

Improved quantification of forest range shifts and their implications to ecosystem function in high-elevation forests

Peter James Morley

Biological and Environmental Sciences

Faculty of Natural Sciences

University of Stirling

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**UNIVERSITY of
STIRLING**



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Abstract

Rapid environmental changes are driving shifts in forest distribution across the globe with significant implications for ecosystem function and biodiversity. Despite the prevalence of forest range shifts across the globe, reliable estimations of changes in forest extent and structure at the elevational treeline (the elevational limit of forest distribution) are difficult to obtain due to limited access to mountainous environments. Remote sensing data is well suited to quantifying environmental change across large areas; however, a lack of published research that uses remotely sensed data in studies of mountain forests has led to uncertainty surrounding how much information about forest structure at the mountain treeline can be resolved in remotely sensed data. This uncertainty presents a major obstacle to landscape-scale quantification of forest range shifts and estimation of the impacts forest advance will have on ecosystem function and biodiversity in mountain systems. The distribution of high-elevation coniferous forests in the Central Mountain Range, Taiwan, has changed rapidly with increases in treeline elevation and forest density reported. Climate is considered to be the primary regulatory factor of the treeline in the Central Mountain Range. However, topography modifies the response of treeline advance to environmental change resulting in a structurally diverse treeline. This research combines a network of field observations across the Central Mountain Range, Taiwan, with aerial photography and multispectral satellite imagery to 1) determine which spectral features derived from multispectral satellite remote sensing best explain variation in mountain treeline structure and the effect of sensor spatial resolution on the characterisation of structural variation; 2) quantify variation in rates of forest advance; 3) quantify the accuracy of forest change assessments using a sample-based area estimation and classifying spectral trends identified in a time-series of satellite remote sensing data, and 4) quantify changes in above-ground woody biomass. The results presented here show that the green, red and short-wave infrared spectral bands and vegetation indices derived from these spectral bands offer the best characterisation of vegetation structure across the treeline ecotone with R^2 values reported up to 0.723. Sample-based change assessment using repeat aerial photography shows a 295.0 ha increase in forest area and a 115.1 m increase in the mean elevation of forest establishment between 1963 and 2016. The rate of forest advance is spatially variable with forest establishment occurring most rapidly on east and south facing slopes with gradients of 0-20° and is also temporally variable with the rate of forest establishment peaking between 1980 and 2001. The classification of spectral trends in time-series analysis shows that Landsat-based change estimates underestimate the area of forest advance in the Central Mountain Range. However, the general pattern and direction of habitat change are consistent

with those derived from sample-based estimates of change using repeat aerial photography offering the opportunity for error adjustment. Consequently, the results presented within this thesis show a net gain in above-ground woody biomass of 4688.7 t C in areas above 2400 m a.s.l. in the Central Mountain Range, Taiwan, and a reduction in the area of alpine grassland. The methods presented in this thesis provide a major opportunity to improve the quantification of forest range shifts across mountain systems allowing the estimation of landscape-scale impacts of forest advance on biodiversity and ecosystem function in data-poor mountain regions.

This thesis is presented as a collection of papers. Details and the current status of each paper are shown below:

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

Ecological Informatics **43**: 106–115

Quantifying structural diversity to better estimate change at mountain forest margins

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Contents

List of Figures	11
List of Tables	12
Chapter 1	13
Integrating remote sensing and demography for more efficient and effective assessment of changing mountain forest distribution.....	13
Abstract.....	15
1.1 Introduction	16
1.1.1 The impact of treeline advance	18
1.2 Interpreting the mountain treeline in remotely sensed imagery.....	21
1.2.1 Suitability of remotely sensed data	21
1.2.2 Ecological relevance of classification.....	25
1.2.3 Training and validation	29
1.3 Research priorities	34
1.3.1 Suitability of remotely sensed data	35
1.3.2 Ecological relevance of classification.....	36
1.3.3 Training and validation	37
1.4 Conclusion.....	38
1.5 Acknowledgements	39
1.6 Literature cited	39
Thesis aims.....	47
Chapter 2	49
Quantifying structural diversity measures to better estimate change at mountain forest margins	49
Abstract.....	51
2.2 Methods.....	57

2.2.1 Study location	57
2.2.2 Field data.....	57
2.2.3 Earth observation data	60
2.2.4 Statistical analysis	64
2.3 Results.....	65
2.3.1 Textural features.....	65
2.3.2 Spectral bands.....	67
2.3.3 Vegetation indices.....	69
2.3.4 Multiple regression	71
2.3.5 Data visualisation	73
2.4 Discussion.....	79
2.5 Conclusion.....	82
2.6 Acknowledgments.....	83
2.7 Literature cited.....	83
Supplimentary Information 1.....	91
Chapter 3	93
Identifying variation in patterns of forest advance in a high-elevation ecosystem	93
Abstract:.....	94
3.1 Introduction	95
3.2 Methods.....	98
3.2.1 Study area	98
3.2.2 Aerial photography	100
3.2.3 Change assessment.....	100
3.3 Results.....	103
3.3.1 Landscape-scale change estimates	103
3.3.2 Change estimates by terrain strata.....	105
3.3.3 Variation in the rate of change	106

3.4 Discussion	113
3.5 Conclusion.....	117
3.6 Acknowledgements	118
3.7 Literature cited	118
Chapter 4	124
Forest range shifts are increasing carbon sequestration potential in a subtropical mountain region.....	124
Abstract:	125
4.1 Introduction	126
4.2 Methods.....	128
4.2.1 Study area	128
4.2.2 Change assessment of forest area.....	129
4.2.3 Above-ground biomass estimation.....	131
4.3 Results.....	131
4.3.1 Area change assessment.....	131
4.3.2 Above-ground biomass estimate	134
4.4 Discussion	135
4.5 Conclusion.....	139
4.6 Literature cited	140
Appendix 4.1: Topographic Illumination Correction	145
Literature Cited	146
Appendix 4.2: Spatial Resolution Enhancement.....	148
Literature cited	149
Chapter 5	150
An integrated approach to assessments of montane forest range shifts	150
5.1 Introduction	151

5.2 Suitability of remote sensing data	152
5.3 Ecological relevance of classifications	154
5.4 Effectiveness of training and validation procedures	156
5.5 An integrated approach to change assessments in montane forests	157
5.6 Future directions.....	158
5.7 Conclusion.....	160
5.8 Literature cited.....	161

List of Figures

Chapter 1

Figure 1.1	Images showing treeline structural variation	18
Figure 1.2	Illustrated depiction of forest structural components	29
Figure 1.3	Roadmap of research priorities and advances	35

Chapter 2

Figure 2.1	Plots of stand biomass, tree height and tree density	60
Figure 2.2	Relationship between GRVI and forest / non-forest response with estimated probability of occurrence	75
Figure 2.3	Relationship between GRVI and full structural class response with estimated probability of occurrence	76
Figure 2.4	Relationship between GRVI and simplified structural class response with estimated probability of occurrence	77
Figure 2.5	Relationship between GRVI and above-ground biomass response with estimated biomass	78

Chapter 3

Figure 3.1	Aerial photography of study area	99
Figure 3.2	Plots of strata proportions	101
Figure 3.3	Aerial photography of change in vegetation class over time	102
Figure 3.4	Temporal changes in area and elevation of vegetation classes	104
Figure 3.5	Temporal changes in proportion of area occupied by each vegetation class by aspect and gradient	106
Figure 3.6	Temporal variation in the rate of recent forest establishment	108
Figure 3.7	Temporal variation in the rate of rapid forest establishment	110
Figure 3.8	Temporal variation in the rate of advanced forest establishment	112

Chapter 4

Figure 4.1	Map of vegetation change in Mt. Hehuan study area	134
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List of Tables

Chapter 1

Table 1.1	Summary of studies using passive optical remote sensing data to study mountain treelines	32
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Chapter 2

Table 2.1	Merits of different definitions of vegetation structure at the treeline	55
Table 2.2	Description of structural classes	58
Table 2.3	Spectral features used to investigate the relationships between statistical distribution of spectral values and vegetation structure	63
Table 2.4	Coefficient of determination from relationships between textural features derived from GeoEye sensor and vegetation structure	66
Table 2.5	Coefficient of determination from relationships between mean response of spectral bands and vegetation structure	68
Table 2.6	Coefficient of determination from relationships between mean response of vegetation indices and vegetation structure	70
Table 2.7	Coefficient of determination from relationships between multiple predictors of spectral response and vegetation structure	72
Table S.1	Coefficient of determination from relationships between textural features derived from SPOT-7 sensor and vegetation structure	91
Table S.2	Coefficient of determination from relationships between textural features derived from Sentinel-2 sensor and vegetation structure	92

Chapter 3

Table 3.1	Number of sample plots in each strata	100
Table 3.2	Description of vegetation classes	102
Table 3.3	Proportion of change in vegetation classes	105

Chapter 4

Table 4.1	Definition of vegetation change classes	130
Table 4.2	Area estimates for each vegetation change class	133
Table 4.3	Error matrix from Landsat time-series classification	133
Table 4.4	Estimated above-ground woody biomass	135

Chapter 1

Integrating remote sensing and demography for more efficient
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Authors: Peter J. Morley^a, Daniel N.M. Donoghue^b, Jan-Chang Chen^c, Alistair S. Jump^a

^aBiological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK.

^bDepartment of Geography, Durham University, Durham, DH1 3LE, UK.

^cDepartment of Forestry, National Pingtung University of Science and Technology, Pingtung 912, Taiwan.

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 shifts of elevational 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.

1.1 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 0.3-4.8 °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 the 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 while Harsh 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 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 5.5–7.5 °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; Figure 1.1). 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.

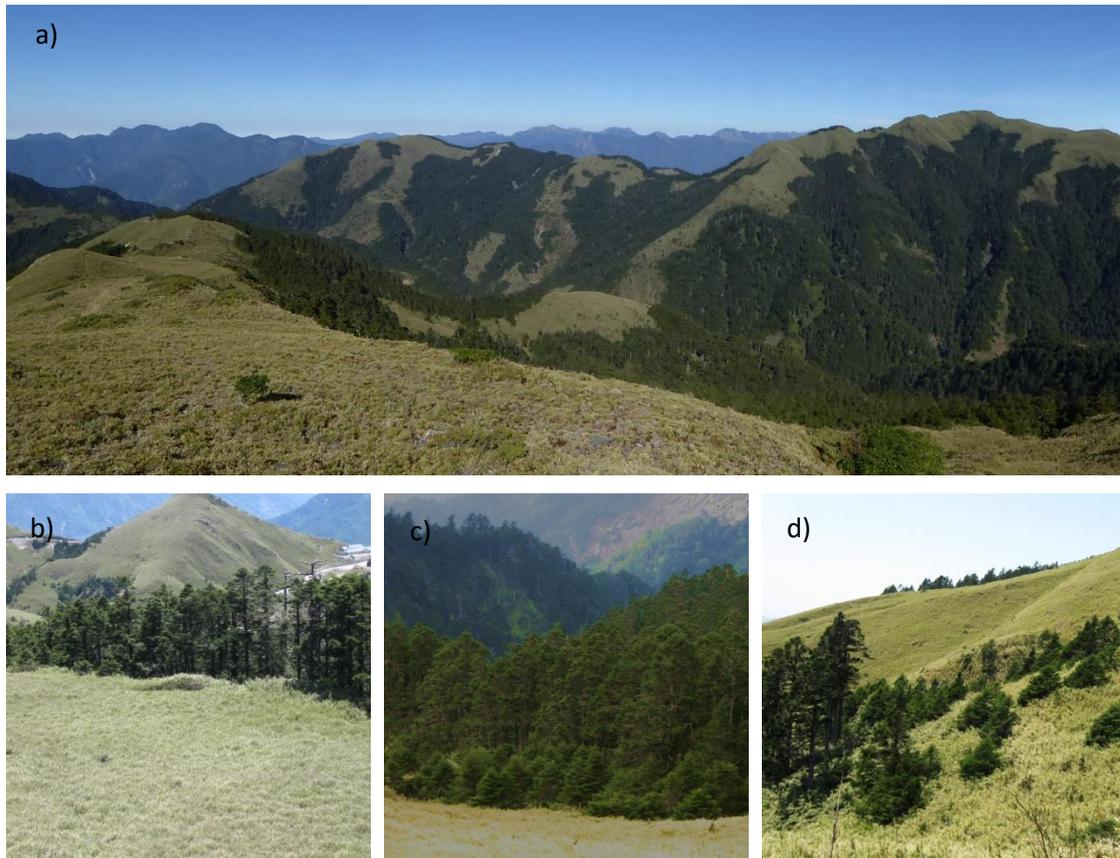


Figure 1.1: Treeline position varies over short distances on mountain slopes (a) with different structural treeline forms identified (b-d). Static forms (b) have a sharp boundary between old growth forest and grassland, abrupt advancing forms (c) are characterised by a high density of establishing juveniles 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.

1.1.1 The impact of treeline advance

Shifts in montane 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 a loss of species with narrow environmental tolerances (Jump et al. 2012).

In addition to the loss of biodiversity, shifts in montane forest distribution are expected to impact on ecosystem function (Greenwood and Jump, 2014). High elevation 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 are expected to increase biomass in montane forests and their ability to act as carbon sinks may be increased as a result (Devi et al., 2008).

Ultimately, variation in montane 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 the precision and global coverage of remotely sensed data to aid monitoring of environmental change. While 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 repeat aerial photography 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 that established temperature as the primary control of the treeline in field surveys (Baker and Weisberg, 1995) has been similarly advanced using remotely sensed data analysed over time 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 leads to uncertainty in the suitability of remotely sensed data to assess change in montane 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.

1.2 Interpreting the mountain treeline in remotely sensed imagery

1.2.1 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.

1.2.1.1 *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, while 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 (Dubayah et al., 2014; Coyle et al., 2015) 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.

1.2.1.2 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.

1.2.1.3 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, while 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).

1.2.1.4 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 AVHRR 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 1.1). 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

1.2.1.5 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 whereas 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.

1.2.2 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).

1.2.2.1 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 1.1). 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 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 (Figure 1.2).

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 (Figure 1.2). 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-scale studies. However, the work of Greenwood *et al.* (2014) demonstrates promise that such classification might be automated in the future.

1.2.2.2 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 type 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 for boundary detection 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, while discrete classification techniques are the most commonly used classification method in the literature (Table 1.1), 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 are 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.

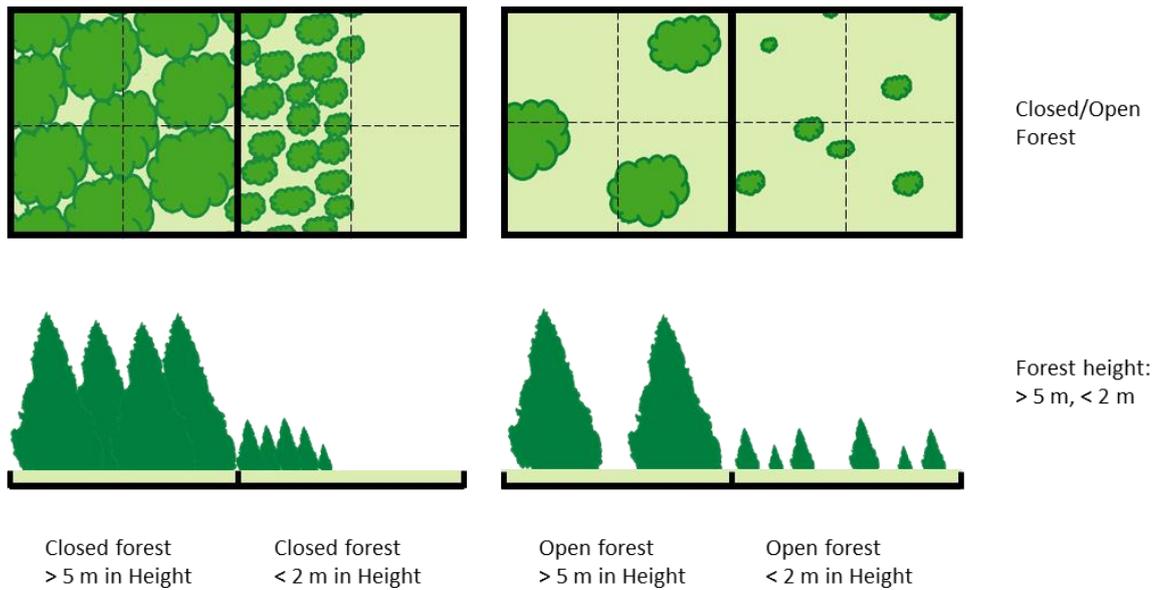


Figure 1.2: Categorising mountain treelines using a single characteristic limits the interpretation of classified products. A forest classified by canopy cover alone may indicate how tree density differs over an area but both old growth forest and areas of new establishment can share the same forest 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 characteristics 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.

1.2.3 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 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.*, 2014, 2013). 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 1.1).

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 Lou 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.

Table 1.1: 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 <i>et al.</i> , 2012	Landsat MSS Landsat TM	60 30	30	Species	Discrete Classification	Field survey	Quantitative
Mihai <i>et al.</i> , 2017	Landsat ETM Landsat OLI Sentinel 2 MSI	30 30 10	13	Species	Discrete Classification	Romanian National Forest Inventory, Global Forest Loss Product (Hansen <i>et al.</i> 2013)	Quantitative
Hill <i>et al.</i> , 2007	SPOT 5 HRG	10	NA	Canopy cover	Soft Classification	Limited field assessment, 2.5 m NDVI	Quantitative
Greenwood <i>et al.</i> , 2014	Aerial Photographs	0.3 – 1	26 -33	Canopy cover and Height	Discrete Classification	Field survey	Qualitative
Resler <i>et al.</i> , 2004	Digital Orthophoto Quadrangle	2	NA	Canopy cover and growth form	Discrete Classification	Photo interpretation	Quantitative
Dinca <i>et al.</i> , 2017	Landsat TM Landsat ETM	30 30	34	Canopy cover	Discrete Classification	Photo interpretation	Quantitative
Mathisen <i>et al.</i> , 2014	Aerial Photographs Quickbird Worldview	2 0.6 0.5	48-50	Height	Discrete Classification	Limited field survey	Qualitative

Chen <i>et al.</i> , 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

1.3 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 (Figure 1.3). 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.

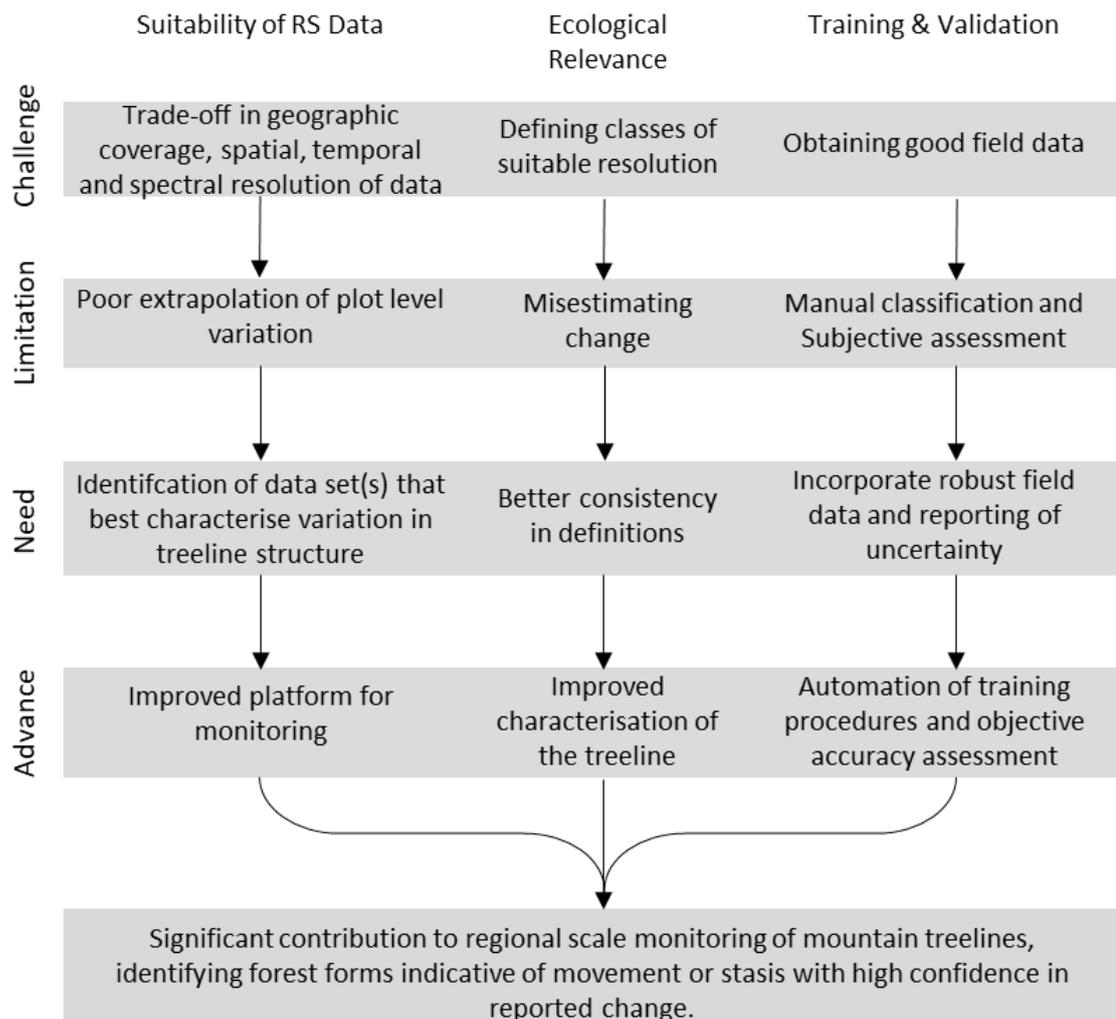


Figure 1.3: Roadmap to advance regional scale monitoring of fine-scale variation in treeline advance by integrating remote sensing methods, ecological perspective, and robust field data. Whilst each of the three strands makes a modest advance in our ability to monitor treelines more effectively, when 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.

1.3.1 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 while 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-scale shifts in montane forest distribution.

In establishing the most appropriate methodologies for monitoring montane 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 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.

1.3.2 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 elevational 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; Figure 1.1). 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. In a review by Harsh and Bader (2011) a hierarchy of mechanisms are described that are hypothesised to cause in 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 to the local 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.

1.3.3 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 validation 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.*, 2014, 2013). However, low incorporation of field data and a quantitative accuracy assessment is a persistent problem in the literature (Table 1.1). While 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.

1.4 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 the 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 (Figure 1.3). 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.

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Thesis aims

Three major research priorities have been identified where research is needed to improve the integration of remote sensing data into assessments of forest range shifts at mountain treelines to enable the quantification of the impacts that forest range shifts will have on biodiversity and ecosystem function (chapter 1). These priorities are the need to identify the suitability remote sensing data, the ecological relevance of maps derived from satellite image classifications, and the effectiveness of validation methods to achieve precise estimates of change. These priorities encompass a broad spectrum of research needs including methodological innovation as well as greater consistency in approaches taken to define geographic variation in forest range shifts in the broader research community. Therefore in this thesis, I focus on a set of research objectives that contribute toward filling the wider research gaps identified in chapter 1, enabling the quantification of forest range shifts and estimates of the impacts that forest advance will have on biodiversity and ecosystem function in the Central Mountain Range of Taiwan.

This thesis aims to improve estimates of montane forest range shifts by combining field observations with repeat aerial photography and multispectral Earth observation data across the Central Mountain Range of Taiwan. In chapter 2 I determine which spectral features derived from multispectral satellite Earth observation data best characterise variation in forest structure at the mountain treeline and quantify the effect of sensor spatial resolution on the characterisation of forest structure. In chapter 3 I quantify changes in forest area and elevation and identify variation in the rate of forest advance using repeat aerial photography. The precision of estimates of forest range shifts derived from repeat aerial photography and from Landsat time-series data is assessed in chapter 4, thereby enabling the quantification of landscape-scale changes in above-ground woody biomass. The suitability of remote sensing data is investigated primarily in chapters 2 and 4 where the effect of sensor spatial resolution is quantified, and the precision of change assessments derived from repeat aerial photography and Landsat time-series data are quantified. By identifying the suitability of remote sensing data sets, this thesis makes recommendations that seek to improve the consistency in approaches to defining geographic variation in forest range shifts. The ecological relevance of classifications is assessed throughout this thesis by quantifying 1) the degree of structural information that can be identified in multispectral remote sensing data (chapter 2); 2) variation in forest range shifts and changes in habitat area using repeat aerial photography (Chapter 3) and 3) changes in above-ground woody biomass at the mountain treeline (chapter 4). To improve the validation of forest range shifts, the precision of changes assessments from repeat aerial photography and

Landsat time-series are quantified and recommendations made to reduce the uncertainty in landscape-scale assessments of forest range shifts in mountain systems (chapters 3 and 4).

