools available in cloud computing platforms, such as Google Earth Engine, to allow for annual monitoring of changes (Wei et al., 2020).

High-resolution mapping of treeline has the potential to quantify the processes underlying observed change to single-tree scales, including demography, species interactions, and distribution of suitable microsites for tree regeneration. LiDAR data obtained from treeline environments have been successfully adopted to measure tree density and heights along the ecotone (Coops et al., 2013) and to monitor the vertical and horizontal structure of forest change over short time scales, obtaining an accuracy (R^2) in LiDAR-derived height estimation between 0.63 and 0.85 (Antonova et al., 2019; Coops et al., 2013) or a RMSE of 18% using UAV-derived structure from Motion (Brieger et al., 2019). Tree crown estimation errors were <25% for both the crown diameter and surface area in other studies (Brieger et al., 2019; Eysn et al., 2012). UAVs represent another recent frontier in treeline RS applications. Fixed-wing UAVs proved to be a powerful tool to map land cover at a local scale in different seasons in the Scandes Mountains (Mienna et al., 2022). UAVs can be used to define individual trees to the species level or combined with LiDAR data to map and determine the height of individual tree crowns (Mishra et al., 2018). However, accuracy assessment based on field measurements revealed that UAV-based stereophotogrammetry performed better in estimating tree heights than tree crown areas in Northwestern Russia (Brieger et al., 2019). Treeline dynamics can be indirectly reconstructed by mapping tree age cohorts or by integrating spatially-explicit tree-ring data (i.e., dendrochronology) with RS measurements obtained from UAVs and high-resolution satellite images (Cazzolla Gatti et al., 2019). Recently, integrating different forest definitions into deep learning models based on VHR aerial images enabled mapping transitions from closed-canopy forests to shrub forests at treeline ecotones in Switzerland (Nguyen et al., 2022).

Limits of RS approaches and future research agenda

The papers we reviewed adopted various RS tools and classification methods to characterize the structure of treeline ecotones (Fig. 7). Given the ever-increasing availability of RS data, image classification approaches, and computational power, what limits the further use of RS applications in treeline ecology? Several limitations arise when using RS methods to measure treeline position, structure, and change in an ecologically meaningful way. A frequent issue is the mismatched spatiotemporal scale between treeline patterns and the characteristics of the available RS data. At the global to regional scale (Fig. 7A and B), spatial information on treeline ecotones at coarse resolution is commonly limited to vegetation productivity and phenology, given that vegetation types can only be loosely characterized. The inability of coarse-resolution RS data to characterize spatial patterns of vegetation communities is compensated by the opportunity to study drivers acting at broad spatial scales, such as climate and topography, with a high temporal resolution and throughout several decades. Although new technologies and platforms have allowed to acquire RS data at high spatial and temporal resolutions over large spatial extents, classical RS data should still be applied within a multiscale and multidisciplinary approach to assess multiple drivers of treeline dynamics.

Treeline patterns at the regional to landscape scale (Fig. 7B and C) are often investigated using moderate-resolution multispectral imagery, where pixels with tens of meters dimension contain mixtures of vegetation, bare

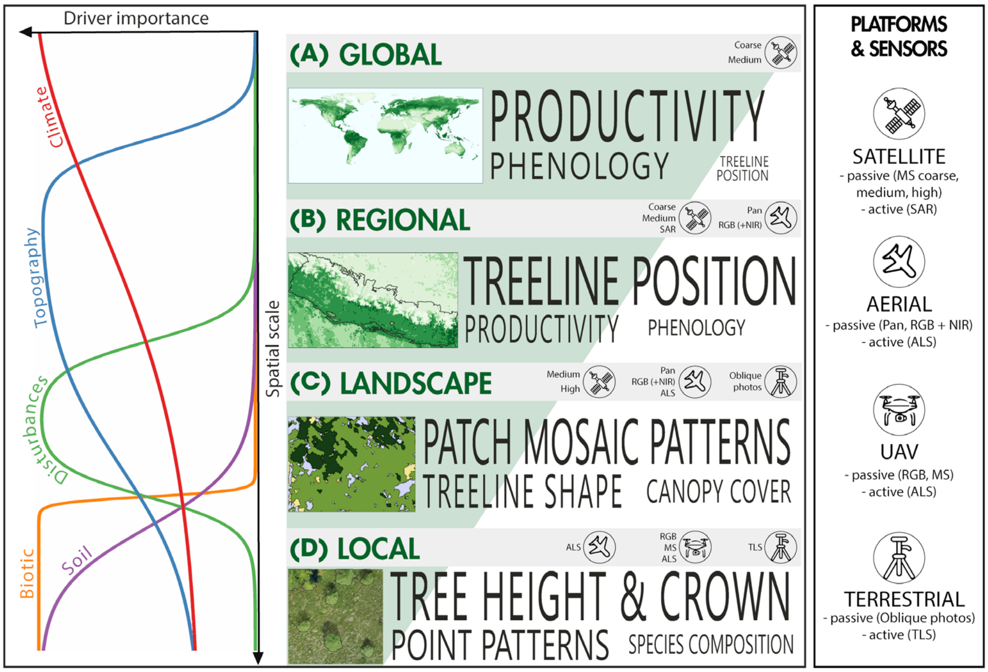

Figure 7. Conceptual model of a multiscale approach for measuring treeline patterns and processes by using remote sensing data sources. Left panel: Relative importance of ecological drivers (horizontal axis) where the vertical axis represents increasing spatial resolution. Central panel = Relative importance of treeline attributes importance by spatial scale (A–D) is expressed proportionately to font size. Right panel = legend of remote sensing sensors and platforms.

