Durham Research Online

Deposited in DRO:

03 January 2018

Version of attached file:

Published Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Morley, Peter J. and Donoghue, Daniel N.M. and Chen, Jan-Chang and Jump, Alistair S. (2018) 'Integrating remote sensing and demography for more efficient and effective assessment of changing mountain forest distribution.', Ecological informatics., 43 . pp. 106-115.

Further information on publisher's website:

https://doi.org/10.1016/j.ecoinf.2017.12.002

Publisher's copyright statement:

© 2017 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/BY/4.0/).

Additional information:

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a link is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the full DRO policy for further details.

Durham University Library, Stockton Road, Durham DH1 3LY, United Kingdom
Tel : +44 (0)191 334 3042 | Fax : +44 (0)191 334 2971
https://dro.dur.ac.uk

Ecological Informatics 43 (2018) 106–115

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Integrating remote sensing and demography for more efficient and effective assessment of changing mountain forest distribution

Peter J. Morley[a], Daniel N.M. Donoghue[b], Jan-Chang Chen[c], Alistair S. Jump[a,*]

[a] Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK
[b] Department of Geography, Durham University, Durham DH1 3LE, UK
[c] Department of Forestry, National Pingtung University of Science and Technology, Pingtung 912, Taiwan

ARTICLE INFO

Keywords:
Treeline
Monitoring
Regional
Accuracy
Biogeography

ABSTRACT

Species range shifts have been well studied in light of rising global temperatures and the role climate plays in restricting species distribution. In mountain regions, global trends show upward elevational shifts of altitudinal treelines. However, there is significant variation in response between geographic locations driven by climatic and habitat heterogeneity and biotic interactions. Accurate estimation of treeline shifts requires fine-scale patterns of forest structure to be discriminated across mountain ranges. Satellite remote sensing allows detailed information on forest structure to be extrapolated across mountain ranges, however, variation in methodology combined with a lack of information on accuracy and repeatability has led to high uncertainty in the utility of remotely sensed data in studies of mountain treelines. We unite three themes; suitability of remote sensing products, ecological relevance of classifications and effectiveness of the training and validation process in relation to the study of mountain treeline ecotones. We identify needs for further research comparing the utility of different remotely sensed data sets, better characterisation of treeline structure and incorporation of accuracy assessment. Collectively, the improvements we describe will significantly improve the utility of remote sensing by facilitating a more consistent approach to defining geographic variation in treeline structure, improving our ability to link processes from stand to regional scale and the accuracy of range shift assessments. Ultimately, this advance will enable better monitoring of mountain treeline shifts and estimation of the associated to biodiversity and ecosystem function.

1. Introduction

Climate plays a key role in limiting plant species' distribution (Pearson and Dawson, 2003). Changes in temperature and precipitation will, therefore, lead to the exacerbation or alleviation of plant stress resulting in alterations to recruitment, growth rates, and adult mortality at climate-limited range edges (Lenoir et al., 2009; Peñuelas et al., 2007). Climate change scenarios predict a mean global temperature increase between 0.3 and 4.8 °C by 2100 compared to the 1985–2005 mean (IPCC, 2013). Consequently, shifts in the geographical distribution of a wide range of species are expected as climate change contributes to range expansion, retraction or fragmentation (Lenoir and Svenning, 2013; Masek, 2001). Regional variation in temperature anomalies means mountain ranges are expected to experience a higher than average temperature increase than other areas of the globe, making them particularly important for research into impacts of climate change (Dirnböck et al., 2011; IPCC, 2007).

Understanding the role that contemporary climate change has played in species range shifts has been the focus of much activity over recent decades (Chen et al., 2011a; Gottfried et al., 2012; Lenoir and Svenning, 2015; Parmesan and Yohe, 2003). In mountain ranges across the globe, average elevational range shifts have been estimated between 6.1 m (Parmesan and Yohe, 2003) and 12.2 m (Chen et al., 2011a) per decade. Although global average values demonstrate a general uphill shift of species, they hide important variation in this response between species and geographical locations. For example, Chen et al. (2011a) report that 25% of species showed downhill shifts of elevational range limits whilst Harsch et al. (2009) report that of 166 treeline sites investigated 52.4% showed upward treeline shifts, 46.4% showed no change and 1.2% showed movement downslope. The scientific literature on this topic shows a significant bias in research effort towards North American and European mountain ranges. Southern hemisphere and Asian ranges are less well studied and, consequently, strongly under-represented in the literature (Chen et al., 2011a; Harsch et al., 2009). The underrepresentation and omission of large mountain ranges combined with interspecific variation in range shifts results in

* Corresponding author.
E-mail address: a.s.jump@stir.ac.uk (A.S. Jump).

https://doi.org/10.1016/j.ecoinf.2017.12.002
Received 16 March 2017; Received in revised form 31 October 2017; Accepted 6 December 2017
Available online 07 December 2017
1574-9541/ © 2017 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/BY/4.0/).

high uncertainty in the extent and impacts of species distribution shifts in mountain ranges at a global scale.

The altitudinal treeline has been used as an indicator for assessing species range shifts in mountainous regions for decades. The separation between closed-canopy subalpine forest and open vegetation at higher altitudes and the sensitivity to climatic change make mountain treelines ideal candidates for monitoring species range shifts across wide geographic areas. Changes in altitudinal treeline position such as those reported in the meta-analysis of Harsch et al. (2009) tell only part of the story of how mountain forests respond to changes in climate. In areas where mountain treelines have not advanced upward, forests have been shown to respond to climatic change through increased tree density below the upper tree limit or by lateral expansion across mountain slopes (e.g. Bharti et al., 2012; Klasner and Fagre, 2002). Consequently, when assessing mountain forest range shifts there is a need to identify both lateral and altitudinal movement in the treeline.

Non-uniformity in species range shifts is partly driven by high habitat heterogeneity in mountain areas. Temperature is routinely noted as the key limiting factor in plant species distribution (Chen et al., 2011a; Gottfried et al., 2012; Lenoir and Svenning, 2015; Parmesan and Yohe, 2003). At a global scale treeline position can be approximated by temperature alone with a mean growing season temperature between 5.5 and 7.5 °C limiting tree growth (Körner and Paulsen, 2004) and winter temperatures playing a key role in juvenile survival (Kullman, 2007; Rickebusch et al., 2007). However, in mountainous systems, topographic and geological controls play important roles alongside climate in limiting species distribution (Chen et al., 2011b; Forero-Medina et al., 2011; Pounds et al., 2006). Topography alters local temperature and precipitation regimes resulting in cooler conditions on poleward facing slopes (Malanson et al., 2011; Suggitt et al., 2011). Rain shadows created on the leeward side of mountains may result in a moisture limited system where the response to climatic change would be expected to differ from systems where temperature is the primary limiting factor (Foden et al., 2007). Topographic modification of regional climate regimes leads to a variable treeline position in mountain regions that differs with slope and aspect at a landscape scale (e.g. Butler et al., 2007; Case and Buckley, 2015; Germino et al., 2002; Greenwood et al., 2014; Fig. 1). Furthermore, at the plot level, differences in micro-climate arising from sheltering caused by slight topographic differences and neighbouring vegetation influences seedling establishment, leading to complex patterns of treeline advance or stasis (e.g. Germino et al., 2002; Greenwood et al., 2015).

Non-thermal regulators lead to significant variation of within-species range shifts where 42–50% of species show inconsistencies in the direction of range shifts between different geographic regions despite similar warming trends (Gibson-Reinemer and Rahel, 2015). At the mountain treeline, non-thermal controls may restrict treeline response to climatic change or cause a downslope retreat due to local differences in resource availability (e.g. McNown and Sullivan, 2013; Sullivan et al., 2015), radiative stress (Bader et al., 2007), drought stress (e.g. Johnson and Smith, 2007; Leuschner and Schulte, 1991; Millar et al., 2007), competitive dynamics (Wardle and Coleman, 1992) and disturbance regimes (e.g. Cullen et al., 2001; Daniels and Veblen, 2003) despite increased temperatures. In some cases, the stand structure of the treeline itself can modulate response to climatic change through constraint or facilitation of tree establishment, growth, and mortality within the ecotone (Camarero et al., 2016). We cannot, therefore, assume that treeline shifts will be uniform within or between mountain ranges.

1.1. The impact of treeline advance

Shifts in mountain forest distribution, whether due to climatic change or release from a non-thermal control, are expected to impact on local biodiversity (Greenwood et al., 2014). The relative isolation of mountainous areas and highly heterogeneous habitats means that mountain systems can harbour disproportionately high numbers of endemic species and retain many rare species (Steinbauer et al., 2016). Encroachment of forest into non-forested areas will threaten mountain plant species through alterations to competitive dynamics where grassland species are likely to be out-competed for space and substrate by tree species as the forest advances (Grabherr et al., 1994) resulting in loss of species with narrow environmental tolerances (Jump et al., 2012).