In chapter 5, I synthesise the knowledge gained in this thesis that aims to improve the application of remote sensing data in assessments of montane forest range shifts and provide some key directions for future research. By integrating remote sensing data into estimates of forest range shifts at mountain treelines, this thesis aims to provide much needed research that will improve our ecological and biogeographic understanding of forest range shifts and enable estimates of the impacts that forest advance will have on biodiversity and ecosystem function in mountain systems.

Chapter 2

Quantifying structural diversity measures to better estimate
change at mountain forest margins

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Title: Quantifying structural diversity measures to better estimate change at mountain forest margins

Authors: Peter J. Morley^a, Daniel N.M. Donoghue^b, Jan-Chang Chen^c, Alistair S. Jump^a

^aBiological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK.

^bDepartment of Geography, Durham University, Durham, DH1 3LE, UK.

^cDepartment of Forestry, National Pingtung University of Science and Technology, Pingtung 912, Taiwan.

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Abstract

Global environmental changes are driving shifts in forest distribution across the globe with significant implications for biodiversity and ecosystem function. At the upper elevational limit of forest distribution, patterns of forest advance and stasis can be highly spatially variable. Reliable estimations of forest distribution shifts require assessments of forest change to account for variation in treeline advance across entire mountain ranges. Multispectral satellite remote sensing is well suited to this purpose and is particularly valuable in regions where the scope of field campaigns is restricted. However, there is little understanding of how much information about forest structure at the mountain treeline can be derived from multispectral remote sensing data. Here we combine field data from a structurally diverse *treeline ecotone* in the Central Mountain Range, Taiwan, with data from four multispectral satellite sensors (GeoEye, SPOT-7, Sentinel-2 and Landsat-8) to identify spectral features that best explain variation in vegetation structure at the mountain treeline and the effect of sensor spatial resolution on the characterisation of structural variation. The green, red and short-wave infrared spectral bands and vegetation indices based on green and short-wave infrared bands offer the best characterisation of forest structure with R^2 values reported up to 0.723. There is very little quantitative difference in the ability of the sensors tested here to discriminate between discrete descriptors of vegetation structure (difference of R^2_{MF} within 0.09). Whilst Landsat-8 is less well suited to defining above-ground woody biomass (R^2 0.12-0.29 lower than the alternative sensors), there is little difference between the relationships defined for GeoEye, SPOT-7 and Sentinel-2 data (difference in $R^2 < 0.03$). Discrete classifications are best suited to the identification of forest structures indicative of treeline advance or stasis, using a simplified class designation to separate areas of old growth forest, forest advance and grassland habitats. Consequently, our results present a major opportunity to improve quantification of forest range shifts across mountain systems and to estimate the impacts of forest advance on biodiversity and ecosystem function.

2.1 Introduction

Rapid changes in global climate and land-use are driving shifts in forest distribution (Améztegui *et al.*, 2016, 2010; Harsch *et al.*, 2009). Mountain ecosystems are expected to experience higher than average temperature increases (Dirnböck *et al.*, 2011; IPCC, 2013; Pepin *et al.*, 2015) and are often subject to land abandonment as agricultural practices change (Haddaway *et al.*, 2014; MacDonald *et al.*, 2000). Naturally occurring elevational treelines (limits of forest distribution) are predominantly climatically determined (Körner and Paulsen, 2004), while the exact position of the treeline and response to environmental change varies due to topographic or geological controls (Butler *et al.*, 2007; Malanson *et al.*, 2011) as well as anthropogenic land-use (Améztegui *et al.*, 2016, 2010). Consequently, shifts in mountain forest distribution have been used as indicators of the impacts of global environmental change (Martin and Bellingham, 2016). Increased forest area and tree growth rates in mountain areas are expected to alter ecosystem service provision, most notably increasing the carbon storage potential of montane forests (Devi *et al.*, 2008; Peng *et al.*, 2009; White *et al.*, 2000). However, forest expansion is considered one of the most significant threats to grassland biodiversity world-wide (Bond and Parr, 2010) and is of concern in mountain ecosystems where disproportionately high numbers of endemic and rare species are found (Steinbauer *et al.*, 2016).

There is limited understanding of how shifts in forest distribution will impact biodiversity and ecosystem function across entire mountain ranges due to variation in the response of mountain forests to environmental change both within-species and between geographic areas (Greenwood and Jump, 2014). A meta-analysis of forest responses at the upper elevational and latitudinal treelines, found that of 166 sites investigated, 52.4 % show upward or poleward migration of forest, 46.4 % show no change and 1.2 % show downslope movement (Harsch *et al.*, 2009). In areas where change in treeline elevation is not exhibited, increased tree density below the upper limit of forest distribution and across-slope movement have been observed (e.g. Bharti *et al.*, 2012; Klasner and Fagre, 2002). Accurately identifying geographic variation in mountain forest response to environmental change is, therefore, essential to improve the understanding of drivers of forest change and to enable assessments of the impacts of changing treeline position and structure on biodiversity and ecosystem function.

Remote sensing provides an opportunity to expand the scope of field surveys which are often restricted to localised, easily accessible mountain areas due to high time and financial

costs. However, characterising variation in forest structure from remote sensing data presents significant challenges for accurately quantifying variation in forest response to environmental change. In some areas, a sharp, well-defined boundary between the forest and the grassland exists. However, mountain treelines are often represented as an ecotone, with a gradual transition between forest and grassland habitats. Despite the prevalence of gradual forest changes globally, there is no optimal method for characterising structural variation in mountain forest-grassland transitions that lack clear boundaries between vegetation classes (Fortin *et al.*, 2000; Hill *et al.*, 2007).

The type of sensor and platform used to acquire remotely sensed data will impact the degree of forest structural information that can be identified and the geographic extent of investigations at mountain treelines. Airborne Laser Scanning (ALS) data are an attractive remote sensing data source for detecting vegetation boundaries across treeline ecotones because of the ability to determine 3-dimensional vegetation structure (Bolton *et al.*, 2018; Coops *et al.*, 2013; Ørka *et al.*, 2012). ALS data have been used to describe vegetation structure within the treeline ecotone (Coops *et al.*, 2013), have been integrated with multispectral satellite imagery to produce maps of vegetation cover types over large areas (Ørka *et al.*, 2012) and have helped improve the interpretation of spectral trends identified from the Landsat data archive (Bolton *et al.*, 2018). Despite the benefit of capturing 3-dimensional information on vegetation structure and the possibility of integrating ALS data with other remote sensing datasets, ALS data are not widely available in many mountainous areas and acquisition of new data sets can be prohibitively expensive. Consequently, there are relatively few published studies using ALS data in mountain treeline ecotones (e.g. Bolton *et al.*, 2018; Coops *et al.*, 2013; Næsset and Nelson, 2007; Ørka *et al.*, 2012).

Synthetic Aperture Radar (SAR) data are sensitive to vegetation structure and, combined with data available from satellite-borne platforms, are attractive for identifying variation in vegetation structure at the treeline ecotone across large areas. Despite the rapid expansion of SAR data availability and the reducing cost of data acquisition, with data from sensors such as Sentinel-1 freely available and high-resolution SAR data available from commercial providers, the use of SAR data in mountain ranges has been restricted due to challenges associated with image processing in mountainous regions. The use of a directional signal in areas with complex and steep terrain often results in geometric distortion of the land surface and occultation due to layover and radar shadowing (Sinha *et al.*, 2015). The capability of Synthetic Aperture Radar (SAR) to penetrate cloud presents obvious benefits for characterising forest structure at mountain treelines. However, there remain significant

difficulties in obtaining and processing SAR data with suitable geometric and radiometric properties (Shimada and Ohtaki, 2010) that could be used for large area assessments of forest distribution shifts in mountain ranges.

The most common source of remote sensing data used in the assessment of mountain treeline change to date has been aerial photography or multispectral satellite remote sensing data (Morley *et al.* 2018). Many studies examine change in forest distribution by classifying multiple remotely sensed multispectral images into forest / non-forest classes, identifying changes in maximum elevation and forest extent over time (e.g. Dinca *et al.*, 2017; Luo and Dai, 2013; Mihai *et al.*, 2017). The simple forest / non-forest definition is an efficient descriptor of the forest-grassland transition and can provide an accurate indicator of change in forest extent if assessed in images from multiple dates. The definition does not, however, capture sufficient information about forest structure to improve the characterisation or understanding of variation in forest response to environmental change (Table 2.1).

Defining intermediate classes between areas of old-growth forest and treeless habitats improves the representation of structural variation contained within the treeline ecotone. Grouping forest margins into areas that share similar structural characteristics, such as tree canopy cover, density, size and growth form, allows classes to be identified that have reasonably homogeneous within-class forest structure while emphasising between-class variation. Underlying biotic and abiotic processes determine forest structural classes at the treeline (Greenwood *et al.*, 2015, 2014; Harsch and Bader, 2011) and the impact of forest distribution change on biodiversity and ecosystem function will depend on the forest structure (Greenwood *et al.*, 2016; Tomback *et al.*, 2016). Consequently, using structural classes to represent heterogeneity in the treeline ecotone allows us to characterise variation in changes in forest extent and structure in a manner that improves our understanding of shifts in forest-grassland transitions and their implications (Table 2.1). However, this level of structural detail is uncommon in studies utilising remote sensing to examine mountain treelines (e.g. Allen and Walsh, 1996; Klasner and Fagre, 2002; Resler *et al.*, 2004). This deficiency exists despite structural classes being sensible ecological units and being efficient to survey. There is also the possibility to identify classes by image classification or by manual interpretation of aerial photography or satellite images with a spatial resolution of 2 m or better (Table 2.1; Allen and Walsh, 1996).

Defining structural classes requires boundaries to be imposed onto the mountain treeline ecotone. The decision of where to define boundaries along a continuum of differing

tree density, size and spatial arrangement that vary over time is non-trivial (Arnot *et al.*, 2004). Continuous variables can be used to map the mountain forest transition and offer an attractive alternative to structural classes due to the ability to represent vegetation heterogeneity on a continuous scale, avoiding the use of subjective boundaries (DeFries *et al.*, 2000; Hill *et al.*, 2007). Indeed, classifications of continuous forest descriptors have been used to improve the structural representation of the treeline ecotone (Hill *et al.*, 2007; Král, 2009) and to identify changes in vegetation abundance over time (Chen *et al.*, 2015). However, canopy cover, the most commonly used descriptor, is not always appropriate for monitoring change in mountain treelines because of an inability to distinguish differences in tree size class (Morley *et al.*, 2018).

Table 2.1: Relative merits of different definitions of vegetation structure at the treeline ecotone for characterising variation in treeline response to environmental change and potential ecological interpretations.

Treeline Definition	Field survey effort	Sources of Reference Data	Characterisation of structural variation	Ecological interpretations	Confidence
Forest / Non-Forest	Low	Photointerpretation Field Data LiDAR	Low	Distribution, Extent	High
Structural Classes	Medium	Photointerpretation Field Data LiDAR	High	Distribution, Extent, Average Tree Size, Area standardised Stand Density & Biomass	High
Above-Ground Biomass	High	Field Data LiDAR	High	Spatial arrangement, Area standardised Biomass	Medium

While multi-spectral sensors are the most commonly used source of remote sensing data used in studies of the mountain treeline; there are uncertainties in the ability of multi-spectral sensors to resolve structural variation in mountain treelines. This uncertainty had led to a poor understanding of which spectral properties best characterise structural variation within the treeline ecotone (Morley *et al.*, 2018). Vegetation indices are used to transform two or more spectral bands into indices that emphasise key biophysical characteristics of vegetated ecosystems. The Normalised Difference Vegetation Index (NDVI) correlates with Leaf Area Index (Wang *et al.*, 2005) and fractional vegetation cover (Carlson and Ripley, 1997) and has been

used in estimates of tree canopy cover at the mountain treeline (Hill *et al.* 2007). Green-based indices, such as the Green Normalised Difference Vegetation Index (GNDVI) or the Green-Red Vegetation Index (GRVI), show an increased sensitivity to chlorophyll-a concentration, and consequently, have been suggested to improve the characterisation of subtle differences among ecosystem types (Gitelson *et al.*, 1996; Motohka *et al.*, 2010). The characterisation of forest structure has also been improved by using vegetation indices based on short-wave infrared due to an increased sensitivity to foliar moisture and vegetation density (Schroeder *et al.*, 2011). Indices that make use of shortwave infrared bands have been used to monitor vegetation regrowth following disturbance events, with particular emphasis placed on monitoring post-fire recovery. While indices such as the Normalised Burn Ratio Index (NBRI) were first conceived for monitoring vegetation regrowth post-fire, the sensitivity to foliar moisture and vegetation density makes them potential candidates for characterising variation in vegetation structure in areas of ecological succession, such as across the treeline ecotone.

In addition to remotely sensed vegetation indices, textural features that describe the statistical distribution of pixel data within a defined neighbourhood have been shown to correlate with forest structural variables, such as tree density or average stem diameter (e.g. Meng *et al.*, 2016; Ozdemir and Karnieli, 2011). Sensors with a finer spatial resolution allow for textural features to be calculated at the scale of the individual plots. However, consideration is required to determine if the increased number of textural parameters that can be defined from imagery of higher spatial resolution results in data that will be ecologically meaningful if used in image classification algorithms given the high degree of collinearity present in spectral remote sensing data. Identifying spectral features that show the strongest relationship with forest structure is important to maximise the amount of structural information that can be resolved in multispectral remote sensing data.

Delineation of structural variation at forest margins is required to improve our understanding of the underlying processes that govern variation in forest response to environmental change and to estimate the impacts of forest distribution shifts on biodiversity and ecosystem services. Here we focus on the use of multispectral satellite remote sensing data because it is the most accessible form of remotely sensed data for assessing mountain treeline change across large areas. However, the issue of how best to characterise variation in vegetation structure at the mountain treeline using multispectral satellite remote sensing data remains unresolved. To address this knowledge gap, this work aims to improve the characterisation of mountain treeline ecotones by i) determining which spectral features derived from multispectral satellite remote sensing best explain variation in vegetation

structure at the mountain treeline and ii) quantifying the ability of sensors with different spatial resolutions to resolve variation in vegetation structure at the mountain treeline.

2.2 Methods

2.2.1 Study location

The Central Mountain Range of Taiwan has more than 200 mountains over 3000 m a.s.l., the highest of which, Yushan (Jade Mountain), reaches 3952 m. Although Taiwan spans the Tropic of Cancer, the highest elevations experience temperate and alpine conditions. At the highest elevation of forest distribution, the canopy is dominated by four conifer species, primarily *Abies kawakamii* and *Tsuga chinensis* with areas of *Pinus taiwanensis* and *Pinus armandii* establishment. The adjacent grassland is dominated by the bamboo *Yushania niitakayamensis* which extends to the peaks with a low density of shrubby species, of which *Juniperus* spp. and *Rhododendron* spp. are the most common.

Climate is considered to be the primary regulatory factor of the treeline in the Central Mountain Range, with temperature and topographic sheltering identified as two fundamental controls on treeline structure, position and advance (Greenwood *et al.*, 2015, 2014). Natural disturbances caused by small-scale fires and landslides that result in a localised reduction of the treeline and removal of substrate affect the treeline sporadically. However, routine disturbance events are considered to be of low impact at the landscape scale, with little evidence to support widespread anthropogenic disturbance or grazing by large herds of herbivores (domesticated or wild).

2.2.2 Field data

To identify limitations to an accurate characterisation of structural variation this work considers three definitions of vegetation structure at the mountain treeline that have been used across the ecological, biogeographical and remote sensing literature. The forest / non-forest definition is based on the FAO Global Forest Resources Assessment (2018) criteria of a forest with at least 10 % canopy cover and trees higher than 5 m or able to reach these thresholds in situ. The FAO (2018) definition was chosen because the leading edge of forest expansion is often characterised by a few trees less than 5 m in height. Consequently, the FAO's forest definition aligns with ecological and biogeographic studies investigating pattern-process responses of the treeline ecotone because it captures a greater area of the forest-grassland transition than forest definitions with a higher canopy cover threshold. Six structural classes were identified based on criteria proposed by Harsh and Bader (2011) and subsequently adapted by Greenwood *et al.* (2014) for the *A. kawakamii* treeline in Taiwan. Areas of forest advance were first identified

using repeat aerial photography and subsequently defining the structural characteristics of forest plots in field surveys (Greenwood *et al.* 2014; Table 2.2). Structural classes are based on differences in stand density, average tree size and successional stage that the dominant canopy forming species belongs to and include classes that exhibit sharp boundaries as well as diffuse areas (Figure 2.1). Complete species separation was not possible due to insufficient field data for species that are sparsely distributed at high elevation in the Central Mountain Range. Consequently, two forest successional stages are defined; the late successional stage is defined as a canopy dominated by *A. kawakamii* or *T. chinensis* and the early successional stage dominated by *P. taiwanensis* or *P. armandii*. Above-ground woody biomass is investigated as the continuous variable in this analysis because of the correlation with tree size and density from which the categorical groupings are defined (Figure 2.1) and its importance for the estimation of global carbon storage as an Essential Climate Variable (Bojinski *et al.*, 2014).

Field data were collected in the Mt Hehuan area of the Central Mountain Range. A purposive sampling strategy was used to ensure representation of all forest sub-classes present at the Hehuan treeline. A total of 154 plots were sampled, split among the different vegetation classes (Table 2.2). Early successional species are only found in localised areas of low-density establishment, therefore, are only represented in a single structural class. Data from Greenwood *et al.* (2014) were combined with data from an additional survey conducted by the authors in 2016. To retain consistency in plot size, transect data from Greenwood *et al.* (2014) were split into 84 subplots measuring 20 x 20 m returning a sample area of 0.04 ha. The 70 plots surveyed in 2016 used a 10 m fixed radius design returning a sample area of 0.03 ha. Since quantity measures are area-standardised, this difference in plot size has no consequence for subsequent analyses. Field plot location were recorded using a handheld Garmin GPSMAP 62s (best accuracy +/- 3 m). All trees were measured for Diameter at Breast Height (DBH) at 1.3 m and the height of all live saplings less than 1.3 m in height was recorded in all plots. During the 2016 survey, a sample of live trees within each plot was also measured for height. Height was related to DBH using nonlinear least squares regression, thereby allowing estimation of height for any plots where it was not recorded (data not shown). Stand above-ground woody biomass was calculated from stand basal area and median stand height, accounting for differences in specific wood gravity between species. Sapling data were used to inform the designation of structural classes but were not used to calculate stand above-ground biomass values.

Table 2.2: Description of full structural classes based on successional stage and stand structure identified in the Mt Hehuan region of the Central Mountain Range, Taiwan, and the number of sampling plots.

Vegetation Class (Number of plots)	Description
Late – Old growth forest (33)	Canopy dominated by <i>A. kawakamii</i> or <i>T. chinensis</i> . Areas of the forest interior where the forest has persisted for many years and characterised by a few large trees.
Late – Static treeline (12)	Canopy dominated by <i>A. kawakamii</i> or <i>T. chinensis</i> . Forested areas at the forest-grassland boundary with trees representative of old growth and no signs of forest advance. Usually with a sharp boundary with the adjacent grassland.
Late – Abrupt advancing treeline (24)	Canopy dominated by <i>A. kawakamii</i> or <i>T. chinensis</i> . Areas of forest advance that have a high density of establishing trees usually over short distances and a sharp, well-defined boundary with the adjacent old growth forest and grassland.
Late – Diffuse advancing treeline (32)	Canopy dominated by <i>A. kawakamii</i> or <i>T. chinensis</i> . Areas of forest expansion with a low density of establishing trees usually over long distances and a diffuse, poorly defined boundary with the adjacent grassland.
Early – Diffuse advancing treeline (22)	Canopy dominated by <i>P. taiwanensis</i> or <i>P. armandii</i> . Areas of forest expansion with a low density of establishing trees usually over long distances and a diffuse, poorly defined boundary with the adjacent grassland.
Grassland (31)	Areas devoid of tree species but may include a low density of shrubs.

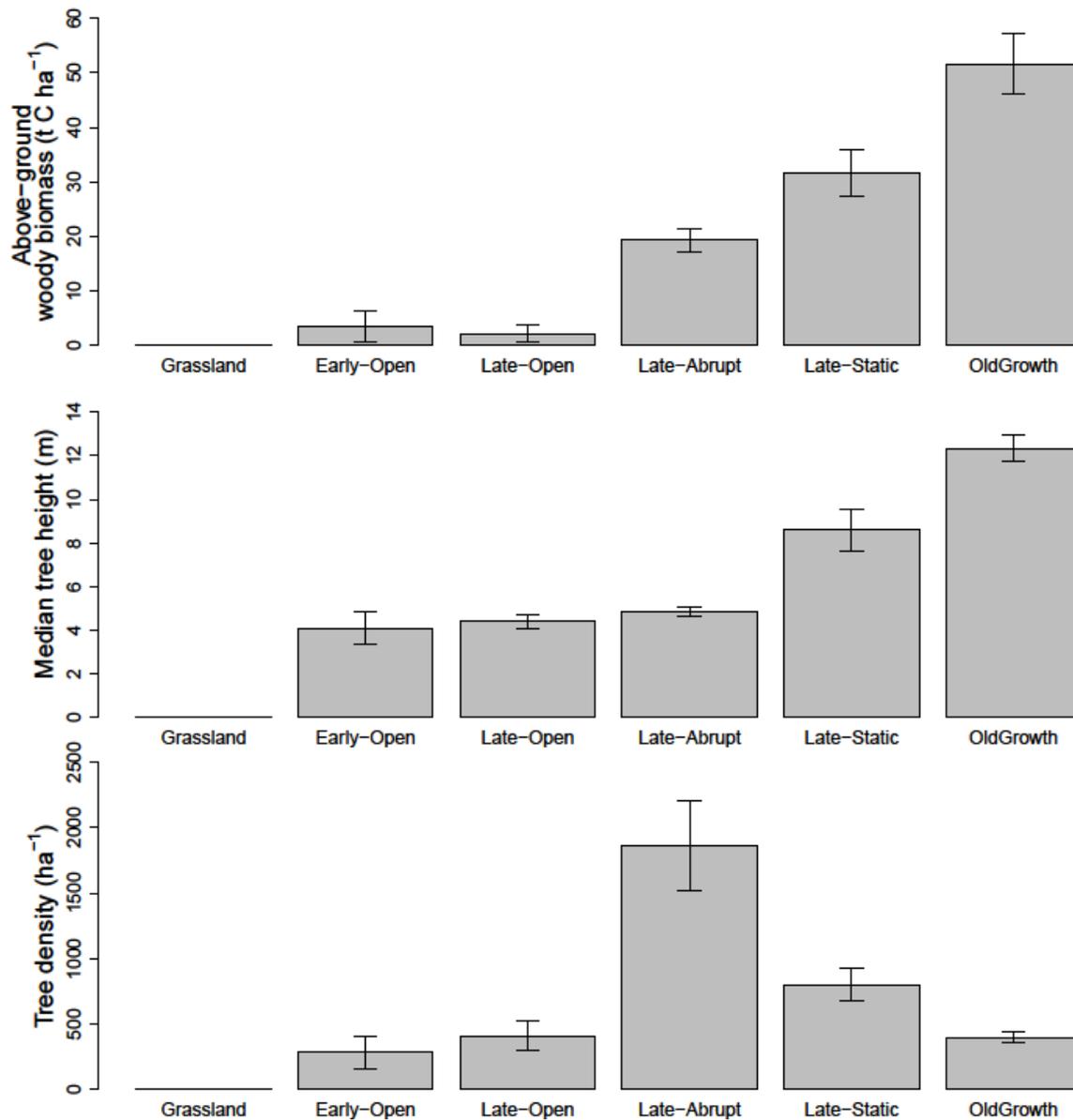


Figure 2.1: Definitions of structural classes are based on differences in tree size and tree density (median values for stand height and tree density are shown with standard error). The combination of tree size and density results in a significant difference in above-ground woody biomass between structural classes (ANOVA: $F(5,148) = 55.96$, $p < 0.001$), with the Early-Diffuse advancing and Late-Diffuse advancing treeline classes not separable due to a similar forest structure but defined by a different successional stage (median values for above-ground woody biomass are shown with standard error).