soil, snow, and shadows. Despite the coarse resolution, land cover fractions and temporal vegetation dynamics can be estimated at a finer scale by using subpixel approaches like spectral unmixing techniques (Chen et al., 2015; Olthof & Fraser, 2007). The integration of medium-resolution multispectral imagery (e.g., Landsat) with LiDAR and field data allows for the production of wall-to-wall information on the spatial distribution of treelines at the regional scale, such as for the entire subalpine zone (Ørka et al., 2012). However, harsh environmental conditions, such as strong shadowing effects due to complex topography and extreme snow cover and moisture variation, further challenge the discrimination between sparse or patchy vegetation and bare soil with medium-resolution RS data.

High-resolution RS approaches are needed to acquire information on individual trees at the local scale (Fig. 7D), including tree height, crown dimension, and species (Fig. 7D). Until recently, these data have been primarily acquired from satellites and planes, with intrinsic limits associated with spatial and temporal coverage, acquisition costs over vast areas, and lack of flexibility in the acquisition timing. Recent advances in RS platforms, such as fixed-wing UAVs, have enabled the acquisition of centimeter-resolution imagery over areas where acquiring optical data is challenging due to persistent cloud cover (Mienna et al., 2022). However, apart from historical aerial images, a crucial limit of high-resolution RS data is their limited availability in past decades and their low temporal resolution. Indeed, dense time series of high-resolution RS data will ultimately help researchers to relate patterns of treeline change to ecological processes at the level of plant demography (e.g., seed production and dispersal) or community interactions (e.g., facilitation and competition).

Alpine treeline ecotones are structured by environmental and ecological influences over multiple scales and thus multiscale and multi-sensor approaches are the most suitable for their analysis (Fig. 7; Weiss et al., 2015). Critical attributes at the local scale, such as canopy cover and species composition, can be easily obtained with RS approaches. However, given the aforementioned limitations, treeline RS applications would strongly benefit from using a multidisciplinary framework, which builds upon the integration with field data coming from climatology, dendrochronology, soil science, and historical ecology. For instance, high-resolution Digital Surface Models (DSMs) combined with field sensor data may be used to investigate the effects of microtopography on climatic characteristics (e.g., McGregor, 1998). Similarly, high-resolution DSMs can locate safe sites for tree regeneration, whose soil mechanical and chemical properties drive water and nutrient availability during the growing season (Tian et al., 2022). These data can be scaled up to calculate a multivariate continuous variable for the classification of treeline spatial patterns from landscape to regional scales (Bader et al., 2021). Increasingly, treeline research demands spatially explicit, local-scale data to large extents. Such datasets will bring us closer to being able to distinguish expanding versus contracting treelines in the climate change context, or natural versus anthropogenic treelines in the context of cultural landscapes (Gehrig-Fasel et al., 2007).

Conclusions

Our meta-analysis of remote sensing applications in treeline ecology studies provides a global overview of approaches and highlights the need for a multiscale and multidisciplinary strategy to better link treeline metrics to ecological questions. Specifically, different platforms and sensors can be combined with field data to increase scale resolution and extent of treeline monitoring. With the increasing availability of high-resolution remote sensing approaches, such as drone photogrammetry and aerial laser scanner, standard tools with high spatial accuracy and precision can be applied to monitor treeline sites. There is the potential for increased availability of high-resolution data over broader extents to foster a new generation of question-oriented treeline studies that span multiple scales of ecological organization. Such studies will enable us to better understand and predict treeline responses to global change.

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Data Availability Statement

Data sources are available as Supporting Information in Table S1.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of 372 selected papers used in our systematic review with an indication of main attributes (Code = Scopus or WoS id number in our dataset; First Author; Year = year of publication; Journal = journal name; Location = mountain range or country of the study area; Category = based on a paper's relevance to our review; see manuscript main text for further explanation).

Table S2. Number and proportion of published papers by scientific discipline.

Table S3. Average (Av) and standard deviation (SD) values for treeline studies measuring temporal changes (Dynamic) and studies that only mapped treelines (Static).

Table S4. Remote sensing sensors adopted by the authors of the selected papers.

Table S5. Statistical details and fitness indices of Non-metric Multidimensional Scaling (NMS): correlation coefficients and stress values for the first three NMS axes. Overall measures of fit are: R^2n (nonmetric fit) = 0.9856; R^2l (linear fit) = 0.8597; R^2m (metric fit) = 0.8410.

Figure S1. NMS biplot of 270 papers reporting the first and third factors (NMS1 and NM3) based on RS attributes (grey vectors – main matrix) and treeline metrics (purple vectors – secondary matrix).