In addition to the loss of biodiversity, shifts in high altitude forest distribution are expected to impact on ecosystem function (Greenwood and Jump, 2014). High altitude forests are important areas for carbon storage and sequestration (Peng et al., 2009; White et al., 2000). However, there has been little research into the impacts mountain treeline advance will have on carbon storage potential (Greenwood and Jump, 2014). Increased tree growth rates, density, and forest expansion is expected to increase biomass in mountain forests and their ability to act as carbon sinks may be increased as a result (Devi et al., 2008).

Ultimately, variation in mountain forest distribution shifts and the associated impacts are driven by the speed and spatial distribution of establishing juveniles at a plot scale. However, changes in forest distribution accumulate across the landscape and as such the impacts are manifested to a greater degree across an entire mountain range (hereafter referred to as regional scale). Accurate estimation of treeline shifts and the impacts, therefore, requires complex patterns of treeline advance or stasis at the plot level to be discriminated at regional scales. The biggest challenge to characterising mountain treeline heterogeneity at a regional scale is the generally poor accessibility of mountain ranges. The best estimation of species range shifts would come from multiple fixed monitoring sites across a mountain range (e.g. Global Observation Research Initiative in Alpine Environments; Grabherr et al., 2000). However, poor access means many studies have been based on incidental historical records covering a limited number of sites (Gottfried et al., 2012). Regional estimations based on limited field surveys alone in highly heterogeneous systems increase the risk of highly inaccurate estimates of change in forest distribution.

Remote sensing, a technique by which observations can be made without direct contact with a feature of interest, is ideally suited to capturing information across large geographic areas and its potential for studying environmental change is well recognised (Buchanan et al., 2015; Donoghue, 2002; Kennedy et al., 2014; Kerr and Ostrovsky, 2003). Considerable investment has been made over recent decades to improve precision and global coverage of remotely sensed data to aid monitoring of environmental change. Whilst the use of remotely sensed data in studies of mountain treeline shifts is not yet extensive, studies that have incorporated remotely sensed data have shown considerable potential for the characterisation of structural variation in the treeline (e.g. Allen and Walsh, 1996; Hill et al., 2007), assessment of distribution change (e.g. Bharti et al., 2012; Luo and Dai, 2013; Mihai et al., 2017), and to better understand how environmental factors act to influence variation in treeline position and structure over differing geographic scales (Weiss et al., 2015).

The integration of spatially explicit data, derived from remotely sensed data, on treeline structural variation and location across entire mountain ranges has significant benefits to better understand patterns and processes that govern treeline movement or stasis. Bader and Ruijten (2008) identified the mountain treeline from a Landsat ETM image and subsequently modelled the role of topography to predict forest cover. By linking a classified map with a digital elevation model Bader and Ruijten (2008) identified altitude as the main determinant of forest cover, with aspect also having a significant effect and areas where water and cold air accumulate resulting in inverted tree lines. Greenwood et al. (2014) used a time series of aerial photographs to identify patterns of treeline advance, highlighting the major role of topography in controlling treeline advance and subsequently, the microsite characteristics influencing variation in tree establishment identified from remotely sensed data (Greenwood et al., 2015). Work

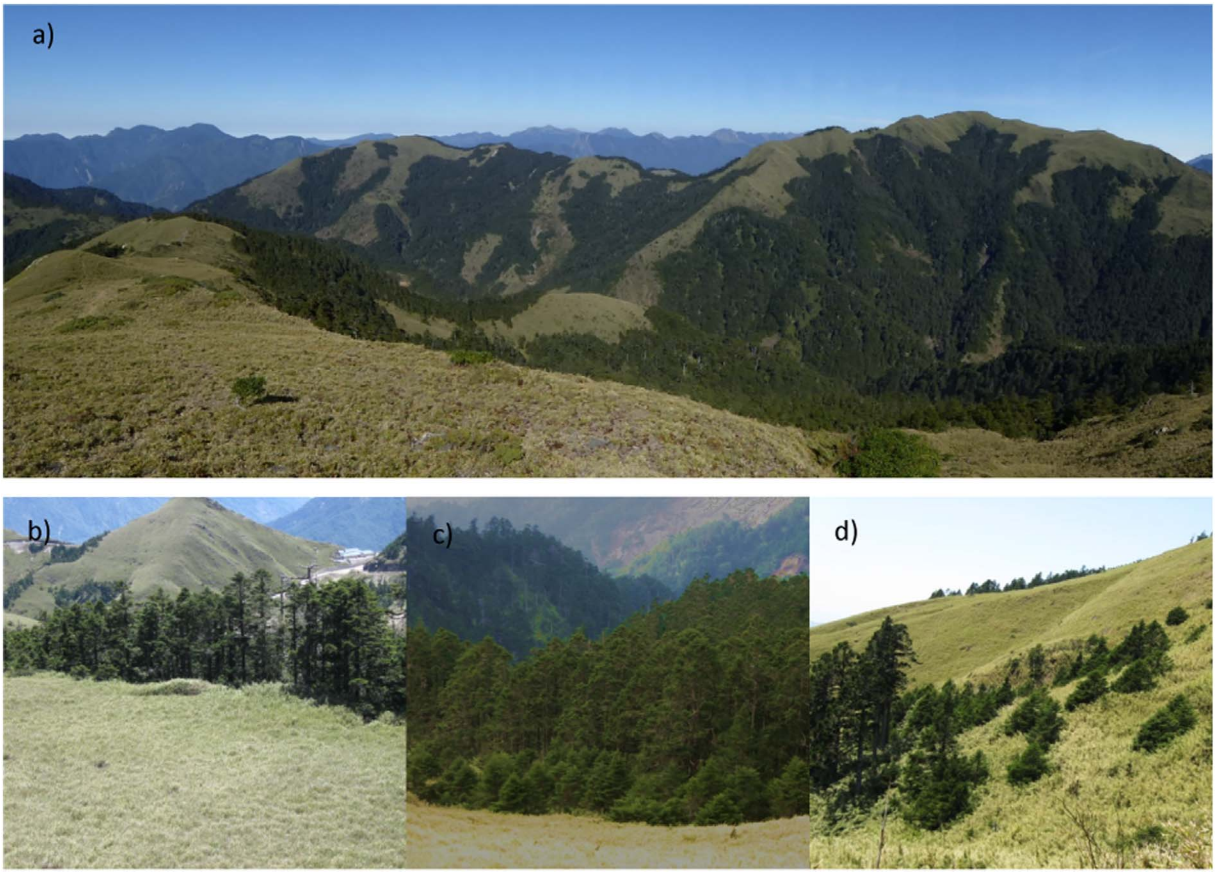

Fig. 1. Treeline position varies over short distances on mountain slopes (a) with different structural treeline forms identified (b–d). Static forms (b) have a sharp boundary between old growth forest and grassland, abrupt advancing forms (c) are characterised by a high density of establishing juveniles over a short distance and diffuse advancing forms (d) have low-density juveniles spread over a long distance. All photographs show mountain forests in Taiwan dominated by the Taiwan fir, *Abies kawakamii*. Photo credit (a) PJM (b–d) S. Greenwood.

that established temperature as the primary control of the treeline in field surveys (Baker and Weisberg, 1995) has been similarly advanced using remotely sensed time-series data with variability in treeline position shown to be attributable to topography at the regional scale (Allen and Walsh, 1996).

It is evident that significant benefits can be gained by incorporating remotely sensed data into studies of mountain treelines; however, spatially explicit data detailing the location and structural variation of mountain forests at the treeline is lacking globally. Our understanding of how processes operate at different spatial scales to influence the heterogeneity of mountain treelines will be advanced by incorporating spatially explicit data into analysis (Malanson et al., 2011). Additionally, our ability to monitor shifts in mountain forest distribution, identify the related impacts, and predict future changes in forest distribution should become more accurate as a result. Despite the considerable benefits gained by using remotely sensed data to monitor change in treeline position and structure, methodological approaches vary considerably in the literature. This variation has coincided with poor training and validation procedures which lead to uncertainty in the suitability of remotely sensed data to assess change in mountain forest distribution. The consequent lack of consistency between studies will present a barrier to accurate and integrated estimations of change and its impacts over coming decades.

To advance our ability to accurately quantify and predict changes in forest structure and distribution in mountain regions, here we synthesise information from three core themes: the suitability of remote sensing data, the ecological relevance of classifications, and the effectiveness of the training and validation process specifically in relation to the study of mountain treeline ecotones. By identifying how we might improve the consistency of current approaches and the ability to relate results to the wider ecological literature, we aim to bridge the gap between global and plot-level studies. In doing so, we endeavour to provide new focus in the use of remote sensing data in mountain regions to improve: (1) our understanding of pattern-process relationships at the mountain treeline, and (2) estimates of species range shifts and the impacts to biodiversity and ecosystem function.