2.2.3 Earth observation data

To investigate the importance of sensor spatial resolution on the characterisation of treeline structural variation, data from four multispectral satellite-borne sensors are compared;

2 m pixel size GeoEye multispectral data captured in October 2012, 6 m pixel size SPOT-7 multispectral data captured in October 2016, 10 m and 20 m pixel size Sentinel-2 MSI data captured in October 2016 and 30 m pixel size Landsat-8 OLI data captured in January 2017. Sentinel-2 and Landsat-8 are delivered as orthorectified products and GeoEye and SPOT-7 images were orthorectified using a 30 m resolution SRTM DEM. The spectral bands were calibrated and converted to top-of-atmosphere reflectance in ENVI 5.3 using gain and offset values, accounting for solar irradiance, sun elevation and time of image acquisition. Atmospheric correction was not implemented as single date images are considered independently and pseudo-invariant features (roads and buildings) did not indicate differences in atmospheric conditions between individual images (Song *et al.*, 2001; data not shown). All images were collected in the same season (Autumn-Winter) to avoid differences in vegetation phenology.

Where available, up to seven spectral bands (blue, green, red, near infrared (NIR), red-edge and two short-wave infrared (SWIR) bands) and four vegetation indices were considered (Table 2.3). The vegetation indices considered were the Normalized Difference Vegetation Index (NDVI), calculated as:

$$NDVI = (NIR - RED)/(NIR + RED) \quad (1)$$

where NIR and RED are the near infrared and red spectral bands respectively; the Green-Red Vegetation Index (GRVI), calculated as:

$$GRVI = (GREEN - RED)/(GREEN + RED) \quad (2)$$

where GREEN and RED are the green and red spectral bands respectively; the Green Normalised Difference Vegetation Index (GNDVI), calculated as:

$$GNDVI = (NIR - GREEN)/(NIR + GREEN) \quad (3)$$

where NIR and GREEN are the near infrared and green spectral bands respectively; and Normalised Burn Ratio Index (NBRI), calculated as:

$$NBRI = (NIR - SWIRII)/(NIR + SWIRII) \quad (4)$$

where NIR and SWIRII are the near infrared and second short-wave infrared (approx. 2200 nm) spectral bands respectively. While the calculation for each of the vegetation indices is the same for each sensor, differences in position and width of each spectral band between sensors (table 2.3) mean that the value of the vegetation indices in any given place will vary between the sensors (Franke *et al.*, 2006). Five measures of statistical distribution were considered as

textural features, the mean, two measures of dispersion (standard deviation and coefficient of variation) and two measures of shape (skewness, kurtosis) were calculated for each spectral band and vegetation index in all sample plots. Due to differences in spatial resolution of the different remote sensing images, we are unable to calculate dispersion and shape statistics for all sample plots. Consequently, the number of sample points that are used in the analysis of the dispersion and shape statistics varies; 154 plots for GeoEye and SPOT-7 and 101 for 10 m pixel size Sentinel-2 (Table 2.3). It was not possible to calculate dispersion and shape statistics at the plot scale from 20 m pixel size Sentinel-2 data or 30 m pixel size Landsat-8 data, consequently, only the mean spectral response is considered and no other descriptors of spectral response are investigated. Statistical descriptors of spectral response were calculated in R (R Core Team, 2017) using packages raster (Hijmans, 2016) and rgdal (Bivand *et al.*, 2016).

Table 2.3: Remote sensing spectral features used to investigate the relationship between the statistical distribution of spectral values and vegetation structure at the mountain treeline. The textural features of the centre (mean), dispersion (standard deviation, coefficient of variation) and shape (skewness, kurtosis) were calculated from the pixel values recorded within the boundary of field plots.

Satellite	Pixel size (m)	Spectral Bands	Wavelength (nm) (min – max, centre)	Vegetation Indices	Textural features (Number of observations)
GeoEye	2	Blue, Green, Red, Near-infrared	450 – 510, 480 510 – 580, 545 655 – 690, 673 780 – 920, 850	NDVI, GNDVI, GRVI	Mean (154), Standard Deviation (154), Coefficient of Variation (154), Skewness (154), Kurtosis (154)
SPOT-7	6	Blue Green Red Near-infrared	455 – 525, 490 530 – 590, 560 625 – 695, 660 760 – 890, 825	NDVI, GNDVI, GRVI	Mean (154), Standard Deviation (154), Coefficient of Variation (154), Skewness (154), Kurtosis (154)
Sentinel-2 MSI	10	Blue Green Red Near-infrared	448 – 546, 497 537 – 583, 560 646 – 684, 665 762 – 908, 835	NDVI, GNDVI, GRVI	Mean (154), Standard Deviation (101), Coefficient of Variation (101), Skewness (101), Kurtosis (101)
	20	Red Edge Short-wave infrared I Short-wave infrared II	731 – 749, 740 1542 – 1686, 1614 2081 – 2323, 2202	NBRI	Mean (154)
Landsat-8 OLI	30	Blue Green, Red, Near-infrared, Short-wave infrared I Short-wave infrared II	450 - 515, 482 525 – 600, 561 630 – 680, 655 845 – 885, 865 1560 – 1660, 1609 2100 – 2300, 2201	NDVI, GNDVI, GRVI, NBRI	Mean (154)

2.2.4 Statistical analysis

Each spectral feature was regressed independently to assess the strength of the relationship between each band or vegetation index and the forest biophysical properties due to the high degree of correlation between spectral bands. The relationship between the forest / non-forest definition and spectral features was assessed using binomial logistic regression with a logit link function. Multinomial logistic regression was used to investigate the probability of separating different structural classes (Table 2.1) from the spectral data. The results from multinomial regression of the full structural classes indicated that some forest classes could not be separated and consequently, class simplification was carried out. The simplified class structure considered three vegetation classes in multinomial logistic regression: Old-growth forest (an amalgamation of the old-growth forest and static treeline classes), areas of forest advance (an amalgamation of the three classes of forest advance: Early-Diffuse, Late-Diffuse and Late-Abrupt advancing treeline classes) and the grassland class. Least squares regression was used to explore the relationship between above-ground woody biomass and spectral features. The inclusion of zero values of above-ground woody biomass from grassland plots caused heteroscedasticity in model residuals. Consequently, the analysis was conducted as a two-stage procedure, first considering the forest / non-forest definition through binomial logistic regression and subsequently conducting least squares regression on data points from the forest class with a log transformation on above-ground woody biomass.

Multiple regression was carried out for each of the four definitions of vegetation structure (Forest / non-forest, full and simplified structural classes and above-ground woody biomass) to ascertain if the characterisation of structural variation at the treeline could be significantly improved by using multiple spectral predictors. Multi-collinearity was tested for using variance inflation factors and, where present, spectral variables were removed to reduce the severity of multi-collinearity. Model simplification was carried out using partial F-tests to identify the minimum adequate model required to explain variation in the response. To identify potential strengths or limitations of the different forest definitions, the probability of class assignment or above-ground woody biomass was estimated for a subset of the Mt. Hehuan study area using the GRVI derived from Sentinel-2 imagery. All statistical analyses were carried out in R (R Core Team, 2017) using packages *boot* (Canty and Ripley, 2016) and *nnet* (Venables and Ripley, 2002), variance inflation was tested for using the *car* package (Fox and Weisberg, 2011). Statistical significance was considered at $p < 0.05$ and the coefficient of determination (R^2) used to gauge the strength of the relationship (the reported R^2 of the binomial and multinomial logistic regression is McFadden's pseudo R^2 - henceforth R^2_{MF}). The reported R^2 for

above-ground biomass are from least-squares regression of biomass against spectral properties in which zero values of biomass in grassland areas were excluded due to heteroscedasticity in the residuals.

2.3 Results

2.3.1 Textural features

Of the textural features considered, the mean spectral response has the strongest relationship with the four treeline ecotone definitions investigated, particularly with the green and red spectral bands and the GRVI (Table 2.4). The dispersion measures (standard deviation and coefficient of variation) of the near-infrared band from the GeoEye sensor show a significant relationship with each of the four definitions of vegetation structure (Table 2.4). However, the strength of the relationship between dispersion measures and forest-grassland definitions is considerably lower when data from either SPOT-7 or Sentinel-2 are considered (e.g. the strongest measure for forest / non-forest: GeoEye NIR Coef. of Var. R^2_{MF} 0.464, $p < 0.01$; SPOT NIR Coef. of Var. R^2_{MF} 0.200, $p < 0.01$; Sentinel-2 NIR Coef. of Var. R^2_{MF} 0.086, $p < 0.01$; Supplementary 1). Whilst the strength of the relationship between definitions of vegetation structure and the dispersion and shape features derived from the spectral bands are typically better than dispersion measures derived from vegetation indices, the dispersion measures of the GNDVI measured from GeoEye data have a comparable, significant relationship with above-ground woody biomass (St. dev. $R^2 = 0.452$, $p < 0.01$; Coef. of Var. R^2 0.469, $p < 0.01$; Table 2.4).

Table 2.4: Coefficient of determination from the regression of four definitions of vegetation structure at the mountain treeline against texture features derived from four spectral bands and three vegetation indices from 2m pixel size GeoEye data in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$).

Forest / Non-forest (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.562**	0.554**	0.587**	0.113**	0.417**	0.554**	0.124**
St. dev.	0.032*	0.009	0.030*	0.417**	0.002	0.002	0.139**
Coef. of Var.	0.009	0.097**	0.010	0.464**	0.012	0.105**	0.080**
Skewness	0.011	0.044*	0.002	0.054**	<0.001	<0.001	0.003
Kurtosis	<0.001	0.019	<0.001	0.003	0.021	<0.001	0.017

Full Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.351**	0.375**	0.374**	0.213**	0.182**	0.329**	0.064**
St. dev.	0.062**	0.052**	0.096**	0.167**	0.022*	0.033**	0.132**
Coef. of Var.	0.043**	0.063**	0.049**	0.226**	0.017	0.079**	0.098**
Skewness	0.107**	0.114**	0.117**	0.041**	0.071**	0.084**	0.034**
Kurtosis	0.012	0.018	0.024*	0.073**	0.009	0.009	0.006

Simplified Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.454**	0.489**	0.484**	0.299**	0.210**	0.407**	0.087**
St. dev.	0.085**	0.055**	0.120**	0.221**	0.015**	0.045**	0.156**
Coef. of Var.	0.055**	0.067**	0.051**	0.303**	0.015	0.109**	0.118**
Skewness	0.018	0.030**	0.021*	0.044**	0.054**	0.021*	0.032**
Kurtosis	0.004	0.012	0.006	0.078**	0.011	0.006	0.009

Above-ground biomass, $t C ha^{-1}$ (R^2 ; $n = 123$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.656**	0.704**	0.676**	0.449**	0.162**	0.586**	0.004
St. dev.	0.057**	0.017	0.090**	0.303**	0.150**	0.016	0.452**
Coef. of Var.	0.037*	0.024	0.010	0.561**	0.112**	0.208**	0.469**
Skewness	0.171**	0.156**	0.201**	0.060**	0.366**	0.178**	0.260**
Kurtosis	0.001	0.017	0.014	0.193**	0.014	0.004	<0.001

2.3.2 Spectral bands

When considering the mean response of spectral bands from all the sensors investigated, the blue, green, red and shortwave infrared bands show the strongest relationship with the definitions of vegetation structure at the treeline ecotone (Highest $R^2_{(MF)}$ for forest / non-forest: Sentinel-2 Red 0.642, $p < 0.01$; Full structural Classes: SPOT-7 & Sentinel-2 Blue 0.396, $p < 0.01$; Simplified structural Classes: Sentinel-2 Blue 0.531, $p < 0.01$; Above-ground woody biomass: GeoEye Green 0.704, $p < 0.01$; Table 2.5), whilst the near-infrared and red edge bands show a weak relationship (Table 2.5). The spatial resolution of the sensor has little effect on the strength of the relationship with either the forest / non-forest definition or full structural classes (difference of R^2_{MF} within 0.06 and 0.09 respectively). When the simplified structural classes are considered the difference in R^2_{MF} in the visible wavelengths is < 0.08 , however, in the near-infrared this difference increases to 0.19 due to a reduced strength of the relationship between the mean response of the near-infrared band from Landsat-8 and the simplified structural classes. Similarly, the strength of the relationship between above-ground woody biomass and the visible and near-infrared bands from the Landsat-8 sensor are consistently 0.12-0.29 R^2 lower than the strongest relationship with the alternative sensors considered here. However, the difference in R^2 among the remaining three sensors in the visible range is < 0.03 and in the near-infrared there is a difference in R^2 of 0.1 when above-ground woody biomass is used to describe the treeline ecotone (Table 2.5).

Table 2.5: Coefficient of determination from the regression of the four definitions of vegetation structure at the mountain treeline against the mean response of the spectral bands in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$). Forest / Non-forest (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	Red Edge	SWIR1	SWIR2
GeoEye	0.562**	0.554**	0.587**	0.113**	–	–	–
SPOT-7	0.597**	0.584**	0.629**	0.126**	–	–	–
Sentinel-2	0.599**	0.575**	0.642**	0.090**	0.104**	0.471**	0.573**
Landsat-8	0.604**	0.550**	0.618**	0.066**	–	0.494**	0.547**

Full Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	Red Edge	SWIR1	SWIR2
GeoEye	0.351**	0.375**	0.374**	0.213**	–	–	–
SPOT-7	0.396**	0.389**	0.393**	0.165**	–	–	–
Sentinel-2	0.396**	0.378**	0.389**	0.157**	0.175**	0.300**	0.331**
Landsat-8	0.343**	0.325**	0.339**	0.076**	–	0.272**	0.298**

Simplified Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	Red Edge	SWIR1	SWIR2
GeoEye	0.454**	0.489**	0.484**	0.299**	–	–	–
SPOT-7	0.505**	0.505**	0.514**	0.219**	–	–	–
Sentinel-2	0.531**	0.516**	0.526**	0.214**	0.233**	0.408**	0.450**
Landsat-8	0.518**	0.496**	0.514**	0.113**	–	0.410**	0.451**

Above-ground biomass, t C ha⁻¹ (R^2 ; $n = 123$)

	Blue	Green	Red	NIR	Red Edge	SWIR1	SWIR2
GeoEye	0.656**	0.704**	0.676**	0.449**	–	–	–
SPOT-7	0.653**	0.681**	0.670**	0.345**	–	–	–
Sentinel-2	0.686**	0.681**	0.668**	0.349**	0.368**	0.582**	0.601**
Landsat-8	0.552**	0.552**	0.559**	0.164**	–	0.502**	0.521**

2.3.3 Vegetation indices

When vegetation indices are considered, the mean response of the GRVI and NBRI show the strongest relationships with each of the four forest-grassland transition definitions considered (Highest R^2 for forest / non-forest: Landsat-8 GRVI 0.623, $p < 0.01$; Full structural Classes: GeoEye GRVI 0.329, $p < 0.01$; Simplified structural Classes: SPOT GRVI 0.425, $p < 0.01$; Above-ground woody biomass: GeoEye GRVI 0.586, $p < 0.01$; Table 2.6). The strength of the relationship between the mean response of the Green-Red vegetation index does not depend on the spatial resolution of the sensors compared in this study when categorical definitions are used to describe vegetation structure across the mountain treeline (difference of R^2_{MF} within 0.07 for forest / non-forest; 0.04 for full structural classes; 0.05 for simplified structural classes, Table 2.6). However, when above-ground woody biomass is used the difference in R^2 between sensors tested here increases to 0.12 (Table 2.6).

Table 2.6: Coefficient of determination from the regression of the four definitions of vegetation structure at the mountain treeline against the mean vegetation index response in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$).

Forest / Non-forest (R^2_{MF} ; $n = 154$)

	NDVI	GRVI	GNDVI	NBRI
GeoEye	0.417**	0.554**	0.124**	–
SPOT-7	0.442**	0.600**	0.159**	–
Sentinel-2	0.510**	0.590**	0.272**	0.581**
Landsat-8	0.451**	0.623**	0.173**	0.531**

Full Structural classes (R^2_{MF} ; $n = 154$)

	NDVI	GRVI	GNDVI	NBRI
GeoEye	0.182**	0.329**	0.064**	–
SPOT-7	0.170**	0.324**	0.056**	–
Sentinel-2	0.190**	0.287**	0.088**	0.283**
Landsat-8	0.207**	0.302**	0.077**	0.273**

Simplified Structural classes (R^2_{MF} ; $n = 154$)

	NDVI	GRVI	GNDVI	NBRI
GeoEye	0.210**	0.407**	0.087**	–
SPOT-7	0.231**	0.425**	0.079**	–
Sentinel-2	0.271**	0.378**	0.133**	0.388**
Landsat-8	0.258**	0.381**	0.090**	0.403**

Above-ground biomass, $t C ha^{-1}$ (R^2 ; $n = 123$)

	NDVI	GRVI	GNDVI	NBRI
GeoEye	0.162**	0.586**	0.004	–
SPOT-7	0.146**	0.577**	<0.001	–
Sentinel-2	0.189**	0.468**	0.021	0.506**
Landsat-8	0.275**	0.522**	0.047**	0.482**

2.3.4 Multiple regression

When considering the GeoEye sensor, the use of multiple spectral bands as predictor variables leads to a significant increase in variance explained across all four of the definitions of vegetation structure considered here (Table 2.7). However, when considering the alternative sensors tested in this study the benefit of including multiple spectral bands as predictors depends on the definition used to describe vegetation structure across the treeline ecotone. For example, for SPOT-7 and Sentinel-2 the strength of the relationship between spectral bands and both the full and simplified structural class definitions increases when using multiple regression (Table 2.7). However, when a simple forest / non-forest or above-ground woody biomass definition is used to describe the vegetation structure at the treeline ecotone, linear models with R^2 above 0.6 can be derived from a single spectral band such as the green or red spectral bands (Table 2.7). When spectral bands from Landsat-8 are used, the minimum adequate model uses only a single spectral band due to multi-collinearity in the spectral data. However, when vegetation indices are derived from Landsat-8 spectral bands, the combination of GRVI and the NBRI in regression models significantly improves the strength of the relationship with the full structural classes, simplified structural classes and above-ground woody biomass (Table 2.7).

Table 2.7: Coefficient of determination from the regression of the four definitions of vegetation structure at the treeline ecotone against multiple predictors derived from either the spectral bands or vegetation indices in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$).

Forest / Non-forest

Satellite	Spectral Bands	R^2_{MF}	Vegetation Indices	R^2_{MF}
GeoEye	Red Mean + NIR Coef. of Var.	0.619**	GRVI Mean	0.554**
SPOT-7	Green Mean	0.645**	GRVI Mean	0.600**
Sentinel-2	Red Mean	0.642**	GRVI Mean	0.590**
Landsat-8	Red Mean	0.618**	GRVI Mean	0.623**

Full Structural classes

Satellite	Spectral Bands	R^2_{MF}	Vegetation Indices	R^2_{MF}
GeoEye	Green Mean + NIR Coef. of Var.	0.413**	GRVI Mean + GNDVI St. Dev	0.351**
SPOT-7	Red Mean + NIR Coef. of Var.	0.440**	GRVI Mean	0.324**
Sentinel-2	Green Mean + Red Mean + NIR Coef. of Var.	0.451**	GRVI Mean + NDVI Coef. of Var.	0.341**
Landsat-8	Red Mean	0.339**	GRVI Mean + NBRI Mean	0.312**

Simplified Structural classes

Satellite	Spectral Bands	R^2_{MF}	Vegetation Indices	R^2_{MF}
GeoEye	Green Mean + Red Mean + NIR Coef. of Var.	0.551**	GRVI Mean + GNDVI St. Dev.	0.431**
SPOT-7	Green Mean + Red Mean + NIR Coef. of Var.	0.564**	GRVI Mean	0.425**
Sentinel-2	Green Mean + Red Mean	0.554**	GRVI Mean + NDVI Coef. of Var.	0.413**
Landsat-8	Red Mean	0.514**	GRVI Mean + NBRI Mean	0.463**

Above-ground biomass, t C ha⁻¹

Satellite	Spectral Bands	R^2	Vegetation Indices	R^2
GeoEye	Green Mean + NIR Coef. of Var.	0.723**	GRVI Mean + GNDVI St. Dev	0.668**
SPOT-7	Green Mean	0.682**	GRVI Mean	0.577**
Sentinel-2	Green Mean	0.681**	GRVI Mean + NBRI Mean	0.526**
Landsat-8	Red Mean	0.559**	GRVI Mean + NBRI Mean	0.533**

2.3.5 Data visualisation

The probability of class assignment and above-ground woody biomass were estimated to identify potential strengths or limitations of the different definitions of forest structure at the mountain treeline. Tables 2.5 and 2.6 indicate that several spectral bands or vegetation indices would be suitable for this purpose, with the green and red spectral bands and GRVI amongst the highest performing spectral variables considered. While the NBRI shows a similar strength of relationship to the GRVI, it is only possible to calculate the NBRI from two of the four sensors considered (Sentinel-2 and Landsat-8, Table 2.6). Therefore, the GRVI is used to compare definitions of forest structure at the mountain treeline because the GRVI is the best performing vegetation index that can be derived from all four of the sensors investigated in this study.

The estimated probability of the forest / non-forest binomial logistic regression shown using the GRVI derived from Sentinel-2 imagery highlights significant areas of the grassland that would be estimated as forest under a definition based on 10 % canopy cover if a maximum probability classifier were implemented (Figure 2.2). The increased probability of forest occurrence in areas that can be visually identified as grassland coincides with increased standard error compared to neighbouring forested areas (Figure 2.2). Based on a maximum probability classification, the mean response from the GRVI would be expected to identify up to three of the six classes considered here: grassland, late-diffuse advancing treeline and old growth forest (Figure 2.3). This approach does not determine differences in community composition between the early- and late-successional stages in the diffuse advancing structure, areas of late-abrupt advance or differences between the static treeline and old growth forest (Figure 2.3). Simplifying intermediate classes, by amalgamating the late-static class with the old growth forest as well as combining the three classes indicative of forest advance, results in a better distinction between old growth forest and grassland areas as well as a reduction in the area of grassland that would be incorrectly classified as forested under a forest / non-forest approach (Figure 2.4). While the simplified class structure leads to better discrimination of areas of forest advance from areas of old-growth, this approach is unable to resolve heterogeneity in forest structure at the mountain treeline due to overlap in the spectral properties of forest structural classes (Figure 2.3). The estimation of above-ground biomass indicates an improved ability to estimate differences in structural heterogeneity at the mountain treeline showing good correspondence to the true colour image. However, the characterisation of areas with biomass values above 25 t C ha⁻¹ are likely to be inaccurate due to a saturation effect that occurs in the relationship between biomass and the spectral properties (Figure 2.5). In addition, the

spectral signature of some grassland areas still results in an elevated above-ground woody biomass estimation in areas not undergoing forest expansion. However, estimated biomass values of these grassland areas are reduced when compared against the neighbouring forested areas (Figure 2.5).

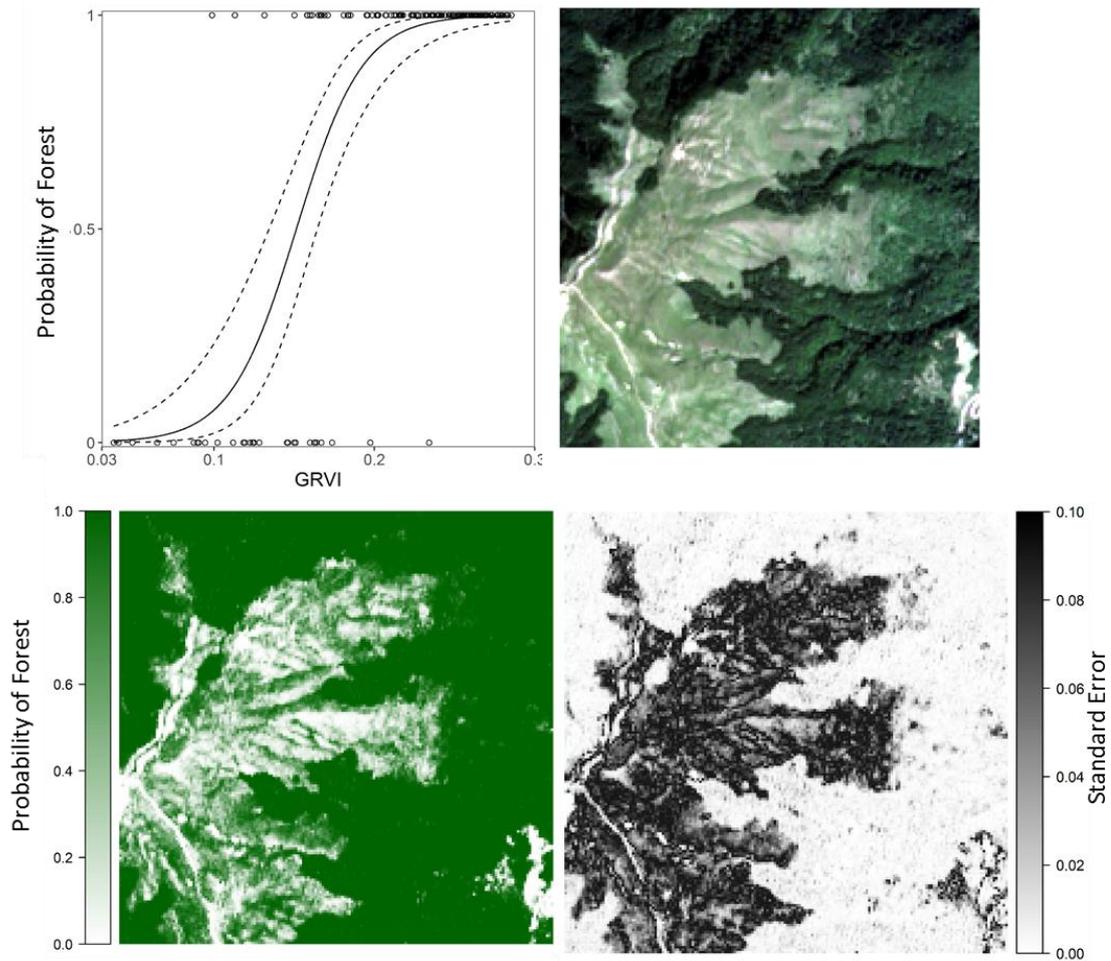


Figure 2.2: The relationship (Binomial logistic regression) between GRVI derived from Sentinel-2 (Oct 2016) and forest / non-forest response and 95 % confidence intervals (top-left, $R^2_{MF} = 0.59$, $p < 0.01$), true colour composite of the Mt Hehuan North Peak (top-right) and corresponding estimated probability of forest occurrence (bottom-left) and uncertainty in the estimated probability shown as standard error (bottom-right).

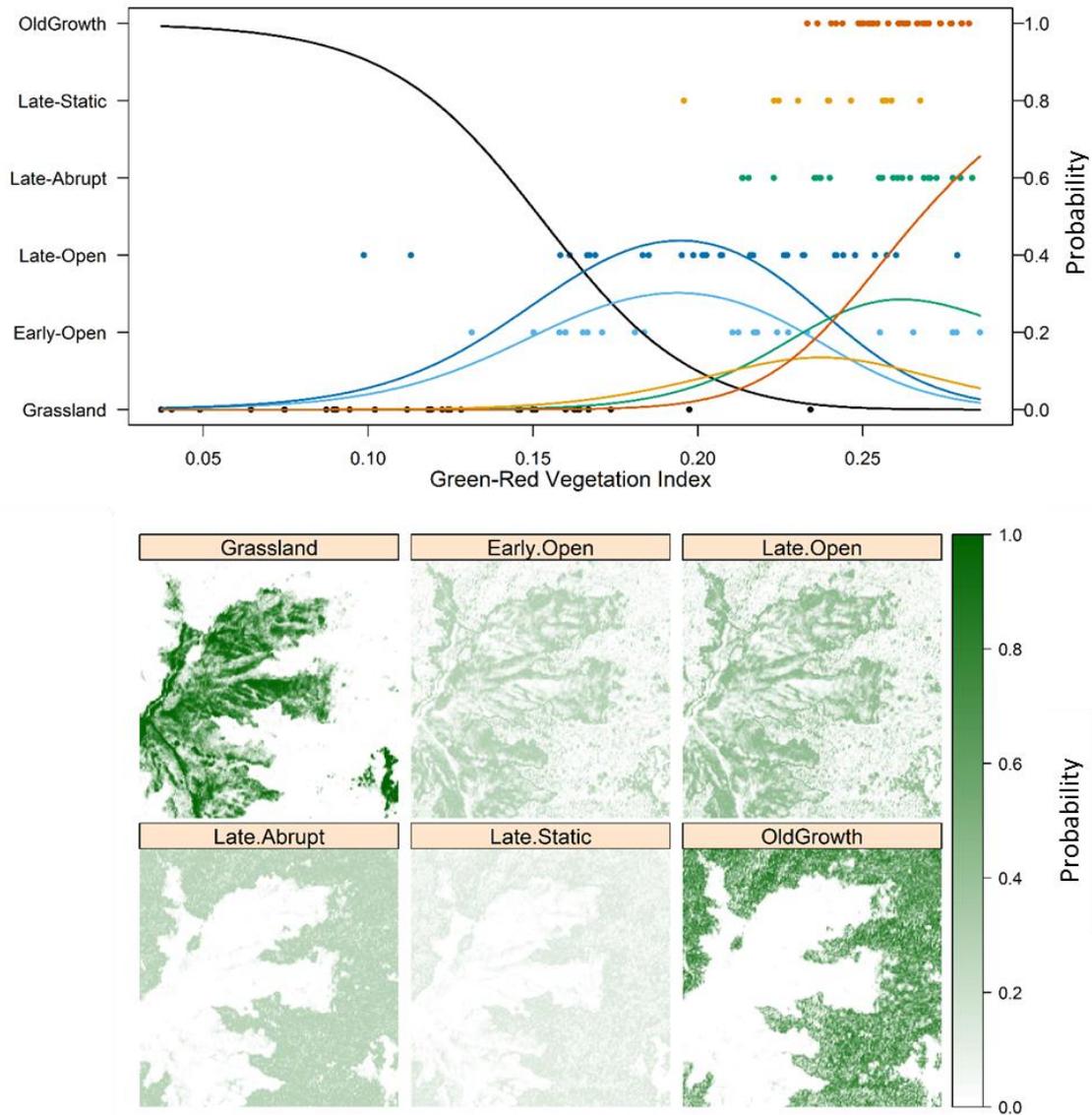


Figure 2.3: The relationship (multinomial logistic regression) between GRVI derived from Sentinel-2 (Oct 2016) and structural classes showing estimated class probability (top, $R^2_{MF} = 0.287$, $p < 0.01$) and the estimated probability of membership to each of the six structural classes in the Mt Hehuan North Peak (bottom). Based on a maximum probability approach, three of the six vegetation classes would be estimated while the early-diffuse advance, late-abrupt advance and Late-static forest structural classes are unlikely to be identified.

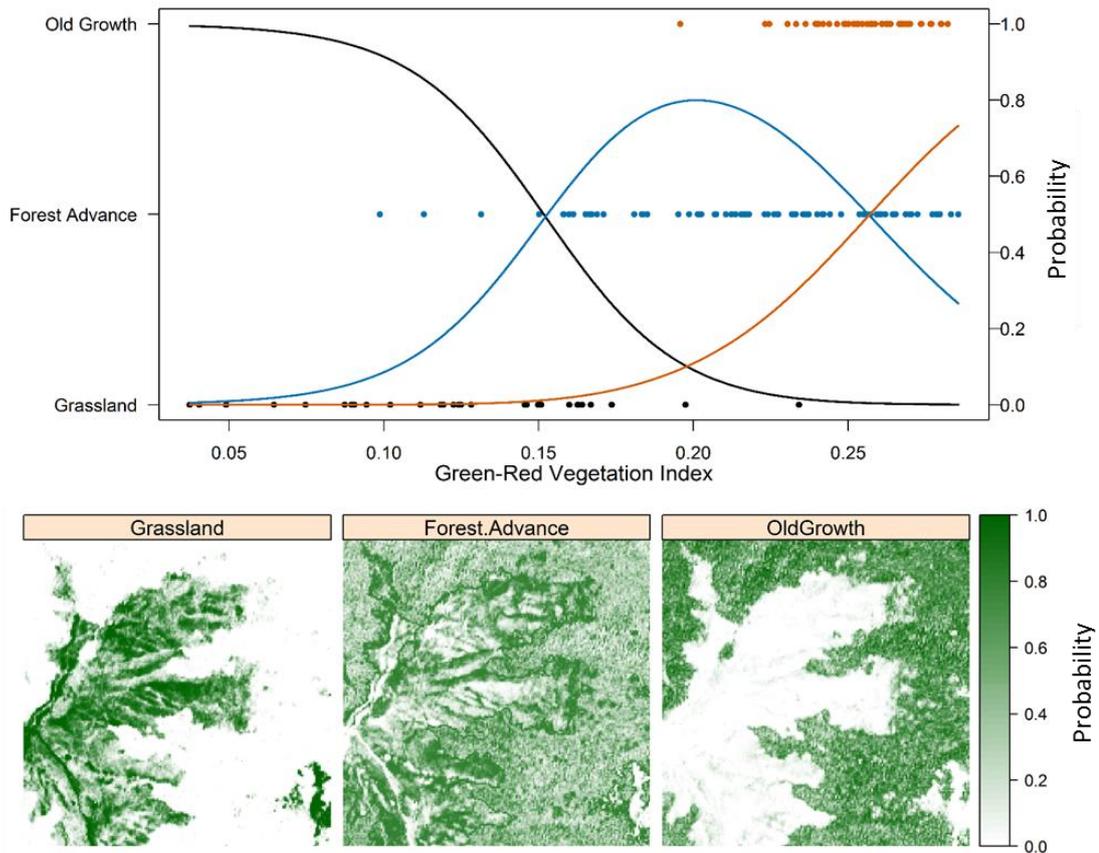


Figure 2.4: The relationship (multinomial logistic regression) between GRVI derived from Sentinel-2 (Oct 2016) and simplified structural classes showing estimated class probability (top, $R^2_{MF} = 0.378$, $p < 0.01$) and the estimated probability of membership to each of the three structural classes in the Mt Hehuan North Peak (bottom). Based on a maximum probability approach, all three vegetation classes would be estimated with an increased probability of forest advance occurring at the old growth forest margins.

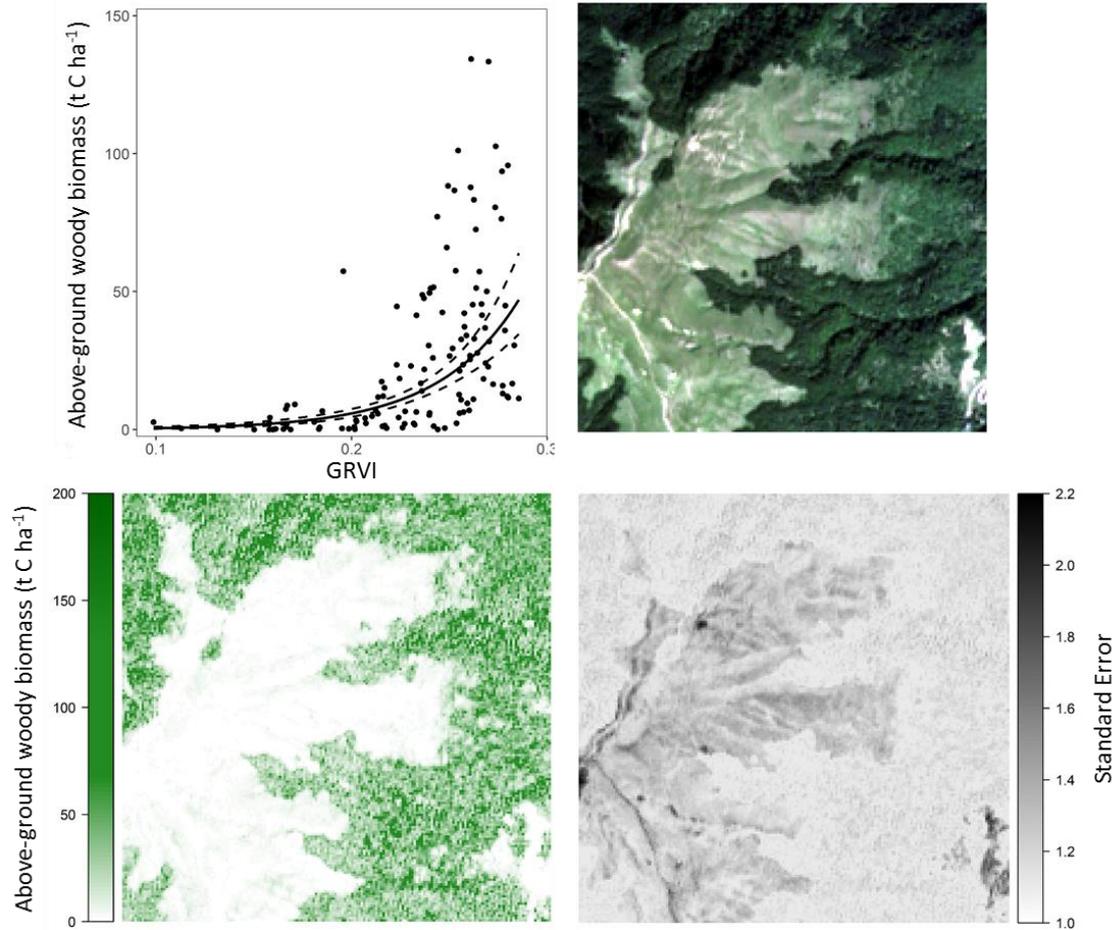


Figure 2.5: The relationship (least-squares regression) between GRVI derived from Sentinel-2 (Oct 2016) and above-ground woody biomass and 95 % confidence intervals (top-left; $R^2 = 0.468$, $p < 0.01$); true colour composite of the Mt Hehuan North Peak (top-right) and corresponding estimated above-ground woody biomass values (bottom-left) and uncertainty in the estimated probability shown as standard error (bottom-right).

2.4 Discussion

Here we show that the ability to identify variation in forest structure at the mountain treeline using multispectral satellite remote sensing data is best achieved when above-ground woody biomass is used to describe variation in vegetation structure (Tables 2.4 – 2.7). Furthermore, we show that a simplified class structure that considers areas of forest advance separately to old growth forest improves the discrimination of areas indicative of forest advance or stasis. The relationships defined here between four definitions of vegetation structure at the mountain treeline and spectral features highlight little quantitative difference between the remote sensing sensors tested here (difference of $R^2_{(MF)}$ within 0.03 for forest / non-forest; 0.11 for full structural classes; 0.05 for simplified structural classes; 0.16 for above-ground woody biomass; Table 2.7). Consequently, effective use of multispectral satellite remote sensing data presents a major opportunity to improve the ecological understanding of range shifts in mountain forests and estimate their subsequent impacts to biodiversity and ecosystem function.

The relationship between treeline definition and spectral variables is strongest when using above-ground woody biomass or the forest / non-forest definition to describe the forest-grassland transition (strongest R^2 for above-ground woody biomass: GeoEye Green mean & NIR Coef. of Var. 0.723, $p < 0.01$; strongest R^2_{MF} for forest / non-forest: SPOT-7 Green mean 0.645, $p < 0.01$; Table 2.7). However, both definitions show limitations in the ability to characterise areas indicative of forest advance or stasis across forest-grassland transitions in mountain ecosystems. When using a forest / non-forest definition, thresholds of canopy cover used to delineate a forest boundary in an ecotone are difficult to define because areas of grassland and areas with a low forest canopy cover can have similar spectral responses which in turn influences estimates of forest extent (Figure 2.2; Arnot *et al.*, 2004; Hill *et al.*, 2007). Song *et al.* (2014) found that varying the threshold of canopy cover from 20 to 30 % resulted in considerable disagreement in forest cover estimates, resulting in a significant under-representation of diffuse forest expansion when a threshold of 30 % canopy cover was used. Treeline ecotones are often characterised by areas with sparse and discontinuous tree cover and, consequently, assessments of change must be able to identify areas of diffuse forest expansion accurately. The sensitivity of the canopy cover threshold used to define the forest / non-forest boundary highlighted above not only leads to high uncertainty in estimates of forest expansion but also understates the variety of responses of the mountain treeline, restricting the ecological interpretation of forest change in mountain treeline ecotones (Holtmeier and Broll, 2017, 2007).

The representation of the mountain treeline ecotone is improved when using above-ground woody biomass to characterise vegetation structure. However, using above-ground woody biomass to represent the treeline ecotone is likely to under-estimate biomass in areas of old growth forest because spectral reflectance has an asymptotic relationship with plant biomass, which leads to a saturation effect in dense vegetation (Figure 2.5; Asner *et al.*, 2003; Huete *et al.*, 1997). In upland plantations, Puhr and Donoghue (2000) highlighted that the spectral signature of conifer trees converges with increasing size and as the canopy approaches closure. Consequently, once coniferous forest stands approach 13 m in height and the basal area exceeds 40 m² ha⁻¹ identifying differences in forest structure is problematic, and predictions are likely to become unreliable (Puhr and Donoghue, 2000). The saturation of GRVI indicated in Figure 2.5 coincides with the class average biomass values of the abrupt advancing treeline where trees establish in high density and reach canopy closure quickly (Figure 2.1). Consequently, it may be possible to identify changes in above-ground woody biomass in areas undergoing forest expansion and so improve the characterisation of vegetation structure. However, characterisation of areas with biomass values above 25 t C ha⁻¹ are likely to be inaccurate and thus limits the use of above-ground biomass as a single predictor of forest structure at mountain treeline ecotones.

Structural classes that define intermediate classes between areas of old-growth forest and treeless habitats have not been widely used in studies using remote sensing data to identify shifts in mountain forests. Consequently, there was uncertainty surrounding the degree of structural information that multispectral satellite remote sensing is able to resolve (Morley *et al.*, 2018). The high spectral similarity between the late successional - old growth forest, late-static treeline and late-abrupt advancing treeline classes indicates a saturation in the spectral properties during the transition between the closed canopy, abrupt advancing treeline and old growth forest structures (Figure 2.3). Amalgamating the static treeline and old growth forest classes leads to an improvement in the ability to identify areas of old-growth forest (Figure 2.4). Similarly, amalgamating the early-diffuse, late-diffuse and late-abrupt advancing forest classes leads to an improved ability to separate areas at the leading edge of forest advance from areas of old-growth forest (Figure 2.4). Consequently, we find that the use of simplified structural classes improves the characterisation of areas indicative of treeline advance or stasis. However, overlap in the spectral properties means that it is not possible to identify variation in forest structure within areas of forest advance using discrete classes.

The spectral similarity highlighted by the probability estimates of the forest / non-forest regression persists between areas of diffuse forest advance and some areas of the grassland

(Figure 2.3). At the leading edge of forest advance, the diffuse advancing treeline class is characterised by a few trees less than 5 m in height. Consequently, the size and density of establishing trees are not sufficient to provide a significant difference in spectral reflectance in some grassland areas when using a single date image, leading to an over-estimation in the extent of diffuse treeline advance (Figure 2.3 & 2.4). The spectral similarity between some grassland areas and the diffuse advancing treeline exists in areas where changes in forest extent and structure are occurring most rapidly. Consequently, the identification of areas of forest advance can be improved by comparing images over time (e.g. Dinca *et al.*, 2017; Mihai *et al.*, 2017; Bharti *et al.*, 2012). The Landsat archive offers the most consistent source of multispectral satellite data with images dating back to the 1980s at 30 m pixel size. Concerns had been raised over the potential suitability of data from the Landsat archive to characterise vegetation heterogeneity due to the spatial resolution of the spectral data (Bharti *et al.*, 2012; Buchanan *et al.*, 2015; Chen *et al.*, 2015). It is often perceived that imagery with a high spatial resolution will improve the characterisation of habitat heterogeneity because of the ability to identify small objects, e.g. individual trees. However, we show that spectral features derived from Landsat-8 data have a comparable strength of relationship to higher resolution imagery when simple structural classes are used, despite the ability to include multiple measures of spectral texture at the plot scale from imagery with a high spatial resolution (difference of R^2_{MF} between sensors tested within 0.03 for forest / non-forest and 0.05 for the simplified structural classes, Table 2.7; Donoghue and Watt, 2006). Consequently, exploiting the long-term, open-access Landsat archives to identify changes in forest extent over time will improve estimates of forest distribution change at the leading edge of forest-grassland transitions (e.g. Dinca *et al.*, 2017; Mihai *et al.*, 2017).

While exploiting the Landsat archive is beneficial for identifying areas of treeline change, there are still difficulties in characterising variation in forest structure within areas of change using structural classes. Identifying change between simplified class assignment over time using archived Landsat data would allow estimation of the extent of forest change and stand age of advancing forest, however, this approach would not directly characterise forest structure. An alternative solution is to estimate above-ground woody biomass directly using imagery of higher resolution within areas identified as advancing forest. Whilst data from the GeoEye sensor returns the highest correlation coefficient with above-ground woody biomass ($R^2 = 0.723$, $p < 0.01$), the difference in correlation coefficient using data from Sentinel-2 or SPOT-7 are within 0.04 ($R^2 = 0.681$, $p < 0.01$; $R^2 = 0.682$, $p < 0.01$ respectively). Consequently, there is an opportunity to make use of freely available Sentinel-2 data to estimate above-ground

woody biomass at the stand scale, thereby allowing variation in forest structure to be characterised within areas undergoing forest advance at the mountain treeline. This two-stage approach would allow variation in vegetation structure at the mountain treeline to be estimated with higher confidence than using either a forest / non-forest classification, which overestimates forest cover, or the direct estimation of above-ground woody biomass, which would give an unreliable estimate of biomass past a saturation threshold.

Structural classes are broad enough to be used at a global scale, and while not necessarily present in every mountain forest, are suitably flexible to be adapted to the local community and structural composition. Here the spectral similarity of conifer species meant it was not possible to distinguish between the early successional – diffuse advancing treeline and the late successional – diffuse advancing treeline. However, Bharti *et al.* (2012) have shown the ability of multispectral Landsat imagery to separate coniferous and broadleaf species at other elevational treelines. Therefore, in other mountain areas, broader species differences could be incorporated to account for species-specific responses to environmental change providing suitable training data are available. When adapting structural classes, the spectral similarity between classes highlighted above emphasises the importance of independent accuracy assessments, the process by which image classification algorithms are trained and validated using subsets of the ground-truthing data set (see Castilla, 2016; Olofsson *et al.*, 2014, 2013). While accuracy assessments are required of any study using remotely sensed data to estimate land-surface properties; they remain an element absent from many previous studies of mountain treelines (Morley *et al.*, 2018). At the leading edge of mountain forest distribution, some areas respond to environmental change very quickly while other areas slowly or not at all (e.g. Greenwood *et al.*, 2014; Harsch *et al.*, 2009; Lloyd, 2005). Consequently, as the uptake of remote sensing technology in assessments of changing mountain forest distribution increases, there is a need to ensure that conclusions drawn about changes in forest extent and structure at forest margins are reliable when scaled up to assess entire mountain ranges.