2. Interpreting the mountain treeline in remotely sensed imagery

2.1. Suitability of remotely sensed data

When considering how appropriate an individual remote sensing data set is for treeline research three key requirements need to be considered. The first is the ability to characterise heterogeneity in forest structure that occurs over short distances; the second is the ability to quantify change that occurs over decadal periods; and the third is the need to capture a large area (i.e. a mountain range) repeatedly and consistently enough to allow for knowledge acquired in the field to be extrapolated across a mountain range. There is usually a compromise to be made between spatial, temporal and spectral resolution, geographic coverage and cost. Therefore, there is a need to identify which data set (s) are the most appropriate to address the need for characterisation of treeline structural heterogeneity and variable response rates across a mountain range.

2.1.1. Sensor type

Passive optical data are the primary choice of remote sensing data for use in mountainous regions. Passive optical sensors normally collect data in the visible and infrared spectrum during daylight when sunlight is reflecting off surfaces on the ground, recording different wavelengths of the spectrum into individual data bands. By capturing multiple spectral bands, the spectral properties of different vegetation types may be analysed by looking at the relationships between different bands. More bands may be beneficial for identifying subtle differences in vegetation structure, however, the increasing data complexity requires greater processing capacity and cost. Consequently, consideration should be given to determine whether the increase in spectral information that comes with additional bands provides data that will be ecologically meaningful.

There are significant challenges to overcome when using multispectral data in mountainous areas. The presence of cloud and cloud shadow in images frequently inhibits mapping from multispectral images. To overcome this problem, multiple images collected over a short time period may be mosaicked (stitching overlapping images together) to produce a single cloud-free image that can be used for analysis. Shadowing caused by steep terrain is also problematic in multispectral data. The effect of shadowing caused by mountain slopes can be reduced by topographic illumination correction, the use of spectral indices that take ratios between individual spectral bands, or by including shadow as a class during discrete classification procedures. It is also necessary to correct for differences in geometry between images that are used for mosaicking or for making comparisons between images of different resolution or ages. Differences in the sensor position at the time of acquisition relative to the area of interest can lead to differences in the relative distances between features within an image. This effect is magnified in mountainous terrain where slopes are stretched disproportionately depending on their aspect in relation to the sensor. Consequently, the resulting data sets may not overlay accurately despite being in the same coordinate system, causing problems in analysis or incorrect results if this distortion is not picked up early during data processing.

Active sensors emit their own signal that interacts with and is received back from ground surfaces. Synthetic Aperture Radar (SAR) emits microwave signals that are able to penetrate cloud making SAR imagery attractive for the study of persistently or seasonally cloudy areas. However, SAR data suffers from geometric distortion and shadowing in areas with steep terrain because the sensors use directional signals, which when combined with high cost and the historically low spatial resolution of available data has restricted the use of SAR to monitor vegetation in mountainous environments (Halperin et al., 2016; Sinha et al., 2015). To our knowledge, SAR has not been used to study the mountain treeline. However, ongoing improvements in resolution and data availability make further investigation of the utility of SAR for this purpose a priority.

Light Detection and Ranging (LiDAR) is an active optical sensor that is widely used for the characterisation of forest structure (e.g. Coops et al., 2013; Donoghue and Watt, 2006; van Leeuwen and Nieuwenhuis, 2010). Whilst there are significant benefits to using LiDAR data to characterise structural variation at the treeline, data accessibility is a major constraint. LiDAR data is typically acquired from airborne or terrestrial platforms, is expensive to acquire and not routinely acquired in mountain ranges globally restricting the use of such data. Consequently, LiDAR has not been widely used to study mountain treelines and has only been used to study relatively small areas (e.g. Coops et al., 2013 covered approximately 700 ha of a valley in the Swiss Alps). Using the satellite-borne LiDAR Geoscience Laser Altimeter System (GLAS), Simard et al. (2011) produced a global forest canopy height dataset. However, whilst this dataset represents a significant milestone in mapping global forest canopy height, the 1 km resolution is not suitable for the application of characterising heterogeneity in the mountain treeline. The anticipated launch of the Global Ecosystem Dynamics Investigation (GEDI) LiDAR sensor in 2018 will provide a significant improvement in resolution over the GLAS sensor (Coyle et al., 2015; Dubayah et al., 2014) and thus further investigation once data sets become available will be a priority to assess the potential suitability of LiDAR data sets from the GEDI sensor for characterisation of mountain treeline structure.

2.1.2. Geographic coverage

When seeking to monitor changes in species distribution across a mountain range, the platform on which a sensor is based has important implications for the geographic extent of a study. Sensors may be borne on satellite, manned aircraft, remotely piloted airborne systems (RPAS) or used on the ground. As terrestrial platforms must be set up in the field they are limited to sections of a mountain range with good access, consequently, they are useful for surveys of individual plots but have limited use in regional-scale studies. RPAS can provide very high-resolution data, however, they are most suited to local scale studies, covering individual mountains, as they are limited by good weather conditions with light winds and short flight times. Aerial photography missions can cover a wide spatial area with high-resolution data captured. However, the use of aerial photography for regional-scale analyses is extremely limited since assembling a complete regional dataset is not only time consuming and costly but also logistically highly challenging due to the limited number of clear days available for survey and time required to fly each mission. Therefore, satellite-borne sensors are the preferred platform for detecting environmental change over wide geographic areas due to the repeatable and predictable orbit pattern that ensures frequent global coverage.

2.1.3. Temporal resolution

Changes in mountain vegetation distribution can be slow. Consequently, the longevity and consistency of a data source over decadal time periods is highly important when identifying historical shifts in distribution and accounting for variation in rates of advance. Where historical photographic records exist, aerial photographs often offer the longest time record of remotely sensed data. However, the use of aerial photography is limited in regional scale assessments due to poor consistency of data between the dates of image acquisition and patchy geographic coverage that results in a small subset of a study region being covered by multiple records. Archives from satellite-borne sensors are preferable because of the data consistency and wide area coverage; however, whilst some historic declassified high-resolution spy satellite data are available in some parts of the world, most new commercial satellites have not been operational long enough to allow a robust assessment of change in mountain treelines. The Landsat archive is the most complete medium resolution satellite-borne archive, making 80 m pixel size imagery freely available dating back to 1973, and 30 m pixel size data available since 1982 (Wulder et al., 2016). The longevity and consistency of the Landsat archive means that landscape-scale changes in species ranges can be assessed and tracked as new acquisitions are made available. However, whilst remotely sensed data may be available, the lack of accompanying field data for each image in a series presents a major constraint on analysis utilising images from multiple dates. If only two images, spaced far apart in time, are used, the error around the classification of any individual image could lead to misinterpretation of change that may not be representative of ground conditions. The inclusion of multiple images, separated by shorter time periods, in an analysis will give a better indication of how treeline shifts respond over time and increase confidence in changes detected rather than taking two images at extremes of a study period (Kennedy et al., 2014).

2.1.4. Spatial resolution

The spatial resolution of a sensor is most easily understood as the size of a pixel, although one must be careful when interpreting the ecological meaning of boundaries between pixels (Fisher, 1997). When attempting to correlate field data on stand structure with remotely sensed data it is necessary to ensure that the pixel size is suitably matched to the plot size of interest because the resolution will affect the ability to accurately represent the boundary. For example, very high-resolution sensors allow for individual trees to be identified whereas coarse resolution data give a more general landscape pattern. There is high variation in the rate of mountain treeline advance; however, where advance occurs it is typically in the order of meters to tens of meters over decadal periods. To characterise treeline heterogeneity, we are primarily interested in sensors with resolutions capable of capturing stand-level characteristics that exist at these orders of magnitude. Coarse resolution (250–1000 m pixel size) MODIS or AVHHR imagery, therefore, lacks sufficient resolution for the accurate characterisation of vegetation heterogeneity in mountain systems.

Medium resolution imagery (circa 30 m pixel size), such as Landsat, has been shown to accurately classify mountain treelines into categories that recognised heterogeneity (Allen and Walsh, 1996). However, others have raised concern that Landsat data may lack sufficient detail to detect subtle differences in the treeline that exist over a very short spatial scale (Bharti et al., 2012; Buchanan et al., 2015; Chen et al., 2015). Consequently, there is uncertainty over the ability of data from the Landsat archive to adequately characterise variation in treeline heterogeneity. Imagery with a spatial resolution suitable for detecting features or variation of ecological relevance is widely available due to the development of many high-resolution sensors onboard satellites (Kennedy et al., 2014; Kerr and Ostrovsky, 2003). Indeed, higher resolution imagery (10 m pixel size or smaller) has been frequently used in studies of mountain treelines (Table 1). However, inconsistencies in the treeline definition used amongst the current literature mean that it has not been possible to quantify the spatial resolution at which defining features of treeline structural heterogeneity can be resolved.

2.1.5. Radiometric resolution

The radiometric resolution of a data set is a technical aspect of data storage. Radiometric resolution determines the number of unique values that can be stored by a sensor. 8-bit data hold 256 unique values where-as 16-bit data hold 65,536 values. Although considered of less relevance when choosing a data set, a higher radiometric resolution is beneficial for ecotone characterisation as the higher contrast that comes with a higher bit rate is likely to lead to better characterisation of vegetation heterogeneity and areas of diffuse boundary change. As data storage and processing capabilities improve, modern sensors are shifting to a higher number of bits for storage. A good example of this is Landsat 8 which is recorded in 12-bit data but has retained a 30 m pixel size to maintain consistency in spatial resolution with the previous sensors in the series. Consequently, whilst the spatial resolution of the sensor has not changed the greater radiometric resolution will result in a better characterisation of features with subtle differences.

2.2. Ecological relevance of classification

Remotely sensed data have great potential to enable the production of globally consistent maps that characterise variation in mountain treeline structure and would make significant contributions to resolving two major gaps in the literature. The first is the need for theoretically and methodologically consistent approaches to better define geographic variability in treeline pattern-process relationships (Malanson et al., 2011). The second is the need to monitor impacts of treeline shifts to biodiversity and ecosystem function across mountain ranges (Greenwood and Jump, 2014).

2.2.1. Defining the treeline

A variety of different definitions of the mountain treeline have been used in the literature. Single characteristics such as canopy cover (Hill et al., 2007; Král, 2009), species (Bharti et al., 2012; Luo and Dai, 2013) or height (Mathisen et al., 2014) have been used as well as combinations of such characteristics to return structural classifications of the treeline (Table 1). The definition of treeline ecotone used requires careful consideration since the choices made can impact on any interpretation of the change estimated and the subsequent utility of distribution maps.

Identification of broad areas of change where forest patches share similar structure is important for improving consistency in the

Table 1

Summary of studies using passive optical remotely sensed data to study mountain treelines. Studies using a discrete classification define discrete classes of vegetation type, those using a soft classification return a proportional representation of the criteria used for classification. Map accuracy assessment was considered quantitative if the authors returned a numerical indicator of accuracy either through a traditional accuracy assessment or through regression as was the case in Hill et al. (2007). However, lack of good quality training validation data limits the interpretation of some quantitative assessments and so the table is filtered top to bottom to indicate the relative robustness of the validation process based on the quality of validation data and type of accuracy assessment.

Author	Remote sensing data	Spatial resolution (m)	Time series (years)	Criteria for treeline classification	Method	Training and validation data	Map accuracy assessment
Allen and Walsh, 1996	Landsat TM	30	12	Canopy cover and growth form	Discrete classification	Field survey and photo interpretation	Quantitative
Luo and Dai, 2013	Aerial photographs Quickbird	0.5 0.6–2.4	44	Species and height	Discrete Classification	Field survey and photo interpretation	Quantitative
Bharti et al., 2012	Landsat MSS Landsat TM	60 30	30	Species	Discrete classification	Field survey	Quantitative
Mihai et al., 2017	Landsat ETM Landsat OLI Sentinel 2 MSI	30 30 10	13	Species	Discrete classification	Romanian National Forest Inventory, Global Forest Loss Product (Hansen et al., 2013)	Quantitative
Hill et al., 2007	SPOT 5 HRG	10	NA	Canopy cover	Soft classification	Limited field assessment, 2.5 m NDVI	Quantitative
Greenwood et al., 2014	Aerial photographs	0.3–1	26–33	Canopy cover and height	Discrete classification	Field survey	Qualitative
Resler et al., 2004	Digital orthophoto quadrangle	2	NA	Canopy cover and growth form	Discrete classification	Photo interpretation	Quantitative
Dinca et al., 2017	Landsat TM Landsat ETM	30 30	34	Canopy cover	Discrete classification	Photo interpretation	Quantitative
Mathisen et al., 2014	Aerial photographs Quickbird Worldview	2 0.6 0.5	48–50	Height	Discrete classification	Limited field survey	Qualitative
Chen et al., 2015	Landsat TM	30	20	Canopy cover and species	Soft classification	Photo interpretation	Qualitative
Klasner and Fagre, 2002	Aerial photographs Digital orthophoto quadrangles	1 1	46	Canopy cover and growth form	Discrete classification	Photo interpretation	Qualitative
Král, 2009	Orthophoto map	0.9	NA	Canopy cover	Soft classification	None	Qualitative

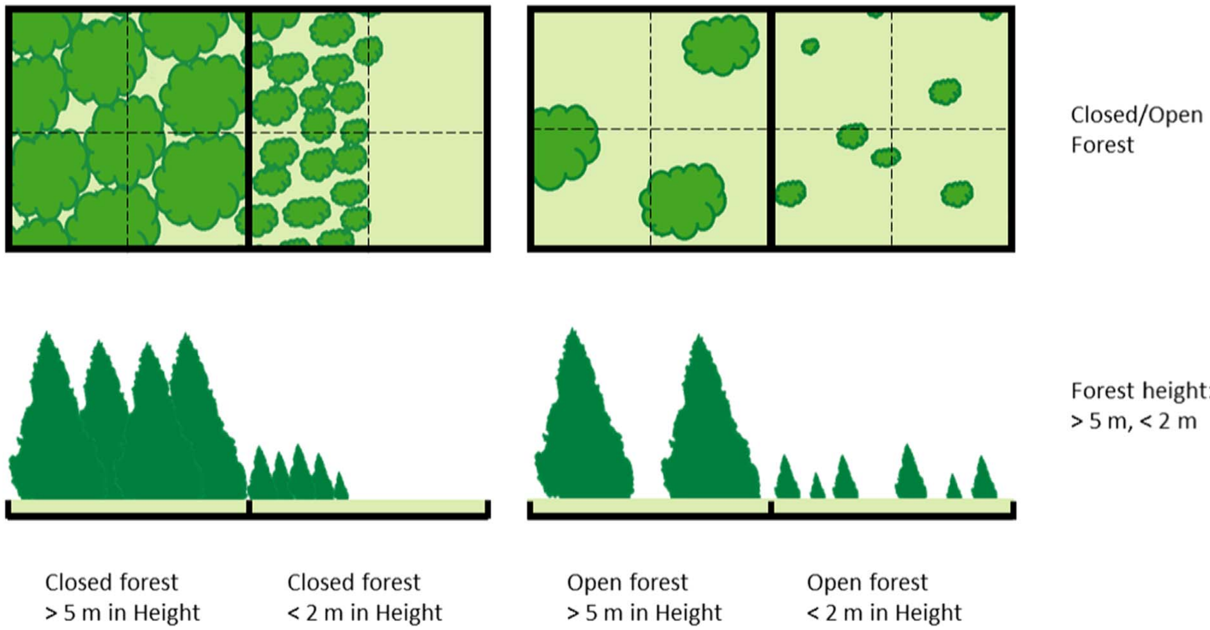

Fig. 2. Categorising mountain treelines using a single characteristic limits the interpretation of classified products. A forest classified by canopy cover alone may indicate how tree density differs over an area but both old growth forest and areas of new establishment can share the same forest class (e.g. closed forest top left, open forest top right). Similarly, if classification occurs by height alone then areas of establishment are identified but the processes that control differences in juvenile density cannot be interpreted. As such, classification based on multiple classifications is required to capture both the spatial distribution and the size of trees/juveniles across the treeline ecotone. The Spatial resolution of remote sensing imagery plays an important role in separating out fine scale differences in forest structure. Coarse resolution (Solid lines) capture information across a wider area and consequently results in mixed pixels where the forested area is smaller than the area covered by a single pixel. Finer resolution imagery, represented by the dashed lines, reduces the error in classifying mixed pixels by capturing a smaller area allowing areas with a homogeneous structure to be identified.

definition of geographic variation in treeline. Individual elements of forest structure return distinct information about the treeline; for example, canopy cover can describe the spatial distribution and density of trees within a plot, tree height indicates areas of forest establishment or growth limitation, and separating out species composition identifies species-specific responses to environmental conditions. However, definitions based on a single characteristic fail to recognise important features of treelines that capture variation in the rate of change within a mountain range (Fig. 2).