2.5 Conclusion

Obtaining estimates of changes in forest distribution over large areas is challenging in mountain areas where steep terrain often restricts the geographical scope of field campaigns. Change assessments must account for variation in forest structure to make reliable estimations of the impacts of distribution shifts on biodiversity and ecosystem function. By comparing different satellite sensors against four definitions of vegetation structure at the mountain treeline that are widely used in the ecology, biogeography and remote sensing literature, we demonstrate that the identification of areas indicative of forest advance or stasis is best

achieved using a simplified class structure while variation in structure within areas of forest advance is best characterised in multispectral satellite remote sensing using above-ground woody biomass to describe forest structure. There is very little difference in the ability of the sensors tested here to discriminate between categorical descriptors of vegetation structure, and while Landsat 8 is less well suited to defining above-ground woody biomass there is little difference between the relationships defined for GeoEye, SPOT-7 and Sentinel-2 data. The results presented here enable structural variation in mountain forest margins to be identified in multispectral satellite remote sensing, facilitating research in mountain areas where significant fieldwork is not possible. Consequently, the methods described in this paper will advance our understanding of the ecological mechanisms driving forest distribution shifts across mountain ranges and improve estimates of the impacts that changes in forest distribution will have on biodiversity and ecosystem function.

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Supplementary Information 1

Table S1: Coefficient of determination from the regression of four definitions of vegetation structure at the mountain treeline against texture features derived from four spectral bands and three vegetation indices from 6m pixel size SPOT-7 data in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$).

Forest / Non-forest (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.597**	0.584**	0.629**	0.126**	0.442**	0.600**	0.159**
St. dev.	0.034*	<0.001	0.021	0.111**	0.077**	<0.001	0.013
Coef. of Var.	0.007	0.061**	0.034*	0.200**	0.112**	0.163**	0.014
Skewness	0.040*	0.016	0.034*	<0.001	0.004	0.004	<0.001
Kurtosis	0.019	0.005	0.007	0.011	<0.001	0.004	0.003

Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.396**	0.389**	0.393**	0.165**	0.170**	0.324**	0.056**
St. dev.	0.075**	0.083**	0.103**	0.063**	0.041**	0.050**	0.017
Coef. of Var.	0.065**	0.092**	0.083**	0.096**	0.054**	0.130**	0.018
Skewness	0.068**	0.060**	0.068**	0.025*	0.014	0.045**	0.006
Kurtosis	0.009	0.008	0.010	0.015	0.007	0.008	0.014

Simplified Structural classes (R^2_{MF} ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.505**	0.505**	0.514**	0.219**	0.231**	0.425**	0.079**
St. dev.	0.097**	0.065**	0.101**	0.059**	0.057**	0.055**	0.008
Coef. of Var.	0.066**	0.061**	0.057**	0.100**	0.075**	0.180**	0.008
Skewness	0.022*	0.015	0.027*	0.014	0.004	0.007	0.001
Kurtosis	0.010	0.005	0.006	0.006	0.000	0.003	0.004

Above-ground biomass, t C ha⁻¹ (R^2 ; $n = 154$)

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.653**	0.681**	0.670**	0.345**	0.146**	0.577**	<0.001
St. dev.	0.085**	0.063**	0.089**	0.005	<0.001	0.012	0.075**
Coef. of Var.	0.053*	<0.001	<0.001	0.127**	0.006	0.112**	0.067**
Skewness	0.087**	0.103**	0.143**	0.045*	0.025	0.057**	0.029
Kurtosis	<0.001	0.009	0.009	0.002	<0.001	<0.001	<0.001

Table S2: Coefficient of determination from the regression of four definitions of vegetation structure at the mountain treeline against texture features derived from four spectral bands and three vegetation indices from 10m pixel size Sentinel-2 data in the Mt. Hehuan area of the Central Mountain Range, Taiwan. (* $p < 0.05$, ** $p < 0.01$).

Forest / Non-forest (R^2_{MF} ; $n = 101$ (n Mean response = 154))

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.599**	0.575**	0.642**	0.090**	0.510**	0.590**	0.272**
St. dev.	0.023	0.003	0.012	0.053	0.048*	<0.001	0.002
Coef. of Var.	0.001	0.056	0.031	0.086*	0.082*	0.156**	0.008
Skewness	0.008	0.020	0.039	0.011	0.015	0.009	0.051*
Kurtosis	0.004	0.003	0.002	0.007	0.010	0.034	<0.001

Structural classes (R^2_{MF} ; $n = 101$ (n Mean response = 154))

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.396**	0.378**	0.389**	0.157**	0.190**	0.287**	0.088**
St. dev.	0.129**	0.155**	0.158**	0.051**	0.064**	0.038*	0.015
Coef. of Var.	0.103**	0.135**	0.120**	0.055**	0.076**	0.104**	0.012
Skewness	0.042*	0.031	0.055**	0.031	0.018	0.039*	0.027
Kurtosis	0.007	0.007	0.012	0.011	0.008	0.016	0.006

Simplified Structural classes (R^2_{MF} ; $n = 101$ (n Mean response = 154))

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.531**	0.516**	0.526**	0.214**	0.271**	0.378**	0.133**
St. dev.	0.145	0.116	0.158	0.034*	0.089**	0.036*	0.007
Coef. of Var.	0.101**	0.077**	0.085**	0.038*	0.110**	0.147**	0.009
Skewness	0.009	0.018	0.070**	0.025	0.008	0.016	0.024
Kurtosis	0.003	0.003	0.006	0.008	0.009	0.019	<0.001

Above-ground biomass, t C ha⁻¹ (R^2 ; $n = 101$ (n Mean response = 154))

	Blue	Green	Red	NIR	NDVI	GRVI	GNDVI
Mean	0.686**	0.681**	0.668**	0.349**	0.189**	0.468**	0.021
St. dev.	0.067*	0.052*	0.070*	0.010	0.007	0.001	0.036
Coef. of Var.	0.048*	<0.001	0.003	0.133**	0.025	0.030	0.023
Skewness	0.072*	0.042	0.137**	0.036	0.010	0.035	0.006
Kurtosis	<0.001	0.001	<0.001	<0.001	0.020	0.010	0.018

Chapter 3

Identifying variation in patterns of forest advance in a high-elevation ecosystem

Abstract:

Changes in global climate and land-use are driving changes in species distributions. Mountain ecosystems are highly susceptible to global environmental changes because they are expected to experience higher than average temperature increases and are more susceptible to land-use change. Montane forests show a diverse response to environmental change with upward elevational shifts, increased tree density and across-slope movement all reported. However, there is variation in patterns of forest advance both between geographic regions and at local scales. Variation in forest range shifts must be accounted for when estimating changes in forest ranges because local variation in forest range shifts are expected to modify the landscape-scale implications that forest advance will have on montane biodiversity and ecosystem function. This study uses repeat aerial photography analysed with a sample-based change assessment to quantify changes in forest elevation and area and to quantify variation in the rate of forest advance over time and with topography. In the Mt. Hehuan study area of the Central Mountain Range, Taiwan, the non-forest area has declined by 29 % between 1963 and 2016. The decline in non-forest area is driven by a 295.0 ha increase in forest area within the Mt. Hehuan area. While no change in mean forest elevation is reported, the mean elevation of establishing forest has increased at a rate of 2.2 m yr⁻¹ lagging 0.5 m yr⁻¹ behind the estimated change in isotherm position. Topography alters patterns of forest advance in the Mt. Hehuan area. East and south facing slopes have experienced the largest gains in forest area, and 0-20° gradient slopes show an increasing rate of forest establishment up to 2016. However, slopes facing west or with gradients of >46° show negligible increases in forest area. The integration of a probability-based change-sample assessment with repeat aerial photography has enabled the quantification of landscape-scale forest range shifts with high accuracy. The change-sample method offers an unprecedented opportunity to expand the geographic scope in change assessments, reduce uncertainty in future change assessments and make precise estimates of the implications of forest advance.

3.1 Introduction

Changes in global climate and land-use are driving shifts in forest distribution (Améztegui *et al.*, 2016, 2010; Harsch *et al.*, 2009). Global temperatures are predicted to increase between 0.3 and 4.8 °C by 2100 compared to the 1985-2005 mean (IPCC, 2013). However, regional variation in temperature changes alongside elevation-dependent warming means that mountain ecosystems are expected to experience higher than average temperature increases (Dirnböck *et al.*, 2011; IPCC, 2013; Pepin *et al.*, 2015). Mountain ecosystems are also susceptible to land abandonment due to shifts in agricultural practices, local population demographics and socio-economic policies (Haddaway *et al.*, 2014; MacDonald *et al.*, 2000). Consequently, mountain ecosystems are highly susceptible to global environmental change.

Uphill advances in the position of montane forests have been observed at the elevational limit of forest distribution (henceforth the treeline), attributable to increasing temperatures and land-use changes (Améztegui *et al.*, 2016, 2010; Harsch *et al.*, 2009). However, upward shifts in treeline position tell only part of the story of changing forest distribution in mountain ecosystems. There is variation in global patterns of forest advance with 52.4 % of elevational and latitudinal treelines showing upward or poleward migration while a further 46.4 % show no change (Harsch *et al.*, 2009). In areas that do not exhibit increases in forest elevation, increased tree density below the treeline and across-slope movement have often been reported (e.g. Bharti *et al.*, 2012; Klasner and Fagre, 2002). It is, therefore, necessary to quantify changes in both the elevation and area of forest distribution in mountain ecosystems to fully capture species responses to environmental change.

At naturally occurring treelines, temperature has been identified as the global limiting factor on treeline position and advance (Körner and Paulsen, 2004). However, the complexity of controls on forest establishment and advance at the treeline results in local and landscape-scale variation in forest range shifts. In mountain ranges, local climate regimes can be modified by topography causing some slopes to experience climatic conditions that may be cooler, drier or more sheltered than neighbouring areas (Malanson *et al.*, 2011; Suggitt *et al.*, 2011). Variation in resource availability (e.g. McNown and Sullivan, 2013; Sullivan *et al.*, 2015), radiative stress (Bader *et al.*, 2007), and drought stress (e.g. Johnson and Smith, 2007; Leuschner and Schulte, 1991; Millar *et al.*, 2007) at the plot scale also play a role in controlling the establishment and growth patterns of advancing montane forests. Additionally, the structure of a forest stand itself can act as a feedback mechanism to facilitate or constrain patterns of tree establishment, growth and mortality through increased seed availability, modification of the micro-climate and alterations to competitive dynamics (Camarero *et al.*,

2017). While the influence that individual factors have on forest advance or stasis is reasonably well understood, the role that interactions between individual factors and feedback processes play in influencing treeline position and forest advance are less well understood. Specifically, there are needs to improve our understanding of variation in rates of forest advance to better understand how interactions and feedback processes lead to landscape-scale variation in patterns of forest advance (Holtmeier and Broll, 2017; Malanson *et al.*, 2011).

Quantifying variation in forest advance in mountain ecosystems is challenging as some areas show a rapid response to environmental change while others respond slowly or not at all. However, the ability to accurately quantify variation in patterns of forest advance in mountain ranges is crucial for assessing carbon sequestration & emissions, biodiversity conservation and resource management. The relative isolation of mountain environments and high habitat heterogeneity means that disproportionately high numbers of endemic and rare species are found at high elevations (Steinbauer *et al.*, 2016). The upward or across slope advance of montane forests will likely cause a reduction in grassland area and change competitive dynamics in high-elevation ecosystems. Consequently, shifts in forest distribution are expected to result in the range contraction and extirpation of grassland species as species ranges are pushed towards mountain tops (Jump *et al.*, 2012). While forest advance is considered a significant threat to grassland biodiversity, increases in forest area, tree density and growth rates are expected to increase the carbon sequestration potential of montane forests (Zierl and Bugmann, 2007). Therefore, increased forest area and tree growth rates in mountain ecosystems could act as negative feedbacks to global temperature increases through greater carbon sequestration, thus contributing to the mitigation of global climate change (Saxe *et al.*, 2001).

Obtaining accurate estimates of the impacts that forest advance will have in mountain ecosystems is currently limited by our ability to quantify variation in forest range shifts at the landscape scale. Local variation in patterns of forest advance must be accounted for across large areas in order to avoid over- or under-stating the severity of the impacts that forest advance will have on biodiversity and ecosystem function. While rapid forest advance may result in the local extirpation of species with narrow environmental tolerances (Jump *et al.*, 2012); if the ability for trees to establish is restricted in some areas within a mountain range due to non-thermal controls, treeless areas may persist that provide refugia for species from alpine habitats and enable their continued persistence (Bruun and Moen, 2003; Greenwood and Jump, 2014). Consequently, the implications that forest advance will have at a landscape-scale will be dependent on local variation in forest range shifts.

Field observations have steered much of our current understanding of species range shifts and their associated impacts. The best estimates of change and the associated implications typically come from repeat surveys of fixed monitoring sites that are distributed across a mountain range (e.g. Global Observation Research Initiative in Alpine Environments; Grabherr *et al.*, 2000). However, many studies are based on incidental historical records and limited field observations (Gottfried *et al.*, 2012). Mountain ranges are difficult to access, and field surveys are often restricted to accessible sites and sample only limited areas. Assessment of the implications that forest range shifts may have on regional carbon budgets or biodiversity are subject to bias if change assessments rely on limited field data to identify regional patterns of forest advance. At a landscape scale, clustering of habitat changes and rare events that occur sporadically in time or space can skew estimates of change that are based on limited field surveys or incidental observations taken at snapshots through time (Fisher *et al.*, 2008). Furthermore, at a global scale, North American and European mountain ranges have received a greater proportion of research effort than southern hemisphere and Asian mountain ranges which are subsequently under-represented in global estimates of species range shifts (Harsch *et al.*, 2009; Malanson *et al.*, 2011). Our ability to quantify uncertainty in landscape-scale forest range shifts and compare estimates of range shifts between geographic areas is therefore limited. Despite challenges in estimating forest range shifts in largely inaccessible mountain ranges, the development of theoretically and methodologically consistent approaches to defining variation in forest range shifts at a landscape-scale is essential to enable the quantification of uncertainty in change estimates and allow comparisons of range shifts between areas.

The use of remote sensing data to assess changes in forest distribution is attractive to overcome limitations of field surveys imposed by poor accessibility to field sites in mountain ranges. Repeat vertical aerial photographic survey data has previously been used to assess change at mountain treelines by identifying the treeline in individual images and comparing the position of the treeline over time (e.g. Greenwood *et al.*, 2014; Klasner and Fagre, 2002; Luo and Dai, 2013; Mathisen *et al.*, 2014; Resler *et al.*, 2004). Such studies often aim to identify changes in the maximum treeline elevation or tree density. However, many published studies do not provide quantitative estimates of uncertainty in the range shifts reported (Morley *et al.*, 2018). Given that some areas respond rapidly to environmental change while others respond slowly or not at all, the lack of quantitative uncertainty estimates limits the interpretation of the results that would allow for a landscape-scale estimate of changes in forest distribution in mountain ecosystems.

Sample-based change estimates are a long-established technique for assessing changes in habitat area and condition that have been widely adopted by forest monitoring programs interested in quantifying change in forest area and forest degradation (Cochran, 1977; Olofsson *et al.*, 2013; Pickering *et al.*, 2019). This approach to change assessment uses manual interpretation of remote sensing data at sample plots to estimate the area of each habitat type at each survey date and within a given terrain feature or geographic region of interest (henceforth stratum) alongside an uncertainty value for the area estimate. Sample-based change estimates are recognised as a more reliable method for estimating changes in habitat type or condition than change assessments derived from classified maps due to image classification errors (Olofsson *et al.*, 2016, 2013; Stehman, 2013). Therefore, integrating a sample-based approach with repeat aerial photography enables changes in habitat to be identified over time with a high degree of confidence. This unification provides the opportunity to expand the geographic scope of change assessments and reduce uncertainty in estimates of montane forest distribution changes. Here aerial photography is combined with a sample-based change assessment to 1) quantify changes in forest elevation and area over time; 2) quantify the rate of forest advance and 3) identify how the rate of forest advance varies over time and with topography.

3.2 Methods

3.2.1 Study area

This study was conducted in the Mt. Hehuan area of the Central Mountain Range, Taiwan (Figure 3.1). Despite Taiwan spanning the Tropic of Cancer, high-elevation areas of the Central Mountain Range experience temperate conditions that support conifer-dominated forests at elevations higher than 2400 m a.s.l. The high-elevation forests of the Central Mountain Range are dominated by four conifer species, primarily *Abies kawakamii* and *Tsuga chinensis* with areas of *Pinus taiwanensis* and *Pinus armandii* establishment. The Mt. Hehuan study area reaches a maximum elevation of 3560 m a.s.l. with a naturally forming treeline giving way to grassland dominated by the bamboo, *Yushania niitakayamensis*.

Greenwood *et al.* (2015, 2014) found that the high-elevation treeline in Taiwan is predominantly temperature limited, with topography and local sheltering influencing treeline position, structure and advance through a modification of regional temperature regimes. The importance of local topographic controls on the treeline in the Central Mountain Range has resulted in a highly reticulate and structurally diverse treeline. As a consequence, patterns of forest advance within the study area show a high degree of variation over a short distance.

Localised reductions in the treeline position are caused by sporadic, naturally occurring small-scale fires and landslides. However, routine disturbance events across the Central Mountain Range are considered of low impact at the landscape scale with limited evidence to support widespread anthropogenic disturbance or grazing by either domestic or wild herds.

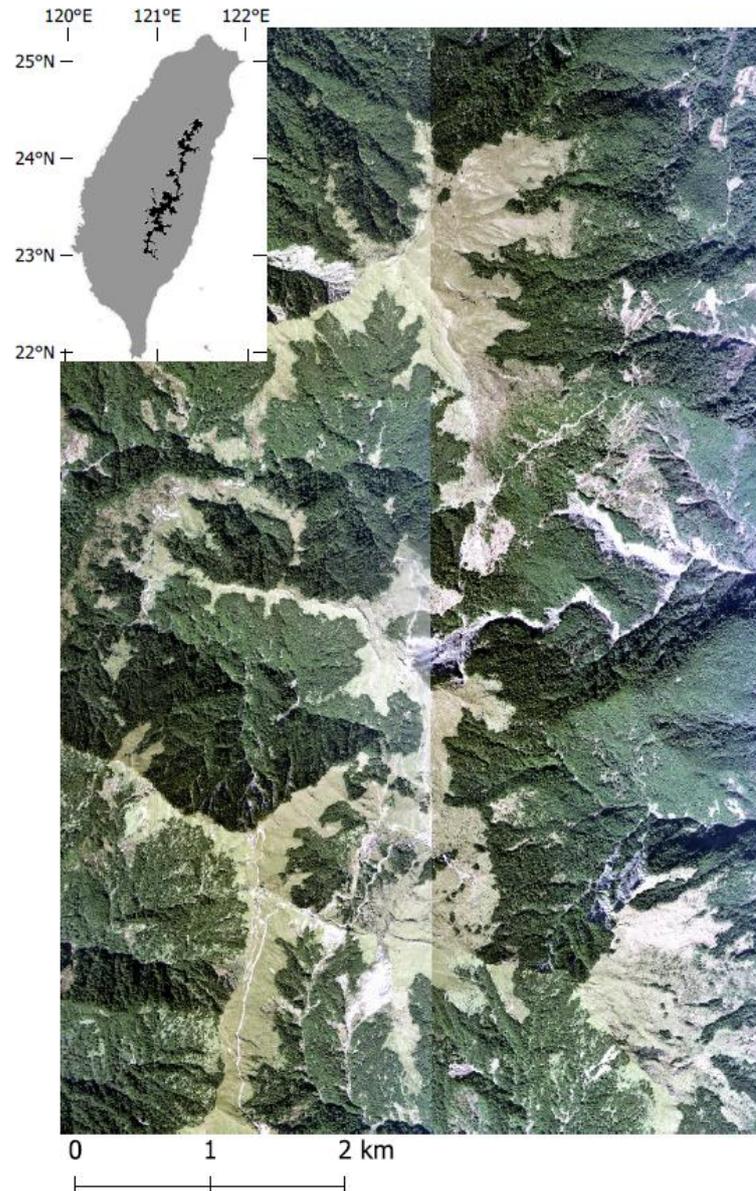


Figure 3.1: Colour aerial photography from 2016 showing the treeline of high elevation conifer forests in the Mt Hehuan study area. The Mt Hehuan study area is located in the North of the Central Mountain Range, Taiwan (the area above 2400 m a.s.l. is shown in black in the inset).

3.2.2 Aerial photography

Black and white aerial photographs were captured in 1963 (0.3 m pixel size) and 1980 (0.25 m pixel size), colour photographs in 2001 (0.5 m pixel size) and four-band multispectral images in 2016 (0.25 m pixel size). Aerial photographs from 1980, 2001 and 2016 were delivered as orthorectified image products by the Taiwanese National Archive and did not require further geometric corrections (minimum accuracy is 2.5 m). The aerial photographs from 1963 were georeferenced to the images captured in 2016 using a spline transformation in the QGIS Georeferencing plugin (Average number of tie points used was 128, ranging between 78 and 207 between image pairs; the mean error in all image pairs was < 1 pixel).

3.2.3 Change assessment

3.2.3.1 Sample Design

A proportional stratified random sampling design was used to assess change in forest distribution. To ensure adequate representation of the entire study area, slope orientation was used as a basis for stratification due to the major role topography has in mediating patterns of forest advance (Greenwood *et al.*, 2015, 2014). Stratification was based on 12 categories of slope gradient and aspect attributes calculated from a high-resolution TanDEM-X Digital Elevation Model (12 m spatial resolution resampled to 15 m pixel size), using four cardinal compass directions ($\pm 45^\circ$ in either direction) and three slope gradient classes (0-20°, 21-45° and 46°+). The number of samples taken in each stratum was proportional to the area of the study region occupied by the slope-gradient combination (Table 3.1, Figure 3.2). Following the removal of sample plots that had to be omitted due to a cloud or shadow impairing the interpretation, a total of 2785 sample plots were interpreted, equivalent to 1.54 % of the total study area.

Table 3.1: The number of sample points from each of the 12 terrain categories used in the change assessment of forest advance in the Mt. Hehuan area of the Central Mountain Range, Taiwan.

Gradient	North	East	South	West
0-20°	67	298	132	59
21-45°	370	706	499	430
46°+	79	47	48	50

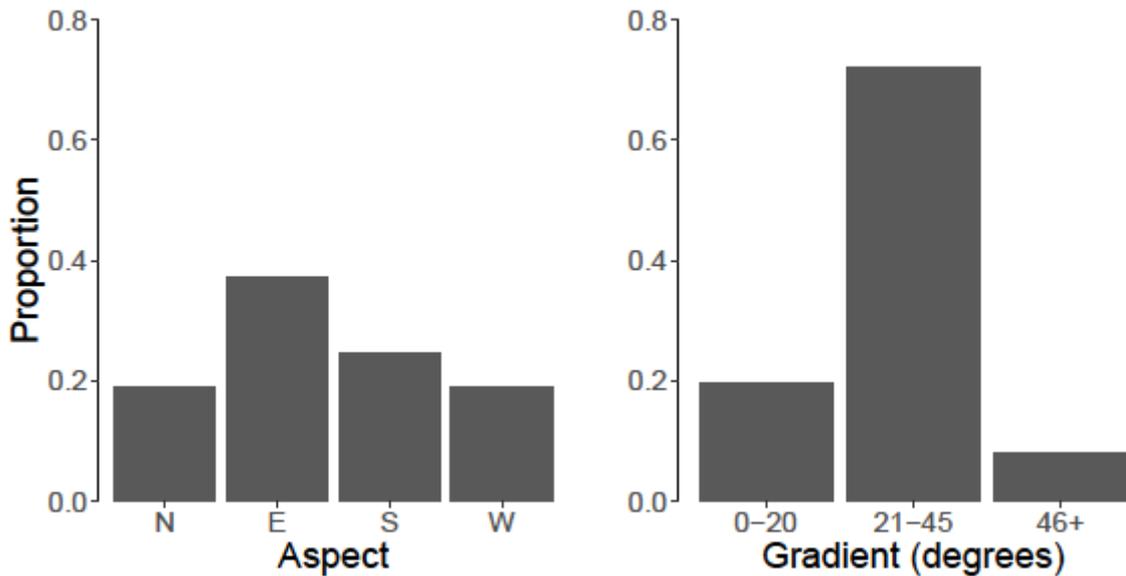


Figure 3.2: The proportion of the Mt. Hehuan study area occupied by each of the four aspects or three gradient classes.