The benefit of definitions that consider multiple structural characteristics over those based on a single characteristic lies in the ability to assess variation in treeline response and ecosystem function. For example, a forest class defined as having a closed canopy may exist both in an old-growth forest and in an area of dense juvenile establishment. Without a distinction between the height of trees within a pixel, change is potentially misrepresented. Likewise, if the focus is solely on height, a better indication of change may be indicated by smaller, establishing trees but the underlying processes that drive differences in tree density within plots cannot be linked to maps classified on height alone (Fig. 2). When considering a discrete separation of treeline structural properties, vegetation classes such as krummholtz, patch forest, continuous forest and forested scree have been successfully classified in multispectral imagery (Allen and Walsh, 1996; Klasner and Fagre, 2002; Resler et al., 2004). However, the separation has primarily been based on canopy cover and growth form with less focus on height and species. Incorporating height into the definition of vegetation classes would represent a significant improvement in the biogeographic and ecological use of the mapped forest classes because it would allow the additional separation of the continuous and patch forest classes into categories that identify differences in growth stage. Without the inclusion of height, reliable assessment of change in forest distribution can only be assessed through a robust analysis over time, provided that remotely sensed images are available with good consistency, temporal and geographic coverage.

Patterns of juvenile establishment have been successfully classified from aerial photographs by Greenwood et al. (2014), who defined different stages of treeline advance including categories where the spatial distribution and quantity of juveniles vary beyond the limit of old growth forest. Unfortunately, issues in the registration of remote sensing imagery meant that the treeline was manually delineated and so the method does not represent a practical solution for regional studies. However, the work of Greenwood et al. (2014) demonstrates promise that such classification might be automated in the future.

2.2.2. Classification techniques

Ecotones can be difficult to delineate in remotely sensed imagery. By their nature, ecotones typically have no discrete boundary between the member classes at either end of a continuous scale (e.g. forest and grassland). Consequently, ecotones are often represented in satellite imagery as mixed pixels, a combination of membership to several different classes (e.g. a mixture of forest and grassland), raising the question of how best to classify such areas.

Boundary detection techniques seek to identify where change in vegetation occurs by seeking out the highest contrast in neighbouring pixel values, however, have not been used in the detection of mountain treelines from remotely sensed images as far as we are aware. Many techniques are well suited to the detection of abrupt changes in vegetation type, however, detection of areas with a gradual gradient between forest and grassland is often more challenging due to the reduction in contrast between neighbouring pixels (Fagan et al., 2003). In areas where the treeline is represented by an abrupt change, boundary detection techniques offer a good option for identifying the position of the treeline, however, they are not as well suited to defining variation in forest structural or function parameters.

Discrete image classification techniques assign pixels to one of a pre-defined set of categories. In areas where the number of boundary pixels between classes is small, discrete classifications give a reasonable estimate of area coverage. However, the mountain treeline ecotone can exist over a long distance and so by assigning a pixel to a fixed category, discrete image classification techniques may not be suitable if the thematic resolution of vegetation classes is too coarse (i.e. forest and grassland only) (Settle and Drake, 1993). Discrete classifications are attractive for treeline research, particularly for the investigation of pattern-process relationships, because of the ability to relate vegetation classes to existing literature that underpins our current understanding of environmental influence on variation in treeline position and structure. Discrete classifications work best where there is an obvious relationship between the spectral data and the ground variable of interest. However, whilst discrete classification techniques are the most commonly used classification method in the literature (Table 1), there has not been a quantitative assessment to identify how much variation in treeline structure is captured in the spectral response.

Soft classification (also known as fuzzy classification) techniques are an attractive alternative for ecotone mapping where no clear boundaries exist between vegetation classes because soft classification assigns individual pixels a score based on the degree of membership that pixel has to a given end member. The resultant data, therefore, describes a continuum in cover between different end members rather than a discrete classification of cover type. However, the resultant maps may not accurately represent actual vegetation cover depending on how the outcome of soft classifications is used (Hill et al., 2007). To describe areas of change, boundaries are often imposed onto soft classifications. However, when using a continuous definition of the treeline the process of defining the boundary requires careful consideration and should be based on detailed understanding of the ecological patterns since the subjective nature of imposing boundaries will impact on landscape metrics calculated from the chosen boundaries (Arnot et al., 2004). If not carefully considered, the utility of such methods may be reduced and the ability to relate classifications to the wider ecological literature may be lost.

2.3. Training and validation

Remote sensing data are highly valuable in mountain environments due to the ability to extrapolate information gathered from detailed surveys in accessible areas to largely inaccessible regions, thereby enabling us to fill the substantial knowledge gaps that we have of the pattern and rate of vegetation change in such regions. Classification of remotely sensed imagery typically uses data from pixel values where the ecological situation on the ground is well known to establish a rule, or set of rules, to extrapolate to pixels that appear spectrally similar. This supervised classification technique works best when there is a large sample of high-quality ground training data to match the imagery and an independent data set, derived from detailed field sampling, against which to assess the accuracy of a classification.

The benefit of good training and validation data and its importance for robust accuracy assessment has been well discussed elsewhere (Castilla, 2016; Olofsson et al., 2013, 2014). However, of the studies highlighted here, only seven (Allen and Walsh, 1996; Bharti et al., 2012; Dinca et al., 2017; Hill et al., 2007; Luo and Dai, 2013; Mihai et al., 2017; Resler et al., 2004) provide a quantitative accuracy assessment of the classification produced, either through a traditional confusion table with percent accuracy or through regression as in Hill et al. (2007). In some cases (e.g. Greenwood et al., 2014), despite the existence of detailed field data, a lack of quantitative accuracy assessment stems from issues registering remote sensing data and consequent manual classification. However, for most remaining cases, a lack of field data appears to be the root of qualitative assessments (Table 1).

Limited access to mountain environments makes acquiring a robust field data set to use for training and validation extremely challenging. Consequently, a variety of approaches have been taken to construct a data set that can be used to train classification algorithms and validate maps. Allen and Walsh (1996) and Luo and Dai (2013) used field datasets that identified forest structural classes, bolstered by additional photo interpreted plots to train and validate their classifications. Mihai et al. (2017) took advantage of existing national forest inventory data in combination with data from the Global Forest Cover product (Hansen et al., 2013) to create their training and validation data. Greenwood et al. (2014) were unable to automate classification, however, classification was based on detailed field knowledge collected from forest inventory data split across pre-defined structural classes. However, the limited accessibility of mountain ranges means that many studies have either carried out classification manually, without the use of training data, or by substituting field data entirely with photo interpreted plots from terrestrial photography (e.g. Klasner and Fagre, 2002) or very high-resolution aerial or satellite images (e.g. Chen et al., 2015).

Photointerpretation can be used to support good field data, especially where challenging terrain limits field campaigns. However, the use of photo interpretation as the sole source of training and validation data risks high uncertainty or subjectivity in classified products. The inclusion of novel remotely sensed data to assess the accuracy of a classified product can, however, be particularly useful in mountain areas where field sites cover a small area of a study region. Hill et al. (2007) used pan-sharpened SPOT 5 red and near-infrared bands to create a high-resolution NDVI product that could be used as a validation data set independently of a classified 10 m resolution image. In doing so, the subjectivity imposed by photo interpretation is reduced and, if backed up by field assessments, offers a complementary approach to accuracy assessment.

3. Research priorities

A lack of clarity in the definition of treeline structural classes that identify areas indicative of forest expansion or stasis has compounded issues in assessing the effectiveness of imagery with different resolutions and pairing that imagery with the most appropriate classification method. Inconsistencies have been exacerbated by a lack of field training and validation data that hinder accuracy assessments and crucially, when combined with poor treeline definitions, the relevance of species distribution maps derived from remote sensing products to the wider community is lost (Fig. 3). Accurate estimates of species range shifts are required if we are to provide information relevant to monitoring forest change with accompanying estimates of uncertainty. If such accuracy assessment is lacking, the validity of subsequent applications is compromised and potentially misrepresents the impacts that species distribution shifts are having on ecosystems, their function, and the ecosystem services that they provide.

3.1. Suitability of remotely sensed data

The trade-offs between spatial resolution, temporal resolution and geographic coverage has meant that the literature to-date generally uses a single data type/resolution whilst a combined approach may be more suitable for mountain ecosystems. By combining recent high-resolution imagery with a time series analysis of medium resolution imagery punctuated by historic aerial photography, an improved characterisation of the structural form and assessment of change may be possible. A key priority is, therefore, to identify the most appropriate method or a combination of methods that will allow for accurate assessments of regional shifts in mountain forest distribution.

In establishing the most appropriate methodologies for monitoring mountain forest shifts, there is a need to determine the resolution at which defining biophysical characteristics of treeline form are unable to be resolved within satellite images of decreasing spatial resolution. The Landsat archives provide the most globally consistent remotely sensed data available with images available since the 1980's at 30 m resolution. However, uncertainty remains over how well Landsat data can characterise structural variation in the treeline, when used either in a time series or as individual images. The recently available Sentinel 2 data represents an improvement in resolution over the Landsat archives giving a pixel size equivalent to 10 m at ground level, however, these data are only available since 2016. Establishing the level of detail

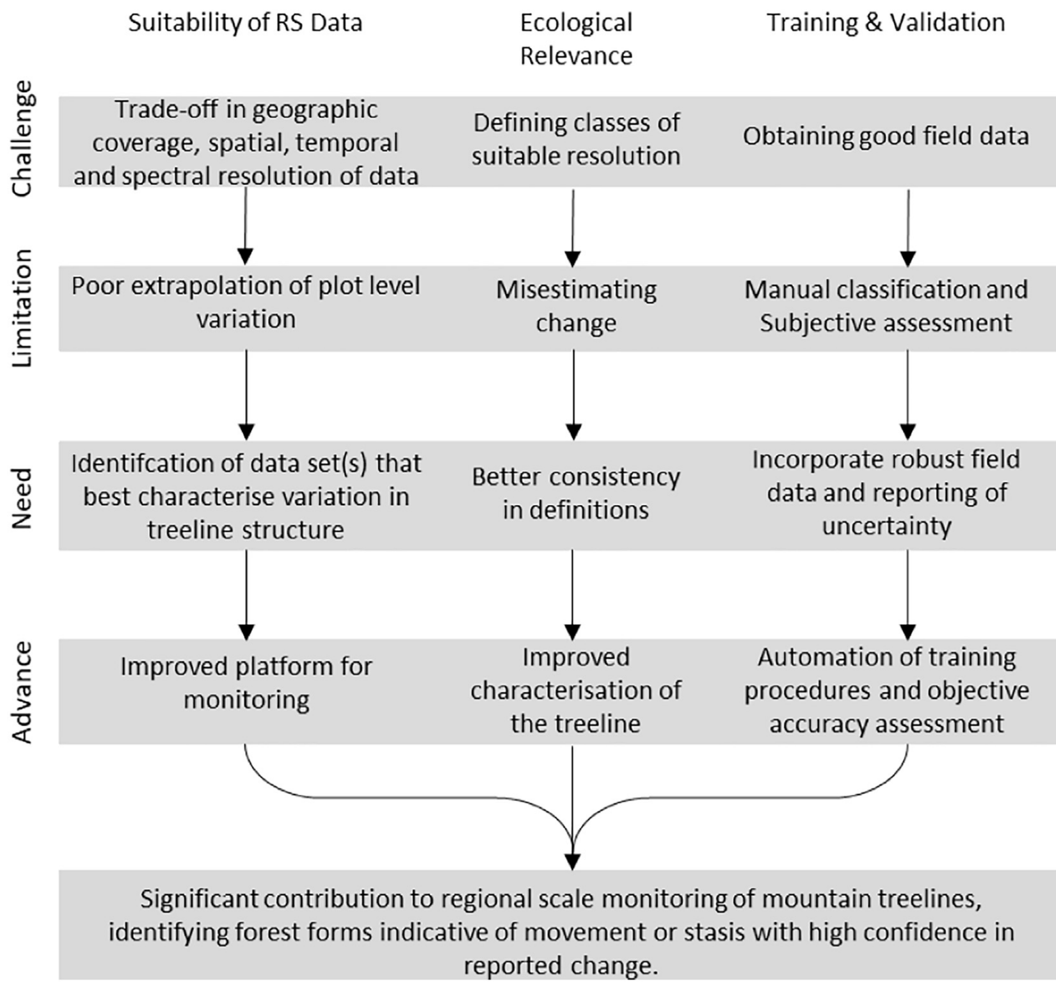

Fig. 3. Roadmap to advance regional scale monitoring of fine-scale variation in treeline advance by integrating remote sensing methods, ecological perspective, and robust field data. Whilst each of the three strands makes a modest advance in our ability to monitor treelines more effectively, when the individual themes are advanced in combination we significantly improve our ability to scale plot-level field data up to a regional scale consistently and in a way that allows results to be linked to the wider ecological literature and national monitoring schemes.

discernible in Sentinel 2 data will be useful to identify the necessity of commercial imagery. Finer spatial resolution imagery is available down to sub-meter pixels, however, this comes with an increase in financial and processing costs and thus its utility must be weighed against the expenditure since the increasing level of detail may not be necessary for distinguishing between treeline forms. Given the necessity of monitoring change over large areas, a key priority is then to identify the appropriate compromise between resolution and cost that still allows sufficient ecological and biogeographical information to be extracted and changes in treeline position that occur over decadal periods to be quantified.

3.2. Ecological relevance of classification

Ultimately the utility of remotely sensed images relies on the ability to separate vegetation into classes that hold ecological relevance. However, within the literature, we find an over-simplification of forest classes in studies of mountain treelines. At the altitudinal limit of forest distribution, treeline shifts, both lateral and elevational, are predominantly reflected by changes to the growth and establishment of the few tree species present, rather than by complex changes in community composition as might be expected in more tree species-rich forests. Recognition of establishing juveniles is therefore required in classifications derived from remote sensing data as it is the quantity and spatial distribution of establishing juveniles that determine the direction and velocity of treeline advance.

Treeline forms are broad structural categories based on patterns of tree and juvenile density, spatial distribution and size (Harsch and Bader, 2011; Fig. 1). Structural classes include diffuse advancing, abrupt advancing, abrupt static, island and krummholtz (Greenwood et al., 2014; Harsch and Bader, 2011). A rich body of literature identifies the underlying controls on the distribution of such classes. A review by Harsch and Bader (2011) described a hierarchy of mechanisms that are hypothesised to cause variation in treeline form. The diffuse form is primarily growth limited by low mean growing-season temperature whereas the krummholtz form incorporates dieback and regrowth of individuals. Abrupt forms are more extensively controlled by seedling mortality (Harsch and Bader, 2011). Identifying treeline forms that include local patterns of tree and juvenile density, distribution and size such as those used by Greenwood et al. (2014) and Harsch and Bader (2011), rather than classes based on adult distribution alone, will significantly advance our ability to characterise mountain treelines at a regional scale and study the impact that climate change is having on species distribution shifts. Whilst these forms will not appear in all mountain areas, they are sufficiently broad to allow a consistency in approaches that can be adapted of the exact ground conditions.

The use of treeline forms supports efforts to make classifications transferable to the wider literature and contribute to future monitoring programs in a consistent manner. Whilst carefully defined discrete categories may be linked to certain ecosystem functions, the ability to directly measure the function of interest would contribute significantly to the current knowledge gaps. Larger projects have identified variables to monitor the impacts of climate change including Essential Climate Variables from the Global Climate Observing System (Bojinski et al., 2014) and the more recently proposed Essential Biodiversity Variables (Pettorelli et al., 2016). However, treeline definitions that directly quantify ecosystem function are lacking in the literature. One example of global importance is above-ground biomass, which is noted for its potential suitability as an Essential Biodiversity Variable (Pettorelli et al., 2016). Changing forest distribution and increased densification at the mountain treeline is expected to increase the carbon storage capacity of mountain forests. As a function of tree density, girth, height and species, above ground biomass is an example of a continuous variable that measures both ecosystem function and accounts for variation in treeline structure. Whilst used extensively elsewhere, research is lacking quantifying changes in above ground biomass at the mountain treeline, yet the classification of above ground biomass from remotely sensed images would make a significant contribution to national monitoring projects.

3.3. Training and validation

Remote sensing classifications make assumptions about ground conditions based on the spectral signature observed. When monitoring inaccessible areas of mountain ranges, a robust field data set is required to reduce subjectivity when training classification algorithms and to independently assess the accuracy of distribution maps. The importance of accuracy assessment has been highlighted previously (Bharti et al., 2012; Castilla, 2016; Olofsson et al., 2013, 2014). However, low incorporation of field data and a quantitative accuracy assessment is a persistent problem in the literature (Table 1). Whilst Olofsson et al. (2014) made clear recommendations for sampling strategies to ensure a robust assessment, in practice, few studies of the mountain treeline either before or since have achieved this level. Consequently, there is a clear need to improve the integration of field and remotely sensed data to return a quantitative accuracy assessment and avoid misrepresentation of change in forest distribution.