3.2.3.2 Change attributes

At each sample location, a sample plot measuring 15 x 15 m was created and interpreted manually for each epoch of change analysis (1963, 1980, 2001, and 2016). Each sample plot was assigned one of four vegetation classes at each survey period (Table 3.2) enabling change between vegetation classes to be tracked over time (Figure 3.3). Areas that meet the FAO Global Forest Resources Assessment (2018) criterion of a forest as an area with at least 10 % canopy cover and trees greater than 5 m in height are classified here as *forest*. Areas with small trees present within the plot that do not meet the thresholds of a forest as set out by the FAO definition were categorised as *establishing forest*. The scale of the aerial photography (≤ 0.5 m pixel size) is sufficient to discriminate differences in tree size based on crown size. Areas with partial removal of the forest canopy between time periods are categorised as *disturbed* and treeless areas are categorised here as *non-forest* areas. The distinction between the forest and establishing forest classes is important. Forest resource assessments rarely comment on areas of forest establishment that do not meet the pre-defined criteria for forest cover. However, ecological and biogeographic studies have a much broader interpretation, and the treeline is often defined by trees greater than 2 m in height and the species limit by the upper-most trees irrespective of tree height. Therefore, the establishing forest class recognises a greater area of the forest-grassland transition that is present at mountain treelines than a simpler forest / non-forest vegetation classification.

Table 3.2: Definitions of vegetation classes used here to assess forest change in the Central Mountain Range, Taiwan.

Class	Description
Forest	An area of trees that meet FAO (2018) criteria of a forest with at least 10 % canopy cover and trees greater than 5 m in height.
Establishing forest	An area of forest establishment, small trees are identifiable in aerial photographs due to their small crown size.
Non-forest	An area that lacks trees.
Disturbed	An area of forest with a reduction in canopy cover but some trees remain.
Omitted	Unable to identify vegetation class due to cloud cover or shadow.

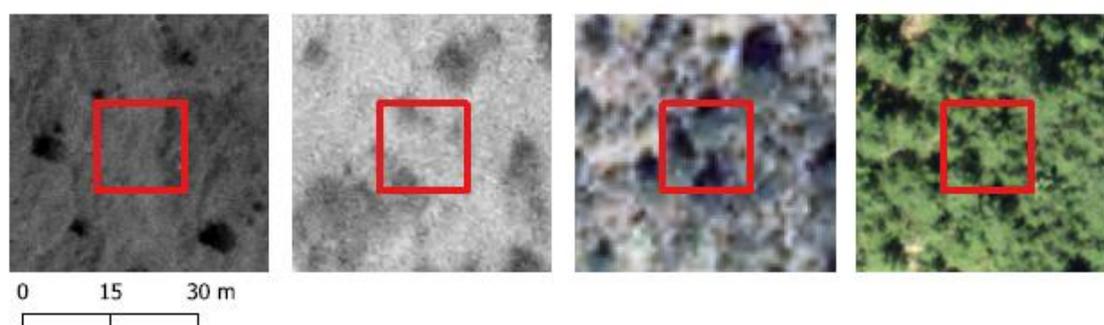


Figure 3.3: Changes in vegetation class over time identified in repeat aerial photographic surveys using 15 x 15 m sample plots (red outline). The images above show non-forest in 1963 (left) transitioning through the establishing forest class (1980 & 2001, middle) and the conversion to the forest class in 2016 (right).

3.2.3.3 Change estimates

Estimates of vegetation change were calculated in R (R Core Team, 2017) using the survey package (Lumley, 2018) to determine weighted estimates of the population total, returning estimated total area (ha) and proportional representation of class membership for each stratum and survey period. The survey package accounts for the effect of stratification by weighting observations according to the sampling probability. The elevation of each plot was identified from a Tan-DEM X Digital Elevation Model and the average elevation of each class calculated for each survey period to quantify the change in class elevation over time. The Tan-DEM X Digital Elevation Model has a relative vertical accuracy of 2m and an absolute vertical accuracy of 10m. The estimated class area in each survey period was compared over time to identify changes in habitat area. Area estimates were calculated for the whole study area and for each terrain stratum to give the proportion of available area occupied by each vegetation class in each of the four aspect strata and three gradient strata. Variation in the rate of habitat change was investigated for three change classes: recent establishment, defined as a change

from non-forest to establishing forest within a change period; rapid establishment, defined as a change from non-forest to forest within a single change period; and advanced establishment, defined as a change from establishing forest to forest within a single change period. Rates of advance were calculated as the proportion of available area occupied by a change class divided by the length of the monitoring period (e.g. the proportion of the non-forest area in 1980 that has converted to forest in 2001 divided by 21 years, returns the rate of rapid establishment between 1980 and 2001). All uncertainty measures reported are at the 95 % confidence intervals unless otherwise stated and area estimates are reported in plan view.

3.3 Results

3.3.1 Landscape-scale change estimates

This sample-based change assessment of the Mt. Hehuan study area reveals that approximately $20.6 \% \pm 2.3 \%$ of the non-forest area in 1963 converted to establishing forest by 2016 with a further $8.2 \% \pm 1.5 \%$ of the non-forest area in 1963 lost to advancing forest by 2016 (Table 3.3). Forest disturbance in the Mt. Hehuan study area is rare, $1.4 \% \pm 0.4 \%$ of the forest area in 1963 has undergone conversion to non-forest while a further $0.7 \% \pm 0.3 \%$ has experienced a reduction in canopy cover between 1963 and 2016 (Table 3.3). There was no evidence indicating anthropogenic causes for forest advance or loss in the Mt. Hehuan study area. In areas of forest loss complete removal of substrate was visible in the aerial photography suggesting that forest loss is primarily caused by landslide events with no direct evidence in the aerial photography to suggest fire caused a loss in forest area. Between 1963 and 2016 forest advance in the Mt. Hehuan study area has led to an estimated net increase in forest area of 295.0 ha and an estimated net decrease in the non-forest area of 332.6 ha (Figure 3.4a). Despite the increase in forest area, the mean elevation of the forest has not changed over time (elevation in 1963 was $2917\text{m} \pm 9\text{ m}$ and in 2016 was $2914\text{ m} \pm 9\text{ m}$; Figure 3.4b). However, the mean elevation of establishing forest has increased over time, rising 115 m in elevation from $2887\text{ m a.s.l.} \pm 26\text{ m}$ in 1963 to $3002\text{ m a.s.l.} \pm 21\text{ m}$ in 2016. While there has been a change in the elevation of establishing forest, the increase in the area occupied by establishing forest is modest with an increase of just 20.1 ha between 1963 and 2016 (Figure 3.4). There has been continued tree growth within areas of establishing forest throughout the study period resulting in $77.8 \% \pm 5.4 \%$ of the area occupied by establishing forest in 1963 converting to forest by 2016 (Table 3.3). The conversion of establishing forest to non-forest is rare in Mt. Hehuan, just $0.9 \% \pm 1.2 \%$ of the area of establishing forest in 1963 returned to non-forest by 2016. However, $21.3 \% \pm 5.3 \%$ of the area of establishing forest in 1963 remained within the establishing forest class in 2016, indicating a limitation on tree growth in some areas (Table 3.3)

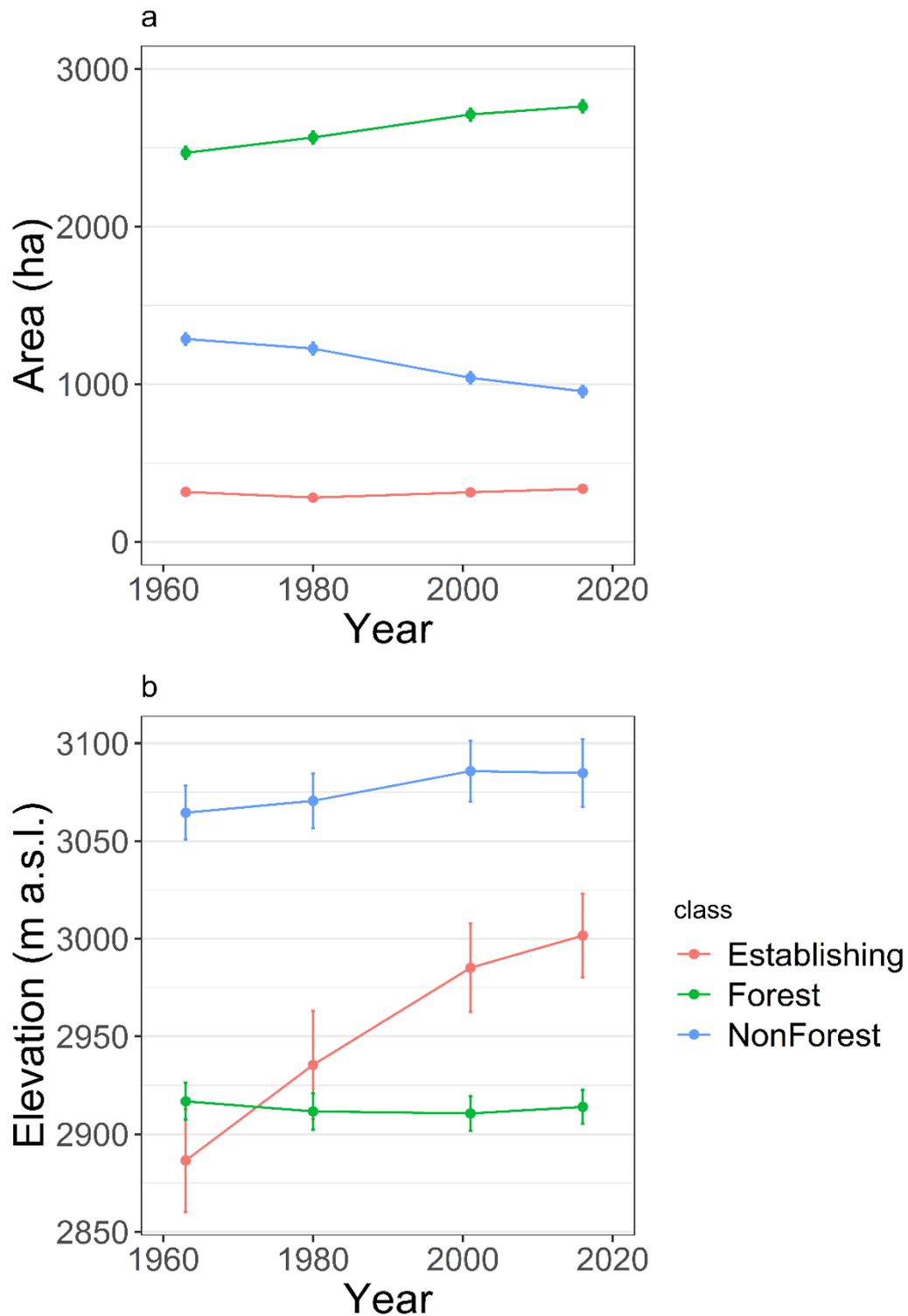


Figure 3.4: Temporal changes in the area occupied (a) and mean elevation (b) of each of the three vegetation classes (forest, establishing forest and non-forest) in the Mt. Hehuan study region of the Central Mountain Range, Taiwan. Uncertainty of the estimates is shown at the 95 % confidence intervals.

Table 3.3: The proportion of changes in vegetation classes between 1963 and 2016. Uncertainty is shown as standard error alongside the estimated proportion of change at the upper (97.5%) and lower (2.5%) 95% confidence intervals.

Class changes from Non-forest					
1963	2016	Proportion	SE	2.5%	97.5%
Non-Forest	Non-Forest	0.7121	0.0132	0.6863	0.7379
Non-Forest	Establishing	0.2058	0.0117	0.1829	0.2288
Non-Forest	Forest	0.0821	0.0080	0.0663	0.0978
Class changes from Establishing forest					
1963	2016	Proportion	SE	2.5%	97.5%
Establishing	Non-Forest	0.0094	0.0063	-0.0030	0.0218
Establishing	Establishing	0.2125	0.0271	0.1595	0.2656
Establishing	Forest	0.7780	0.0275	0.7241	0.8320
Class changes from Forest					
1963	2016	Proportion	SE	2.5%	97.5%
Forest	Non-Forest	0.0142	0.0021	0.0100	0.0184
Forest	Forest	0.9787	0.0026	0.9735	0.9838
Forest	Disturbed	0.0071	0.0015	0.0041	0.0102

3.3.2 Change estimates by terrain strata

East and South facing aspects show the largest change in forest area between 1963 and 2016 resulting in an estimated increase in the proportion of East and South facing slopes occupied by forest of 10.7 % and 8.3 % respectively (Figure 3.5a). Forest area has remained stable on west-facing slopes; however, the proportion of area occupied by establishing forest has increased by 4.3 % resulting in a decrease in the non-forest area over time (Figure 3.5a). When considering slope gradient, forest advance between 1963 and 2016 is greatest on gradients between 0-45° (Figure 3.5b). Gain in forest area over the study period is greater on slopes with 21-45° gradient (221 ha) rather than slopes with 0-20° gradient (76 ha) despite similar changes in the proportion of area occupied by forest. This discrepancy occurs because the 21-45° gradient stratum occupies a larger proportion of the Mt. Hehuan study area (Figure 3.2). The proportion of area occupied by establishing forest has increased from 9.4 % ± 1.3 % in 1963 to 12.4 % ± 1.5 % in 2016 on slopes with 0-20° gradients while there has been a decrease in the proportion of the area of slopes with 21-45° gradient occupied by establishing forest (9.7 % ± 0.7% in 1963 to 6.7 % ± 0.6 % in 2016; Figure 3.5b).

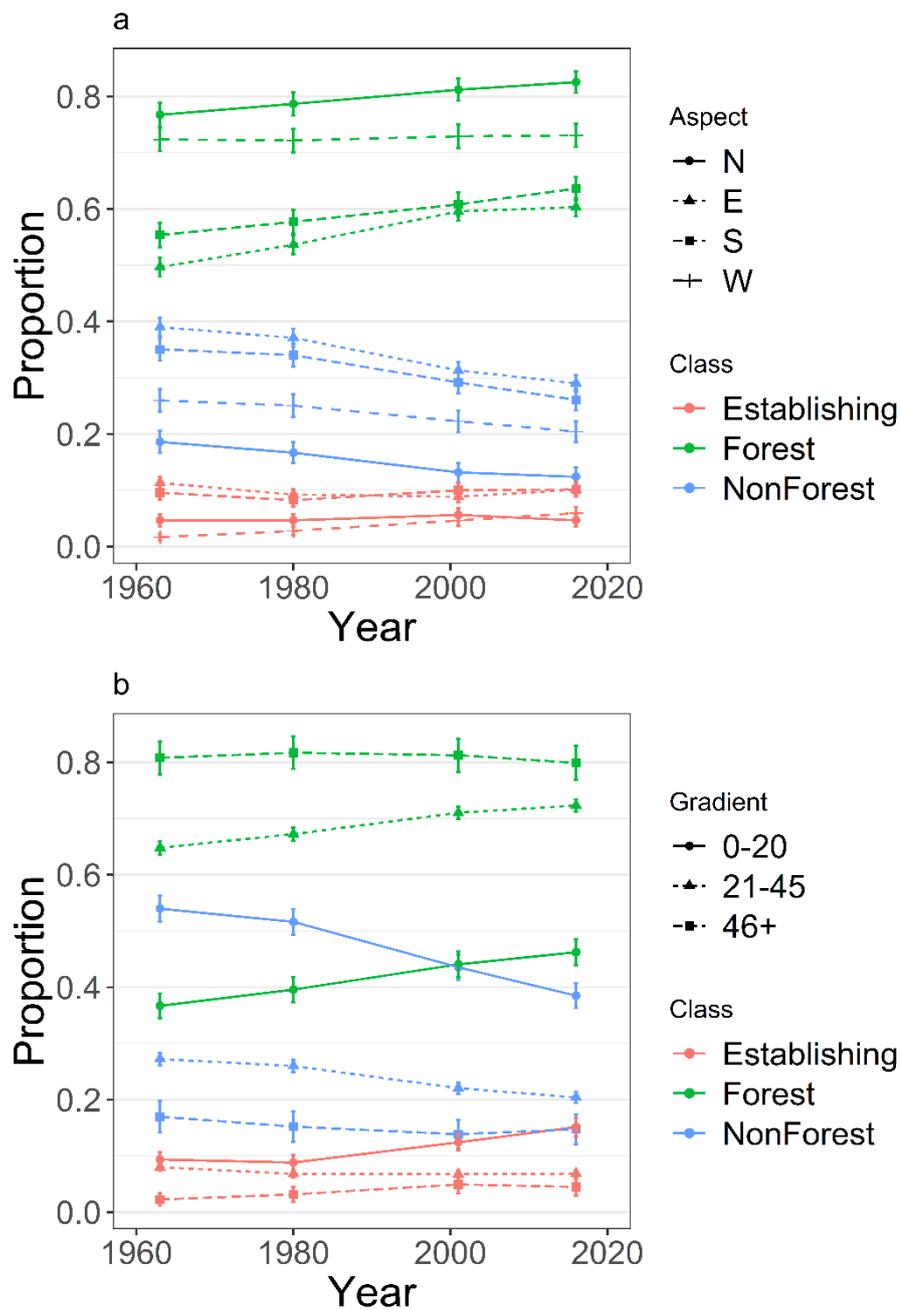


Figure 3.5: Temporal changes in the proportion of aspect (a) and gradient (b) terrain strata occupied by each vegetation class (forest, establishing forest and non-forest) in the Mt. Hehuan area of the Central Mountain Range, Taiwan. Uncertainty of the estimates is shown at the 95 % confidence interval.

3.3.3 Variation in the rate of change

The rate of recent establishment (a change from non-forest to establishing forest within a single change period) peaked across the study area between 1980 and 2001 and remained stable between 2001 and 2016 (Figure 3.6a). For the majority of terrain classes, the patterns of

rates of recent establishment mirror that of the broader study area with only North facing aspects and slopes with gradient $>46^\circ$ deviating from the landscape pattern. Slopes facing North or with a gradient $>46^\circ$ show a sharp peak in recent establishment between 1980 and 2001 followed by a decline in the rate of advance between 2001 and 2016 (Figure 3.6). On East and South facing aspects the rate of recent establishment remained stable following the 1980 and 2001 change period with a small increase in the rate of recent establishment between 2001 and 2016 (Figure 3.6b). The rate of recent establishment on West facing aspects also remains stable after 2001 but shows a slight decline in the rate of recent establishment between 2001 and 2016. The rate of recent establishment on $0-20^\circ$ slopes shows a small increase in the rate of recent establishment after the 1980-2001 change period while $21-45^\circ$ slopes show a small decline in the rate of advance between 2001 and 2016 (Figure 3.6c).

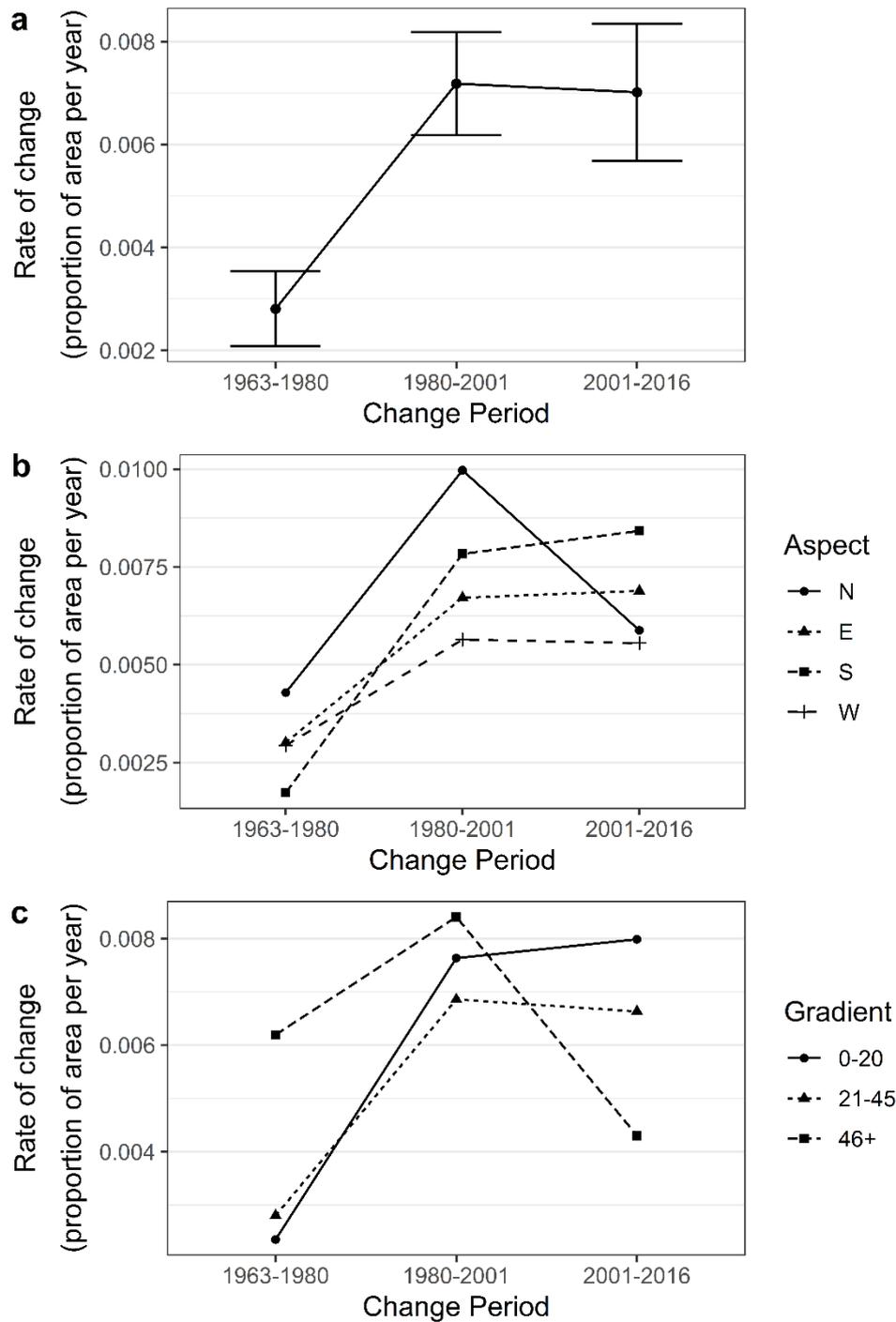


Figure 3.6: Temporal variation in the rate of recent forest establishment, defined as the change from non-forest to establishing within a change period. Three change periods are considered: 1963-1980, 1980-2001 and 2001-2016. Panel a shows the rate of recent forest establishment for the Mt. Hehuan study area as a whole, panel b shows the rate of recent forest establishment separated by aspect strata and panel c shows the rate of recent forest establishment separated by gradient strata. The rate of change is shown as a proportion of available area per year. Uncertainty in the estimates in panel a are shown at the 95 % confidence intervals.

The rate of rapid establishment, defined as the conversion of non-forest to forest in a single change period, is declining over time in the Mt. Hehuan study area (Figure 3.7a). Although there are small variations among terrain strata, a majority of the terrain strata show a decline in the rate of rapid establishment over the whole study period, with the rate of rapid establishment on west facing slopes showing the only increase in rate of rapid establishment over the entire study period. East and South facing aspects show a small rise in the rate of rapid establishment between 1980 and 2001 followed by a subsequent decline in the rate of rapid establishment between 2001 and 2016 (Figure 3.7b). Despite the general trend in decline, the rate of rapid forest establishment increased on west-facing slopes between 2001 and 2016 (Figure 3.7b). All of the slope gradient strata show a decline in the rate of rapid forest establishment between 1963 and 2016 despite a small rise in rapid forest establishment on 21-45° slopes between 1980 and 2001 (Figure 3.7c).

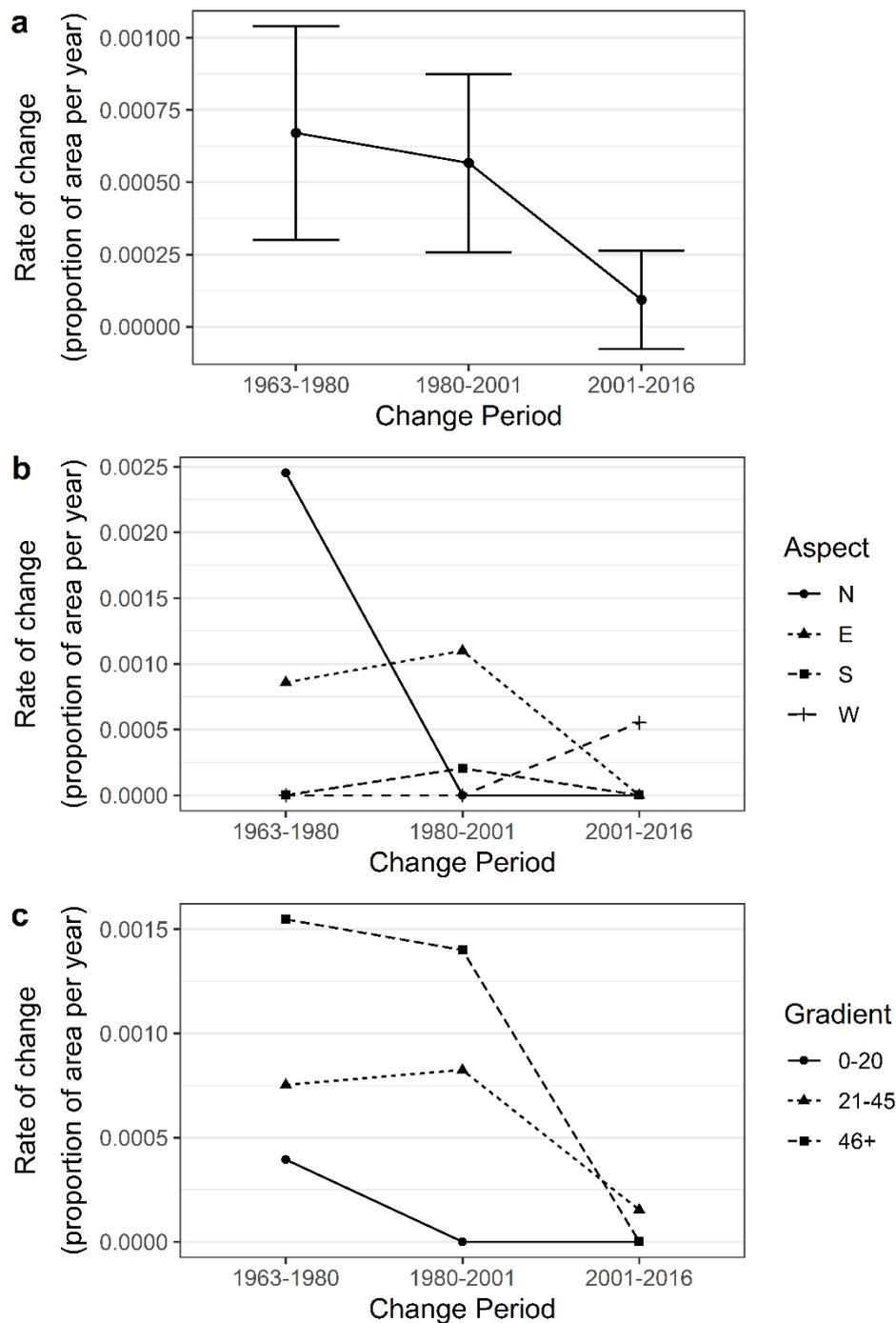


Figure 3.7: Temporal variation in the rate of rapid establishment, defined as the change from non-forest to forest within a change period. Three change periods are considered: 1963-1980, 1980-2001 and 2001-2016. Panel a shows the rate of rapid forest establishment for the Mt. Hehuan study area as a whole, panel b shows the rate of rapid forest establishment separated by aspect strata and panel c shows the rate of rapid forest establishment separated by gradient strata. The rate of change is shown as a proportion of available area per year. Uncertainty in the estimates in panel a are shown at the 95 % confidence interval.

The rate of advanced establishment, defined as the conversion between establishing forest and forest within a single change period, peaks between 1980 and 2001 in Mt. Hehuan (Figure 3.8a). Aspect and slope gradient both show a deviation from the landscape-scale trend. The rate of advanced establishment on East and West facing slopes peaks between 1980 and 2001 followed by a subsequent decline in the rate of advanced establishment between 2001 and 2016 (Figure 3.8b). However, the rate of advanced establishment on North and South facing slopes is stable after 2001 with North facing slopes experiencing a marginal decline in the rate of change between 2001 and 2016 while South facing slopes show a small increase in the rate of advanced establishment between 2001 and 2016 (Figure 3.8b). Slopes with a gradient between 0-45° show an increase in the rate of advanced establishment between 1980 and 2001 (Figure 3.8c). However, slopes with a gradient >46° show the inverse relationship with a strong decline in the rate of change between 1980 and 2001 and higher rates of advanced establishment during the 1963 - 1980 change period and the 2001 - 2016 change period (Figure 3.8c).

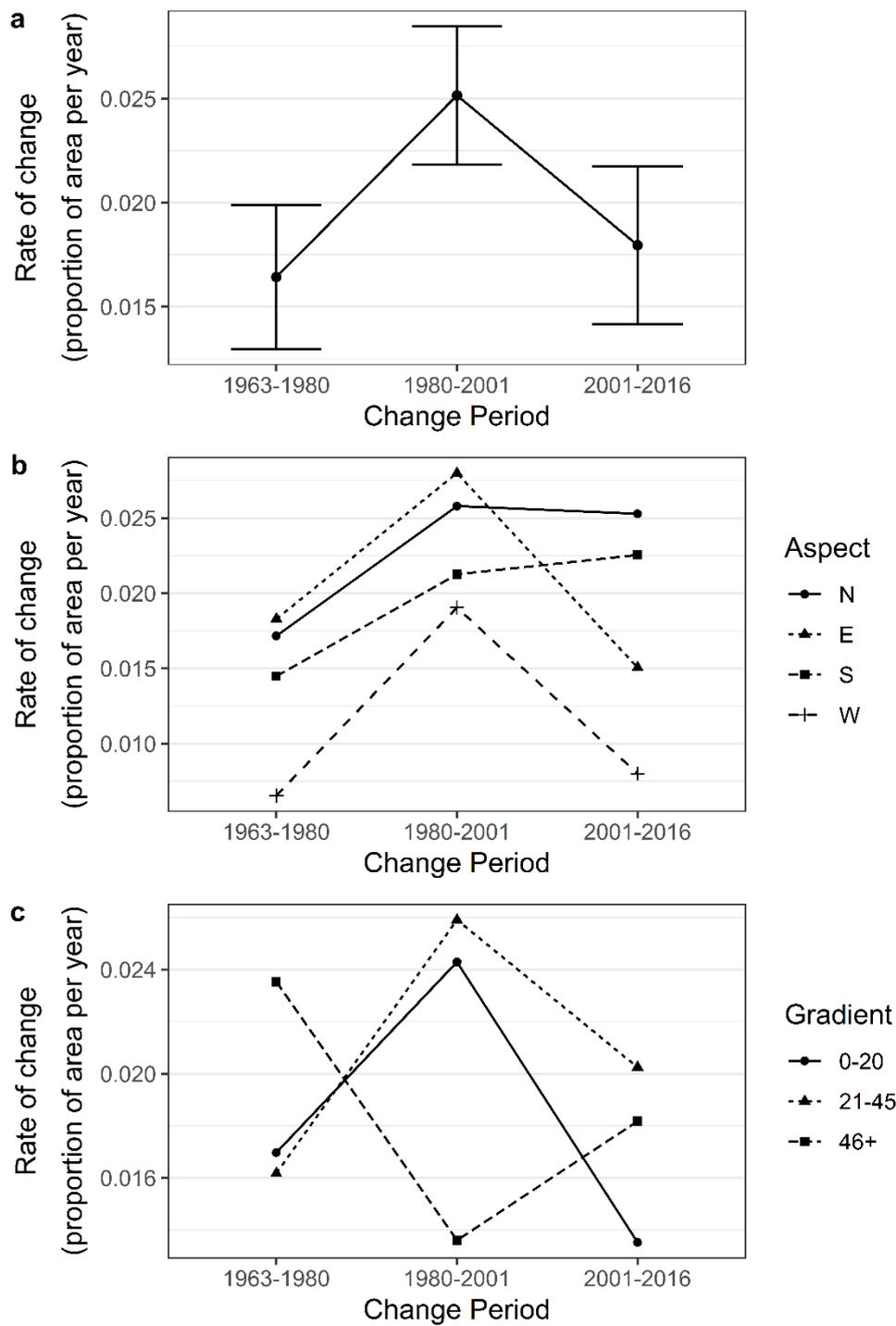


Figure 3.8: Temporal variation in the rate of advanced establishment, defined as the change from establishment to forest within a change period. Three change periods are considered: 1963-1980, 1980-2001 and 2001-2016. Panel a shows the rate of rapid forest establishment for the Mt. Hehuan study area as a whole, panel b shows the rate of rapid forest establishment separated by aspect strata and panel c shows the rate of rapid forest establishment separated by gradient strata. The rate of change is shown as a proportion of available area per year. Uncertainty in the estimates in panel a are shown at the 95 % confidence interval.

3.4 Discussion

Repeat aerial photographic survey data analysed with a sample-based change assessment, reveal that forest advance has led to a loss of 29 % of the non-forest area present in 1963 in the Mt. Hehuan area of the Central Mountain Range, Taiwan (Table 3.3). While there has been an increase in forest area of 295.0 ha between 1963 and 2016 in the Mt. Hehuan area, the mean elevation of the forest class has not changed over the study period. However, the mean elevation of the establishing forest class has increased 115 m between 1963 and 2016 (equivalent to 2.2 m yr⁻¹). Patterns of forest advance vary according to topography, with South and East facing slopes showing the most significant increases in forest area between 1963 and 2016. Slopes with a 0-20° gradient indicate an increasing rate of recent establishment over time, while 21-45° gradient slopes show little change after 2001 and slopes with a gradient greater than 46° show a decrease in the rate of recent establishment following a peak in the rate of establishment between 1980 and 2001.

The substantial increase in forest area, yet stasis in mean forest elevation reported here (Figure 3.4) is consistent with patterns of forest advance previously found in the Mt. Hehuan study region. Greenwood *et al.* (2014) found that forest advance in the Central Mountain Range, Taiwan, predominantly displays infilling below the upper treeline with only modest changes in maximum elevation (27-33 m gain in maximum elevation). The montane forests of the Central Mountain Range, Taiwan, have a highly reticulate treeline owing to strong topographic and micro-climatic controls on treeline position and seedling establishment (Greenwood *et al.*, 2015, 2014). The reticulated nature of the treeline means that the forest has reached its maximum potential elevation in some areas, as determined by mountain ridges, and so it is not possible for the forest to shift further upslope. While changes in treeline elevation are commonly used to indicate the response of montane forests to environmental change, the lack of elevation changes seen in forest cover yet 295 ha increase in forest area emphasises the need for future assessments of montane forest distribution shifts to account for changes in both elevation and area of forest cover.

In the Central Mountain Range, Taiwan, Jump *et al.* (2012) report a rise in temperatures of 1.05 °C to 2009 compared to the 1934-1970 mean. Given the estimated temperature lapse rate for Taiwan calculated by Guan *et al.* (2009) of 0.5 °C 100 m⁻¹, we could expect an increase in forest elevation to be around 200 m between 1934 and 2009 (2.7 m yr⁻¹) if elevational change in forest cover was keeping pace with raises in isotherm position. With an estimated increase in elevation of 2.2 m yr⁻¹, the estimated uphill advance of establishing forest is close to the expected elevation increases based on isotherm data alone and indicates that forest

establishment lags behind temperature increases at a rate of 0.5 m yr^{-1} . If the establishing forest class was not considered separately, the 0.5 m yr^{-1} lag behind temperature increases identified would have been masked, and reported as a more extreme lag, due to the lack of elevation change reported for the forest class. The difference in elevation changes between the forest and establishing vegetation classes highlights the importance of considering growth stage when identifying elevational changes in mountain forests.

The increases in forest area and mean elevation of establishing forest, reported for the study area as a whole mask important variation in patterns of forest advance within the Mt. Hehuan study region. East and South facing aspects show the largest increase in forest area between 1963 and 2016, resulting in an estimated increase in the proportion of East and South facing slopes occupied by forest of 10.7 % and 8.3 % respectively (Figure 3.5a). Similarly, forest advance between 1963 and 2016 is greatest on slopes with gradients between $0-45^\circ$ (Figure 3.5b). However, $0-20^\circ$ slopes have shown a greater decline in the proportion of non-forest area dropping 15.4 % from $53.9 \% \pm 2.3 \%$ non-forest in 1963 to $38.5 \% \pm 2.2 \%$ non-forest in 2016 (Figure 3.5b). This rapid decline in the non-forest area is substantially driven by an increase in the proportion of $0-20^\circ$ slopes that are occupied by establishing forest. Slopes with a gradient of $0-20^\circ$ are the only terrain stratum to show a large increase in the proportion of area occupied by establishing forest over the study period. As temperature thresholds are passed at a given elevation due to rising isotherms, a larger area of habitat is likely to be affected by environmental change when the slope gradient is shallow (Jump *et al.*, 2009). Environmental changes are therefore likely to lead to greater forest establishment and rapid declines in grassland area once a shallow slope becomes favourable for seedling establishment.

The rate of recent establishment (conversion from non-forest to establishing forest within a change period) has remained stable after an initial increase during the 1980-2001 change period, with only North facing aspects and slopes with gradients $>46^\circ$ showing a decline in the rate of recent establishment between 2001 and 2016. However, the rate of rapid establishment (conversion from non-forest to forest within a change period) has declined over time, except on west-facing slopes that show a small increase in the rate of rapid establishment. The seemingly opposite trends in these two patterns of forest advance (recent vs rapid establishment) might be explained by differences in the factors that limit seedling establishment and subsequent growth. The controls on treeline advance in mountain environments are complex, with resource availability (McNown and Sullivan, 2013; Sullivan *et al.*, 2015), radiative stress (Bader *et al.*, 2007), drought stress (Johnson and Smith, 2007; Leuschner and Schulte, 1991; Millar *et al.*, 2007), micro-climate (Greenwood *et al.*, 2015),

competition (Wardle and Coleman, 1992), and topographic sheltering (Greenwood *et al.*, 2014) all known to influence forest advance. However, the importance of any individual control or set of controls is likely to vary over the lifecycle of an individual tree. For example, soil temperature has a positive correlation with the abundance of establishing seedlings yet air temperature has a more important role in the promotion and control of subsequent growth (Greenwood *et al.*, 2015).

While the initial establishment and colonisation of new areas in both recent and rapid advance scenarios are likely to be driven by a release from a temperature limitation, in order for non-forest to convert to forest within a short time period, the newly colonised areas must also have favourable conditions for rapid growth. Consequently, areas that undergo establishment within a change period but do not grow sufficiently to be classified as forest may exist in areas where a threshold for establishment has been surpassed, but the necessary conditions for rapid growth are not met. It is important to note that the conversion of non-forest to forest is considerably less common than the conversion of non-forest to establishing forest within a single change class (there is an order of magnitude difference in the rate of advance; see figures 3.6 & 3.7). Therefore, the proportion of non-forest area that experiences conditions suitable for establishment and subsequent fast growth may be a limiting factor on rapid forest establishment in Mt. Hehuan. Ongoing increases in global temperature are expected by 2100 (IPCC, 2013), and consequently, expansion of this research to incorporate more information on soil nutrient availability, substrate depth and water availability within these two contrasting areas of forest advance would be a beneficial theme for new research. The ability to identify areas that are currently non-forest but match the physical attributes of areas that have undergone rapid establishment would make a significant contribution to our ability to predict future forest range shifts in mountain ecosystems.

The ability to quantify variation in forest range shifts in mountain ecosystems is of critical importance to allow for the implications of forest advance to be predicted. Forest advance is expected to impact biodiversity of the alpine zone and alter ecosystem function in mountain environments (Greenwood and Jump, 2014). Jump *et al.* (2012) show that the elevation of mountain plant species distribution has increased, on average, by 3.6 m yr⁻¹ in Taiwan during the last century. The rate of advance calculated by Jump *et al.* (2012) indicates that the forb and shrub species studied are advancing uphill more rapidly than the montane forest. Despite the rapid uphill advance of montane forb and shrub species reported by Jump *et al.* (2012), forest advance in Mt. Hehuan has reduced the available area of non-forest habitats by 29 % and has caused a 20 - 32 m increase in the mean elevation of remaining non-forest

habitats through range contraction (figure 4; elevation gain increases to 32 m when landslide events are excluded). Given that the mountain peaks limit the maximum elevation of non-forest habitats and that there has been a decrease in the non-forest area across all terrain strata over the study period, the upward shift of montane forests is expected to lead to a reduction in biodiversity as the area, and elevational range of alpine habitats is reduced.

Despite the general trend of declining non-forest area, variation in patterns of forest advance may reduce the impact that forest advance has on biodiversity at a landscape scale. Slopes with gradients of 0-20° are experiencing the most significant losses in non-forest area and show a continuing increase in the rate of recent establishment. However, the substantial increase in establishing forest on 0-20° slopes is not replicated in the other terrain strata considered here. Slopes with a gradient >46° or with a westerly aspect show the smallest reductions in non-forest area due to negligible gains in forest area (figure 5). Areas where establishment rates are low may allow for alpine species to persist despite ongoing forest advance in other areas (Bruun and Moen, 2003). Therefore, it is likely that the presence of refugia in areas of slow forest advance or growth limitation will play an increasingly vital role in the maintenance of alpine biodiversity in mountain systems as forest advance continues. However, even where such refugial areas occur, contraction in population size of alpine species is likely due to a reduction in the non-forest area, risking population loss and diminishing but not removing their risk of local extinction.

Increases in forest area, tree density and growth rates are expected to increase the carbon sequestration potential of montane forests (Zierl and Bugmann, 2007). Morley *et al.* (2019) report a class average above-ground woody biomass of 60 t C ha⁻¹ in mature forests in the Central Mountain Range, Taiwan. The reported increase in forest area of 295.0 ha means there will have been a considerable increase in above-ground woody biomass at high-elevations over the past five decades. Furthermore, alpine soils typically have low levels of carbon and treeline advance is expected to increase below-ground carbon accumulation in mountain systems (Körner, 1998; Michaelson *et al.*, 1996) meaning the impact of forest advance on regional carbon storage and sequestration potential is likely to be significantly greater than the gain in above-ground biomass. However, quantitative data on carbon dynamics that would allow for an ecosystem scale assessment of the ability of montane forests to act as carbon sinks are lacking. To quantify carbon storage and sequestration potential of montane forests, further research is required that incorporates above- and below-ground processes as well as extending the scope of monitoring programs to identify changes across entire mountain ranges.

Despite locally excellent data availability, aerial photography is geographically limited and not a globally available resource. Satellite-borne Earth observation data offers an opportunity to expand the geographic scope of change assessments. However, previous studies that analyse Landsat data over time to estimate forest area change at mountain treelines do so without the benefit of data that provide high precision estimates of change and rates of change. Olofsson *et al.* (2013) and Stehman (2013) set out steps to reduce bias in area estimates derived from Earth observation data using information contained within image classification accuracy assessments, and highlight the importance of stratified sampling to improve the precision of area estimates. Using a sample-based estimator of change should be a pre-condition for using lower resolution imagery, yet few studies that use satellite-borne Earth observation data deliver quantitative assessments of the accuracy of reported changes in forest area or elevation at mountain treelines (Morley *et al.*, 2018). Therefore, improving the unification of satellite-borne Earth observation data with detailed estimates of forest change is essential to enable large-area assessments of the impacts forest advance has on biodiversity and ecosystem function in mountain ecosystems.

3.5 Conclusion

Quantification of variation in forest range shifts in mountain systems is of critical importance to enable accurate estimation of the consequences of forest advance for biodiversity and ecosystem services. The integration of a sample-based change assessment and repeat aerial photography reveals that non-forest area in the Mt. Hehuan study area of the Central Mountain Range of Taiwan has declined by 29 % between 1963 and 2016 due to a 295 ha increase in forest area. The mean elevation of establishing forest has increased at a rate of 2.2 m yr⁻¹ lagging 0.5 m yr⁻¹ behind the estimated change in isotherm position. Forest advance is not uniform within the study area, with slope aspect and gradient leading to variation in the rate of forest advance. Integration of a sample-based change assessment with repeat aerial photography permits the quantification of landscape-scale forest range shifts with high accuracy and reduces previous uncertainty surrounding estimates of forest advance in mountain ecosystems. Extending the sample-based change estimate by incorporating satellite-borne Earth observation data and detailed field data offers an unprecedented opportunity to expand the geographic scope of change assessments, reduce uncertainty in change estimates and improve our understanding of the drivers and consequences of forest range shifts in mountain systems.

3.6 Acknowledgements

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Chapter 4

Forest range shifts are increasing carbon sequestration potential
in a subtropical mountain region

Abstract:

Increases in forest extent in mountain regions driven by changes in global climate and land-use are expected to result in significant increases in above-ground biomass and hence carbon sequestration potential at high elevations. However, quantitative estimates of the impact that shifts in montane forest distribution will have on carbon sequestration potential have been limited because of the restricted scope of most field surveys. A further consequence of restricted field data availability is that the accuracy of estimates of change in montane forest area is poorly understood despite the prevalence of forest shifts globally and the potential to characterise forest range shifts using remote sensing methods. Focussing on the high-elevation forests of Taiwan, this study estimates change in forest area derived from Landsat time-series classification in combination with repeat aerial photography analysed using a sample-based change assessment. By combining these methods, we quantify the accuracy of forest change assessments and estimate changes in above-ground woody biomass. Mapped area estimates derived from Landsat time-series classification underestimate forest advance by 141.9 ha, equivalent to 24.3 % of the area estimated using a sample-based change assessment. However, error-adjustment of mapped area estimates improves area estimates derived from Landsat spectral trends, and the classification of spectral trends reveals a realistic spatial pattern of forest advance in mountain ecosystems. Error-adjusted area estimates reveal that $587.8 \text{ ha} \pm 64.4 \text{ ha}$ of the 4070.8 ha study area is undergoing forest advance, leading to an estimated net increase in above-ground woody biomass of 4688.7 t C between 1987 and 2017. The ability to carry out error-adjustment of mapped area estimates relies on the close integration of change-sample validation data with Landsat time-series data and is an important, yet under-utilised, step to improve the utility of the Landsat archive for estimating gradual forest advance. Integration of Landsat time-series data with high-quality validation and field data, leads to landscape-scale quantification of montane forest range shifts that enable robust estimation of the impacts of montane forest advance on carbon sequestration potential.

4.1 Introduction

Ongoing changes in global climate and land-use are driving shifts in forest distribution (Améztegui *et al.*, 2016, 2010; Harsch *et al.*, 2009). Mountain regions are expected to experience higher than average increases in temperature (Dirnböck *et al.*, 2011; IPCC, 2013; Pepin *et al.*, 2015) and are susceptible to land abandonment (Haddaway *et al.*, 2014; MacDonald *et al.*, 2000) thus increasing the vulnerability of mountain ecosystems to global environmental change. At the elevational and latitudinal limits of forest distribution, upward or poleward shifts have been reported in 52 % of treelines driven by changes in climate and land-use (Harsch *et al.*, 2009). In areas where elevational shifts in montane forest distribution have not been reported, increases in forest area and tree density have been observed below the treeline in response to environmental change (e.g. Bharti *et al.*, 2012; Klasner and Fagre, 2002).

Reported increases in forest area, tree density and growth rates at mountain treelines are expected to increase carbon accumulation in above-ground biomass at high-elevations, potentially increasing the ability of high-elevation forests to act as carbon sinks (Zierl and Bugmann, 2007). Despite this expectation, the impact that changes in montane forest distribution will have on carbon storage and sequestration potential in mountain ecosystems is poorly understood (Greenwood and Jump, 2014). To achieve quantitative assessments of changing carbon sequestration potential of montane forests, precise estimates of changes in forest area and density are required over large areas. However, estimating changes in montane forest area and forest biomass is challenging in mountainous areas because inaccessible terrain limits the scope of field surveys.