Improving the integration of existing forest inventory datasets (e.g. Mihai et al., 2017) with new field campaigns that target treeline structures indicative of forest advance or stasis in accessible areas will increase the representation of vegetation structures of interest. By taking a purposive approach to data collection to first identify how the biophysical properties of the treeline relate to the spectral properties of remotely sensed data, we will be able to develop more robust protocols for data sampling and hypothesis testing. Accuracy reporting may take multiple forms. Presentation of confusion tables that compare the predicted class against that assigned in the field data would be suitable where discrete categories are predicted. If using continuous variables to characterise variation in forest structure reporting and visualising the error of pixel assignment, for example as a range in confidence intervals or the standard error, would contribute to our ability to assess how much is noise versus real change. Ultimately, such improvements will increase the efficiency of subsequent analysis and lead to the robust measurement of accuracy.

4. Conclusion

Ongoing environmental changes demand that we monitor changes in species distributions and identify their impacts over wide geographic areas. Advances in remote sensing technology and data availability provide a major opportunity to achieve regional scale monitoring. However, in mountain regions, their application remains problematic due to high habitat heterogeneity, variable rates of environmental change and poor access that restricts collection of field data. Considering key challenges for monitoring and predicting change in mountain forests, here we identify a need for further research that compares the utility of different remotely sensed data sets, better representation of variation in treeline structure, an improvement in the reporting of accuracy assessment and resource efficiency. Together, these advances will enable a more consistent approach to characterising spatial variation in treeline structure and allow us to more accurately link pattern and process over different geographic scales (Fig. 3). Ultimately, such improvements will enable us to meet a pressing need for better quantification and prediction of changes in species distribution and improved estimation of the impacts such changes will have on biodiversity and ecosystem function in mountainous regions.

Acknowledgements

This work was funded by the Natural Environment Research Council (UK) (NERC IAPETUS DTP NE/L002590/1). We are grateful to the anonymous reviewers for their comments and suggestions to improve this article.

References

Allen, T., Walsh, S., 1996. Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. Photogramm. Eng. Remote Sens. 62, 1261–1268.
Arnot, C., Fisher, P., Wadsworth, R., Wellens, J., 2004. Landscape metrics with ecotones: pattern under uncertainty. Landsc. Ecol. 19, 181–195.
Bader, M., Ruijten, J., 2008. A topography-based model of forest cover at the alpine tree line in the tropical Andes. J. Biogeogr. 35, 711–723.
Bader, M., van Geloof, I., Rietkerk, M., 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. Plant Ecol. 191, 33–45.
Baker, W., Weisberg, P., 1995. Landscape analysis of the Forest-Tundra Ecotone in Rocky Mountain National Park, Colorado. Prof. Geogr. 47, 361–375.
Bharti, R., Adhikari, B., Rawat, G., 2012. Assessing vegetation changes in timberline ecotone of Nanda Devi National Park, Uttarakhand. Int. J. Appl. Earth Obs. Geoinf. 18, 472–479.
Bojinski, S., Verstraete, M., Peterson, T., Richter, C., Simmons, A., Zemp, M., 2014. The concept of essential climate variables in support of climate research, applications, and policy. Bull. Am. Meteorol. Soc. 95, 1431–1443.
Buchanan, G., Brink, A., Leidner, A., Rose, R., Wegmann, M., 2015. Advancing terrestrial conservation through remote sensing. Eco. Inform. 30, 318–321.
Butler, D., Malanson, G., Walsh, S., Fagre, D., 2007. Influences of geomorphology and geology on alpine treeline in the American West—more important than climatic influences? Phys. Geogr. 28, 434–450.
Camarero, J., Linares, J., García-Cervigón, A., Batllori, E., Martínez, I., Gutiérrez, E., 2016. Back to the future: the responses of alpine treelines to climate warming are constrained by the current ecotone structure. Ecosystems 1–18.
Case, B., Buckley, H., 2015. Local-scale topoclimate efects on treeline elevations: a country-wide investigation of New Zealand's southern beech treelines. PeerJ 3, e1334. http://dx.doi.org/10.7717/peerj.1334.
Castilla, G., 2016. We must all pay more attention to rigor in accuracy assessment: additional comment to "the improvement of land cover classification by thermal remote sensing". Remote Sens. 7, 8368–8390 (8, 288).
Chen, I., Hill, J., Ohlemüller, R., Roy, D., Thomas, C., 2011a. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.
Chen, I., Hill, J., Shiu, H., Holloway, J., Benedick, S., Chey, V., Barlow, H., Thomas, C., 2011b. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. Glob. Ecol. Biogeogr. 20, 34–45.
Chen, Y., Lu, D., Luo, G., Huang, J., 2015. Detection of vegetation abundance change in the alpine tree line using multitemporal Landsat Thematic Mapper imagery. Int. J. Remote Sens. 36, 4683–4701.
Coops, N., Morsdorf, F., Schaepman, M., Zimmerman, N., 2013. Characterization of an alpine tree line using airborne LiDAR data and physiological modelling. Glob. Chang. Biol. 19, 3808–3821.
Coyle, D., Stysley, P., Poulios, D., Clarke, G., Kay, R., 2015. Laser transmitter development for NASA's Global Ecosystem Dynamics Investigatoin (GEDI) lidar. In: Proc. SPIE 9612, Lidar Remote Sensing for Environmental Monitoring XV, pp. 961208. http://dx.doi.org/10.1117/12.2191569.
Cullen, L., Stewart, G., Duncan, R., Palmer, J., 2001. Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. J. Ecol. 89, 1061–1071.
Daniels, L., Veblen, T., 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. J. Veg. Sci. 14, 733–742.
Devi, N., Hagedorn, F., Moiseev, P., Bugmann, H., Shiyatov, S., Mazepa, V., Rigling, A., 2008. Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. Glob. Chang. Biol. 14, 1581–1591.
Dinca, L., Nita, M., Hofgaard, A., Alados, C., Broll, G., Borz, S., Wertz, B., Monteiro, A., 2017. Forests dynamics in the mountain-alpine boundary: a comparative study using satellite imagery and climate data. Clim. Res. http://dx.doi.org/10.3354/cr01452.
Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob. Chang. Biol. 17, 990–996.
Donoghue, D., 2002. Remote sensing: environmental change. Prog. Phys. Geogr. 26, 144–151.
Donoghue, D., Watt, P., 2006. Using LiDAR to compare forest height estimates from IKONOS and Landsat ETM + data in Sitka spruce plantation forests. Int. J. Remote Sens. 27, 2161–2175.

Dubayah, R., Goetz, S., Blair, B., Fatoyinbo, T., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., Swatantran, A., 2014. The Global Ecosystem Dynamics Investigation. American Geophysical Union, Fall Meeting 2014. (abstract #U14A-07).

Fagan, W., Fortin, M., Soykan, C., 2003. Integrating edge detection and dynamic modelling in quantitative analyses of eological boundaries. Bioscience 53, 730–738.

Fisher, 1997. The pixel: a snare and a delusion. Int. J. Remote Sens. 18, 679–685.

Foden, W., Midgley, G., Hughes, G., Bond, W., Thuiller, W., Hoffman, T., Kaleme, P., Underhill, L., Rebelo, A., Hannah, L., 2007. A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. Divers. Distrib. 13, 645–653.

Forero-Medina, G., Joppa, L., Pimm, S., 2011. Constraints to species' elevational range shifts as climate changes. Conserv. Biol. 25, 163–171.

Germino, M., Smith, W., Resor, A., 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecol. 162, 157–168.

Gibson-Reinemer, D., Rahel, F., 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. PLoS One 10, e0132103.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J., Coldea, G., Dick, J., Erschbamer, B., Calzado, M., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I., Grabherr, G., 2012. Continent-wide response of mountain vegetation to climate change. Nat. Clim. Chang. 2, 111–115.

Grabherr, G., Gottfried, M., Pauli, H., 1994. Climate effects on mountain plants. Nature 369, 448.

Grabherr, G., Gottfried, M., Pauli, H., 2000. GLORIA: a global observation research initiative in alpine environments. Mt. Res. Dev. 20, 190–191.

Greenwood, S., Jump, A., 2014. Consequences of treeline shifts for the diversity and function of high altitude ecosystems. Arct. Antarct. Alp. Res. 46, 829–840.

Greenwood, S., Chen, J., Chen, C., Jump, A., 2014. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. Glob. Chang. Biol. 20, 3756–3766.

Greenwood, S., Chen, J., Chen, C., Jump, A., 2015. Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. J. Veg. Sci. 26, 711–721.

Halperin, J., LeMay, V., Coops, N., Verchot, L., Marshall, P., Lochhead, K., 2016. Canopy cover estimation in miombo woodlands of Zambia: comparison of Landsat 8 OLI versus RapidEye imagery using parametric, nonparametric, and semiparametric methods. Remote Sens. Environ. 179, 170–182.

Hansen, M., Potapov, P., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., Kommareddy, A., Egorov, A., Chini, L., Justice, C., Townshend, J., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853.

Harsch, M., Bader, M., 2011. Treeline form – a potential key to understanding treeline dynamics. Glob. Ecol. Biogeogr. 20, 582–596.

Harsch, M., Hulme, P., McGlone, M., Duncan, R., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol. Lett. 12, 1040–1049.

Hill, R., Granica, K., Smith, G., Schardt, M., 2007. Representation of an alpine treeline ecotone in SPOT 5 HRG data. Remote Sens. Environ. 110, 458–467.

IPCC, 2007. Climate change 2007: impacts, adaptation and vulnerability. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.K., and New York.

IPCC, 2013. Climate change 2013: the physical science basis. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.K., and New York.

Johnson, D., Smith, W., 2007. Limitations to photosynthetic carbon gain in timberline *Abies lasiocarpa* seedlings during prolonged drought. Can. J. For. Res. 37, 568–579.

Jump, A., Huang, T., Chou, C., 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. Ecography 35, 204–210.

Kennedy, R., Andréfouët, S., Cohen, W., Gómez, C., Griffiths, P., Hais, M., Healey, S., Helmer, E., Hostert, P., Lyons, M., Meigs, G., Pflugmacher, D., Phinn, S., Powell, S., Scarth, P., Sen, S., Schroeder, T., Schneider, A., Sonnenschein, R., Vogelmann, J., Wulder, M., Zhu, Z., 2014. Bringing an ecological view of change to Landsat-based remote sensing. Front. Ecol. Environ. 12, 339–346.

Kerr, J., Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. Trends Ecol. Evol. 18, 299–305.

Klasner, F., Fagre, D., 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. Arct. Antarct. Alp. Res. 34, 49–56.

Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732.

Král, K., 2009. Classification of current vegetation cover and alpine Treeline ecotone in the Praděd reserve (Czech Republic), using remote sensing. Mt. Res. Dev. 29, 177–183.

Kullman, L., 2007. Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. J. Ecol. 95, 41–52.

Lenoir, J., Svenning, J., 2013. Latitudinal and elevational range shifts under contemporary climate change. In: Levin, S. (Ed.), Encyclopedia of Biodiversity (Second Edition). Academic Press, pp. 599–611.

Lenoir, J., Svenning, J., 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography 38, 15–28.

Lenoir, J., Gégout, J., Pierrat, J., Bontemps, J., Dhôte, J., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). Ecography 32, 765–777.

Leuschner, C., Schulte, M., 1991. Microclimatological investigations in the tropical alpine scrub of Maui, Hawaii: evidence for a drought-induced alpine timberline. Pac. Sci. 45, 152–168.

Luo, G., Dai, L., 2013. Detection of alpine tree line change with high spatial resolution remotely sensed data. J. Appl. Remote. Sens. 7, 073520.

Malanson, G., Resler, L., Bader, M., Holtmeier, F.-K., Butler, D., Weiss, D., Daniels, L., Fagre, D., 2011. Mountain treelines: a roadmap for research orientation. Arct. Antarct. Alp. Res. 43, 167–177.

Masek, J., 2001. Stability of boreal forest stands during recent climate change: evidence from Landsat satellite imagery. J. Biogeogr. 28, 967–976.

Mathisen, I., Mikheeva, A., Tutubalina, O., Aune, S., Hofgaard, A., 2014. Fifty years of tree line change in the Khibiny Mountains, Russia. Advantages of combined remote sensing and dendroecological approaches. Appl. Veg. Sci. 17, 6–16.

McNown, R., Sullivan, P., 2013. Low photosynthesis of treeline white spruce is associated with limited soil nitrogen availability in the Western Brooks Range, Alaska. Funct. Ecol. 27, 672–683.

Mihai, B., Săvelescu, I., Rujoiu-Mare, M., Nistor, C., 2017. Recent forest cover changes (2002–2015) in the Southern Carpathians: case study of the Iezer Mountains, Romania. Sci. Total Environ. 599–600, 2166–2174.

Millar, C., Westfall, R., Delany, D., 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Can. J. For. Res. 37, 2508–2520.

Olofsson, P., Foody, G., Stehman, S., Woodcock, C., 2013. Making better use of accuracy data in land change studies: estimating accuracy and area and quantifying uncertainty using stratified estimation. Remote Sens. Environ. 129, 122–131.

Olofsson, P., Foody, G., Herold, M., Stehman, S., Woodcock, C., Wulder, M., 2014. Good practices for estimating area and assessing accuracy of land change. Remote Sens. Environ. 148, 42–57.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Pearson, R., Dawson, T., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371.

Peng, C., Zhou, X., Zhao, S., Wang, X., Zhu, B., Piao, S., Fang, J., 2009. Quantifying the response of forest carbon balance to future climate change in Northeastern China: model validation and prediction. Glob. Planet. Chang. 66, 179–194.

Peñuelas, J., Ogaya, R., Boada, M., Jump, A., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30, 830–838.

Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T., Fernandez, M., Lucas, R., Schaepman, M., Wang, T., O'Connor, B., Jongman, R., Kempeneers, P., Sonnenschein, R., Leidner, A., Böhm, M., He, K., Nagendra, H., Dubois, G., Fatoyinbo, T., Hansen, M., Paganini, M., Klerk, H., Asner, G., Kerr, J., Estes, A., Schmeller, D., Heiden, U., Rocchini, D., Pereira, H., Turak, E., Fernandez, N., Lausch, A., Cho, M., Alcaraz-Segura, D., McGeoch, M., Turner, W., Mueller, A., St-Louis, V., Penner, J., Vihervaara, P., Belward, A., Reyers, B., Geller, G., 2016. Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. Remote Sens. Ecol. Conserv. 2, 122–131.

Pounds, J., Bustamante, M., Coloma, L., Consuegra, J., Fogden, M., Foster, P., La Marca, E., Masters, K., Merino-Viteri, A., Puschendorf, R., Ron, S., Sánchez-Azofeifa, G., Still, C., Young, B., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161–167.

Resler, L., Fonstad, M., Butler, D., 2004. Mapping the alpine treeline ecotone with digital aerial photography and textural analysis. Geocarto Int. 19, 37–44.

Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A., Zimmermann, N., 2007. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. For. Ecol. Manag. 246, 251–263.

Settle, J., Drake, N., 1993. Linear mixing and the estimation of ground cover proportions. Int. J. Remote Sens. 14, 1159–1177.

Simard, M., Pinto, N., Fisher, J., Baccini, A., 2011. Mapping forest canopy height globally with spacebourne lidar. J. Geophys. Res. 116, G04021.

Sinha, S., Jeganathan, C., Sharma, L., Nathawat, M., 2015. A review of radar remote sensing for biomass estimation. Int. J. Environ. Sci. Technol. 12, 1779–1792.

Steinbauer, M., Field, R., Grytnes, J., Trigas, P., Ah-Peng, C., Attorre, F., Birks, J., Borges, P., Cardoso, P., Chou, C., Sanctis, M., de Sequeira, M., Duarte, M., Elias, R., Fernández-Palacios, J., Gabriel, R., Gereau, R., Gillespie, R., Greimler, J., Harter, D., Huang, T., Irl, S., Jeanmonod, D., Jentsch, A., Jump, A., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M., Strasberg, D., Stuessy, T., Svenning, J., Vetaas, O., Beierkuhnlein, C., 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation. Glob. Ecol. Biogeogr. 25, 1097–1107.

Suggitt, A., Gillingham, P., Hill, J., Huntley, B., Kunin, W., Roy, D., Thomas, C., 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120, 1–8.

Sullivan, P., Ellison, S., McNown, R., Brownlee, A., Sveinbjörnsson, B., 2015. Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. Ecology 96, 716–727.

van Leeuwen, M., Nieuwenhuis, M., 2010. Retrieval of forest structural parameters using LiDAR remote sensing. Eur. J. For. Res. 129, 749–770.

Wardle, P., Coleman, M., 1992. Evidence for rising upper limits of four native New Zealand forest trees. N. Z. J. Bot. 30, 303–314.

Weiss, D., Malanson, G., Walsh, S., 2015. Multiscale relationships between alpine treeline elevation and hypothesized environmental controls in the western United States. Ann. Assoc. Am. Geogr. 105, 437–453.

White, A., Cannell, M., Friend, A., 2000. The high-latitude terrestrial carbon sink: a model analysis. Glob. Chang. Biol. 6, 227–245.

Wulder, M., White, J., Loveland, T., Woodcock, C., Belward, A., Cohen, W., Fosnight, E., Shaw, J., Masek, J., Roy, D., 2016. The global Landsat archive: status, consolidation and direction. Remote Sens. Environ. 185, 271–283.