Monitoring and mapping changes in forest canopy cover and biomass using Earth observation data is an intensive field of research, enabling repeat surveys of large areas that are often inaccessible to field surveys (Hansen *et al.*, 2013, 2010). However, many existing methods for quantifying changes in forest area using Earth observation data are better suited to the detection of abrupt changes (e.g. deforestation) rather than gradual changes where the change from one habitat type to another may take several decades to complete (Vogelmann *et al.*, 2016, 2012). At mountain treelines, patterns of forest advance can be highly variable due to the complexity of factors that control tree establishment and growth. In some areas, treelines respond to environmental change quickly and over a long distance but often display low-density establishment where the canopy may not close for several decades. This low-density pattern of forest advance leads to incremental changes in the spectral signature observed in Earth observation data over long periods. In other areas treeline response to environmental change can be limited to short distances (10–30 m) but with high-density tree establishment in

sheltered areas close to the old-growth forest. High-density establishment is likely to result in a relatively stronger response in the spectral signature but requires forest advance to be identified over short distances. Consequently, there is a need to identify forest advance in mountain ecosystems over several decades and at a fine spatial resolution to adequately account for variable patterns of forest advance, requiring Earth observation data sets to have a temporal and spatial resolution appropriate for the ecological phenomenon.

Aerial photographic survey data offer a valuable source of reference data for identifying changes in habitat type in areas with poor accessibility due to the fine spatial scale at which data is collected and in many cases, aerial photographic data represent the earliest available remote sensing data. Repeat aerial photographic survey data have been used to identify changes in forest elevation and tree density in mountain ecosystems (e.g. Greenwood *et al.*, 2014; Luo and Dai, 2013; Resler *et al.*, 2004) and integration with a sample-based change assessment (probability-based sampling is used to identify sample plots that are interpreted to identify changes in habitat across a study area) offers an effective method to estimate changes in montane forest area precisely (Chapter 3). When used with repeat aerial photographic survey data, sample-based change assessments allow for changes in forest area to be estimated over time alongside a quantitative assessment of the accuracy of forest area change reported. If used in combination with detailed field assessment of the impacts that changes in forest distribution will have on biodiversity and ecosystem function, sample-based change assessments enable the robust estimation of the impacts that forest advance will have on ecosystem function at the landscape scale. However, local variation in data availability means that the use of aerial photography is often unfeasible for large area assessments of forest change.

Satellite-borne Earth observation sensors offer frequent and repeat coverage of the Earth's surface and as such offer globally consistent data sets for estimating changes in forest area in mountain systems. The Landsat program has the most extensive archive of satellite-borne Earth observation imagery available, with data available since the 1980s at 30 m pixel size, offering an opportunity to expand change assessments and quantify changes across entire mountain ranges (Wulder *et al.*, 2016). Landsat data are less well-suited to the sample-based change assessment technique when quantifying gradual forest advance because the spatial resolution of the data is not sufficient to manually identify small differences in tree establishment patterns. However, gradual habitat changes can be characterised by identifying trends in spectral indices over time (Vogelmann *et al.*, 2012). While positive, long-term greening trends have been identified in mountain ecosystems using time-series Landsat data, many studies stop short of image classification and do not quantify changes in habitat area (Bolton *et*

al., 2018; Carlson *et al.*, 2017; Gartzia *et al.*, 2016). Consequently, the accuracy at which gradual changes in montane forest distribution can be resolved using spectral trends identified in time-series Earth observation data is poorly described in the literature.

The classification of spectral trends provides the potential to automate large area mapping and provide a visualisation of forest change. Quantitative estimates of area change determined from classified maps typically use a pixel counting technique which determines the number of pixels allocated to a given map class and multiplies this number by the area of an individual pixel. While pixel counting is a simple method for area estimation, bias in mapped area estimates occurs due to classification errors (Czaplewski, 1992; Stehman, 2005). It is, however, possible to correct for bias in mapped area estimates using information contained within an error matrix obtained during accuracy assessment if precise estimates of change are available for validation (Olofsson *et al.*, 2013). However, few published studies that investigate forest change at mountain treelines provide sufficient information on their validation procedures or class-specific classification accuracy that would enable robust estimation of the area of forest change using satellite-borne Earth observation data.

To enable the accurate quantification of changes in carbon sequestration potential of montane forests, here we combine aerial photography analysed with a sample-based change assessment with a time-series of Landsat data to 1) estimate the area of forest change from Landsat time-series classification; 2) estimate the area of forest change from a sample-based change assessment using aerial photography; 3) quantify the precision of forest change assessments and 4) quantify changes in above-ground woody biomass in high-elevation forests.

4.2 Methods

4.2.1 Study area

The Mt. Hehuan study area is located in the North of the Central Mountain Range, Taiwan, and reaches a maximum elevation of 3422 m a.s.l. Despite spanning the tropic of Cancer, high-elevation areas of the Central Mountain Range experience temperate and alpine climatic conditions which support conifer-dominated forests above 2400 m a.s.l. The forest canopy at the highest elevations of forest distribution is dominated by four conifer species, primarily *Abies kawakamii* and *Tsuga chinensis* with areas of *Pinus taiwanensis* and *Pinus armandii* establishment. At the treeline, the conifer forests give way to grassland dominated by the bamboo *Yushania niitakayamensis* which extends to the mountain peaks with a low density of shrubby species, of which *Juniperus* spp. and *Rhododendron* spp. are the most common. The treeline in Taiwan's Central Mountain Range is primarily temperature limited, with topographic

sheltering and microclimate causing variation in patterns of tree establishment and forest advance. Landslide events and small-scale fires affect the treeline sporadically, resulting in local reductions in treeline elevation and removal of the substrate. However, routine disturbance events are of low impact at the landscape-scale, and there is little evidence to suggest anthropogenic controls on treeline position.

4.2.2 Change assessment of forest area

4.2.2.1 Sample-based area estimates

Black and white aerial photography from 1980 and four-band multispectral images from 2016 were captured in the Mt. Hehuan area of the Central Mountain Range, Taiwan and orthorectified by the Taiwanese National Archive (minimum accuracy 2.5 m). Stratified random sampling was used to assess vegetation change between 1980 and 2016. Stratification was based on slope and aspect attributes calculated from a TanDEM-X DEM (12 m pixel size). To ensure adequate representation of changes across the whole study area, terrain variables were binned into four cardinal compass directions ($\pm 45^\circ$ in either direction) and three slope gradient classes (0-20°, 21-45° and 46°+) resulting in 12 category combinations that provided a basis for probability-based sampling. A total of 2785 sample plots measuring 15 m x 15 m were interpreted in both aerial photography surveys (1980, 2016) and assigned one of five vegetation change classes (Table 4.1). *Non-forest* was defined as an area that remained treeless between 1980 and 2016. *Forest* was defined as areas that met the FAO (2018) definition of a forest as an area with at least 10 % canopy cover and trees greater than 5 m in height with no evidence of new tree establishment between 1980 and 2016. *Forest advance* was defined as areas where trees were present and tree canopy cover and/or density has increased between 1980 and 2016. *Forest disturbance* was defined as areas with a partial removal of forest canopy between 1980 and 2016 and *forest loss* as areas with full removal of the forest canopy between 1980 and 2016 (Table 4.1). Area estimates for each vegetation change class were carried out in R (R Core Team, 2017) using the survey package (Lumley, 2018) to calculate estimates of the population total, returning estimated total area (ha) and the uncertainty in the estimated area for each vegetation change class. The survey package accounts for the effect of stratification by weighting observations according to the sampling probability.

Table 4.1: Definitions of vegetation change classes used to assess forest change in the Central Mountain Range of Taiwan.

Class	Definition
Forest	An area that meets the FAO (2018) definition of a forest with at least 10 % canopy cover and trees greater than 5 m in height which show no evidence of new tree establishment between 1980 and 2016.
Forest Advance	An area with trees present that has undergone an increase in tree size and/or stand density. Small, establishing trees are identifiable in aerial photographs due to their small crown size.
Non-forest	Areas that remain treeless between 1980 and 2016.
Disturbed Forest	An area of forest that shows a reduction in canopy cover between 1980 and 2016 but with some canopy cover remaining.
Forest loss	An area with complete removal of forest canopy cover within the study period.

4.2.2.2 Mapped area estimates

Two-monthly cloud free image composites were created between Jan 1987 and Dec 2017 using all available images from Landsat TM (1987 – 2011), ETM+ (2012 – 2013) and OLI (2014 – 2017) sensors resulting in 186 composite images. Image composites were created in Google Earth Engine from Tier 1 surface reflectance data derived from the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS). Tier 1 LEDAPS data products are georeferenced, terrain-corrected and radiometrically calibrated across Landsat sensors and so enable direct comparison of individual pixels over time. A tasselled cap transformation was applied to each image composite to reduce the six spectral bands into three orthogonal indices using band weightings defined by Crist (1985). Each tasselled cap index emphasises distinct physical properties of the land surface. The brightness index is a measure of overall reflectance, the greenness index measures variability in vegetation greenness and the wetness index measures a combination of surface moisture conditions and vegetation moisture.

Time-series analysis is carried out per pixel to identify linear trends in spectral response over time. Pixel time-series data were decomposed to remove the seasonal spectral signature in order to minimise the effect of seasonal variation of topographic illumination, however further illumination correction was not carried out (Appendix 4.1). Least-squares regression was implemented to regress each of the seasonally decomposed Brightness, Greenness and Wetness indices against time to estimate the intercept, slope and p-value of the linear spectral trend. A random forest classifier was implemented on the coefficients from the linear trend analysis using 1000 trees and class weightings to account for unbalanced sample sizes of the vegetation change classes. The random forest classifier was implemented in RStoolbox (Leutner

et al. 2018) using 5-fold cross validation with an out of the box error estimate of 15.14 % and a tune length of three. The cross validation identified the optimum number of variables to use as candidates at each split (mtry) as two. The classification model used 50 % of the sample plots interpreted from the aerial photography sample-based assessment for training and the remaining 50 % for validation of the classified map. Area estimates based on a pixel counting of mapped vegetation change classes are likely to be biased due to classification errors. Consequently, an error-adjustment was applied to the mapped area estimates using the validation data and information contained within the error matrix following the method detailed by Olofsson *et al.* (2013).

4.2.3 Above-ground biomass estimation

Above-ground woody biomass was estimated from 38 forest and 78 forest advance plots sampled from the Mt. Hehuan area of the Central Mountain Range, Taiwan. Data from 71 plots collected by Greenwood *et al.* (2014) measuring 20 x 20 m were combined with data from an additional survey of 45 plots with 10 m fixed radius conducted by the authors in 2016. Across both field surveys, all trees were measured for Diameter at Breast Height (DBH) at 1.3 m, and in the 2016 survey, a sample of live trees within each plot were also measured for height. Height was related to DBH using nonlinear least squares regression to estimate tree height for plots where it was not recorded (data not shown). Stand above-ground woody biomass was calculated from stand basal area and median stand height, accounting for differences in specific wood gravity between species, from which average above-ground woody biomass values were calculated for each vegetation change class. An average class biomass of 0.0 t C ha⁻¹ is assumed for non-forest areas because we only consider above-ground woody biomass in this study. Class average biomass values were estimated for the surface area and plan area covered by each plot. Biomass values expressed in plan area were used to calculate estimates of above-ground biomass for the whole study area because both remote sensing based change assessment methods report the area of each vegetation change class in plan view.

4.3 Results

4.3.1 Area change assessment

The sample-based change assessment using aerial photography indicated that 584.7 ha ± 29.4 ha of the Mt. Hehuan study area has undergone forest advance between 1980 and 2016 (Table 4.2). The mapped area of forest advance from Landsat time-series classification is 442.8 ha, underestimating forest advance by 141.9 ha which is equivalent to 24.3 % of the class area estimated using the sample-based change assessment method (Table 4.2). Map bias is high for

disturbed forest and forest loss classes, with the map bias equivalent to 76.7 % (13.5 ha) and 51.3 % (17.2 ha) of the class area estimated by the sample-based change assessment respectively (Table 4.2).

The map bias reported in Table 4.2 occurs due to classification errors in the vegetation change classes. The overall accuracy of the Landsat time-series classification is $85 \% \pm 2 \%$ yet class specific accuracy measures deviate from this value. The producer accuracy (rate at which reference sample plots are correctly classified) for the forest advance class is 49 %, and the user accuracy (probability that a predicted value on the classification map is actually in the assigned class) is 67 % (Table 4.3); for the disturbed forest class both user and producer accuracies are 0 %, and for the forest loss class the producer accuracy is 25 % while the user accuracy is 100 % (Table 4.3). Error-adjusted area estimates, calculated by correcting the mapped area estimates to account for classification errors, improve the similarity of class area estimates calculated from sample-based and Landsat time-series based assessment of vegetation change (Table 4.2). However, the margin of error associated with the class area estimates is higher for the Landsat error-adjusted area estimates than the sample-based area estimates (Table 4.2). The margin of error for forest advance increases from 5 % when using the sample-based change assessment to 11% in the error-adjusted Landsat time-series based area estimates. For the disturbed forest class the margin of error increases from 32 % when using the sample-based change assessment to 80% in the error-adjusted Landsat time-series based area estimates. For the forest loss class the margin of error increases from 23 % when using the sample-based change assessment to 49 % in the error-adjusted Landsat time-series based area estimates. In the stable vegetation classes (forest and non-forest) the margin of error remains the same for the forest class and increases by only 2 % in the non-forest class due to higher class-specific classification accuracies (Table 4.2). Despite the low class-specific classification accuracies reported for forest advance and forest loss (Table 4.3), visual comparison between the aerial photography survey data and the map derived from Landsat time-series classification shows that the Landsat-based approach resolves a realistic spatial pattern of forest advance and loss in the Mt. Hehuan study area (Figure 4.1).

Table 4.2: Area estimates for each vegetation change class with 95 % confidence intervals and the margin of error (ratio of the confidence interval to area estimate expressed as a percentage) in the Mt. Hehuan study area derived from aerial photography sample-based change assessment and classification of Landsat time-series spectral trends. The mapped area is the area of each class estimated through pixel counting and map bias the difference between mapped and sample-based area estimates.

Vegetation Class	Aerial photography		Landsat time-series			
	Area (ha)	MoE	Mapped Area (ha)	Map Bias (ha)	Error-adjusted Area (ha)	MoE
Non-Forest	921.1 ± 34.5	4 %	945.2	24.1	922.9 ± 57.3	6 %
Forest Advance	584.7 ± 29.4	5 %	442.8	-141.9	587.8 ± 64.4	11 %
Forest	2515.2 ± 39.4	2 %	2662.4	147.2	2507.1 ± 61.9	2 %
Disturbed Forest	17.6 ± 5.7	32 %	4.1	-13.5	17.6 ± 14.1	80 %
Forest Loss	33.5 ± 7.6	23 %	16.3	-17.2	35.3 ± 17.2	49 %

Table 4.3: Error matrix from Landsat time-series classification of vegetation change classes in the Mt. Hehuan study area of the Central Mountain Range, Taiwan. The values expressed are pixel counts; overall accuracy is 85 % ± 2 %

Prediction	Reference					Total
	Non-Forest	Forest Advance	Forest	Disturbed Forest	Forest Loss	
Non-Forest	265	48	14	1	5	333
Forest Advance	23	98	26	0	0	147
Forest	26	54	813	5	4	902
Disturbed Forest	0	0	0	0	0	0
Forest Loss	0	0	0	0	3	3
Total	314	200	853	6	12	1385
Producer Accuracy	84 %	49 %	95 %	0 %	25 %	-
User Accuracy	80 %	67 %	90 %	0 %	100 %	-

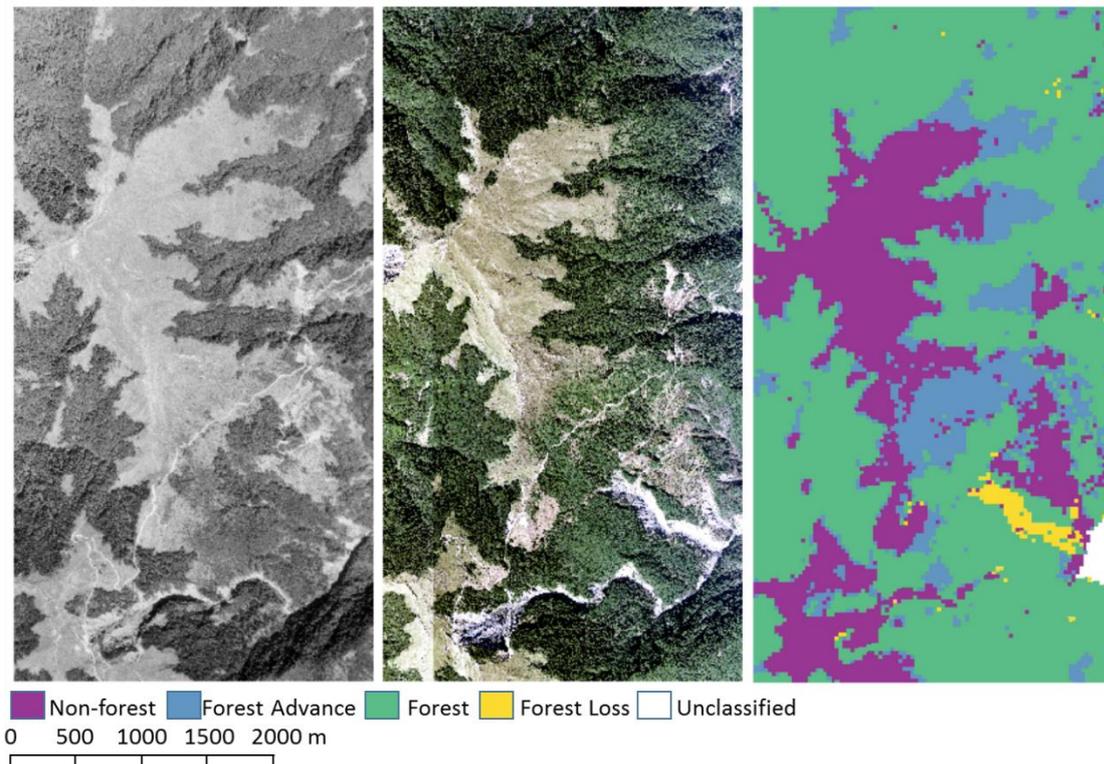


Figure 4.1: Map of vegetation change within the Mt. Hehuan study area of the Central Mountain Range, Taiwan, showing the aerial photography from 1980 (left) and 2016 (middle) with the Landsat derived classification of vegetation change (right).

4.3.2 Above-ground biomass estimate

The estimated area of forest advance (error-adjusted estimate of 587.8 ha \pm 64.4 ha) indicates a gain in above-ground woody biomass in areas above 2400 m a.s.l. of 6877.3 t C \pm 1881.0 t C within the 4070.8 ha Mt. Hehuan study area (Table 4.4). Forest loss has resulted in an estimated reduction in above-ground woody biomass of 2188.6 t C \pm 374.2 t C in the Mt. Hehuan study area between 1986 and 2017 (Table 4.4). It was not possible to quantify losses in above-ground woody biomass attributable to partial removal of the forest canopy because there is no biomass data available for areas of forest disturbance in the Central Mountain Range of Taiwan. The large area of forest advance and relatively small area of forest loss indicates a net gain in above-ground woody biomass of 4688.7 t C in the Mt. Hehuan study area of the Central Mountain Range, Taiwan, between 1986 and 2017 (Table 4.4).

Table 4.4: Estimated average above-ground woody biomass of each vegetation class, with estimated current above-ground woody biomass and estimated gain and loss of above-ground woody biomass in the Mt. Hehuan study region between 1986 and 2017. Estimates for current biomass and gain and loss biomass values are calculated using mean class biomass values adjusted to plan area to allow for integration with the area estimates derived from error-adjustment of the Landsat time-series change assessment. Uncertainty is reported at the 95 % confidence interval.

Vegetation Class	Class biomass (t C ha ⁻¹) surface area	Class biomass (t C ha ⁻¹) plan area	Error-adjusted area (ha)	Current biomass (t C)	Biomass gain/loss (t C)
Non-forest	0.0	0.0	922.9 ± 57.3	0.0	0.0
Forest advance	10.7 ± 2.8	11.7 ± 3.2	587.8 ± 64.4	6877.3 ± 1881.0	6877.3 ± 1881.0
Forest	58.6 ± 10.2	62.0 ± 10.6	2507.1 ± 61.9	155440 ± 26575.3	0.0
Disturbed forest	–	–	17.6 ± 14.1	–	–
Forest loss	0.0	0.0	35.3 ± 17.2	0.0	-2188.6 ± 374.2
Total	–	–	4070.8	162317.5	4688.7

4.4 Discussion

The ability to accurately quantify changes in forest carbon storage potential in mountain ecosystems relies, in part, on our capacity to accurately quantify changes in the area occupied by montane forests at a landscape scale. In the Mt. Hehuan area of the Central Mountain Range, an estimated 587.8 ha ± 64.4 ha of the 4070.8 ha study area is undergoing forest advance leading to an estimated net increase in above-ground woody biomass of 4688.7 t C in areas above 2400 m a.s.l. A comparison of change assessment techniques indicates that mapped areas, derived from the classification of spectral trends captured in Landsat time-series data, underestimate the area of forest advance when compared against a sample-based estimate of forest change using repeat aerial photography. However, the classification of spectral trends shows a realistic spatial pattern of forest advance at the mountain treeline and error-adjustment of mapped area estimates improves the area estimates derived from classification of Landsat spectral trends.

Mountain treelines can respond to environmental change slowly and over short distances (<30 m) thus requiring forest advance to be identified over decadal periods and at high spatial resolution. The <1 m scale of aerial photography used here is sufficient to identify

small differences in vegetation cover over time, such as the appearance of a few small trees or incremental increases in canopy cover. However, the contribution that small changes in tree density or canopy cover make to the reflectance recorded in an individual pixel in the Landsat data are likely to be small, resulting in the reduced classification accuracy reported in Table 4.3. Positive, long-term greening trends have been identified in both treeless areas of alpine grasslands and established montane forests (Bolton *et al.*, 2018; Carlson *et al.*, 2017; Gartzia *et al.*, 2016). Consequently, separating greening trends that occur due to increased tree density from background trends of greening due to increased vegetation productivity will be challenging in image classification routines. At the mountain treeline, the spectral signature observed in satellite-borne Earth observation data saturates when above-ground woody biomass values exceed 25 t C ha^{-1} (Morley *et al.*, 2019), yet mature forests have an average class biomass of $62.0 \pm 10.6 \text{ t C ha}^{-1}$ (Table 4.4). Consequently, in areas with very low-density tree establishment or in areas where forest stands undergoing advance exceed a biomass value of 25 t C ha^{-1} there may not be sufficient difference in the spectral trends to allow forest advance to be resolved during image classification.

Inaccuracies in the classification of spectral trends from Landsat time-series result in mapped class area estimates showing a strong bias that underestimates the area of forest advance, despite producing a map with a realistic spatial pattern of forest advance and loss in the Mt. Hehuan study area (Figure 4.1). This bias in class area estimation would lead to erroneous estimates of changes in forest biomass in mountain regions if not corrected. Error-adjustment of mapped vegetation classes is an important, yet underutilised, step to account for classification errors and improve the utility of satellite-borne estimates of area change in montane forests (Olofsson *et al.*, 2013). However, the margin of error for the forest advance class associated with the sample-based change assessment is 5 % while the margin of error associated with the error-adjusted area estimates from Landsat-based classification of forest advance is 11 %. While the margin of error associated with Landsat-based area estimates is double that of the sample-based assessment, an error of 11 % might be considered acceptable given the gradual nature of forest advance and the subtlety of differences at boundaries between areas of forest advance and old-growth forest or grassland habitats in mountain ecosystems.

Detailed validation data is crucial to adjust area estimates for classification accuracy and quantify the accuracy at which Landsat-based time-series classification can estimate the area of gradual forest advance in mountain ecosystems. However, most studies that use Landsat data to study mountain treelines do so without the benefit of high-quality validation data that can provide precise estimates of change (Morley *et al.*, 2018). The close integration of high-

quality validation data with Landsat time-series based classification, as shown here, is necessary to improve the precision of large-area estimates of forest range shifts and should be a pre-condition of any study using lower resolution imagery.

Several methods exist to improve the spatial resolution of coarse resolution imagery that can provide a benefit to improving the spatial precision of image classification and might improve the precision of subsequent area estimates when using time-series Landsat data (Appendix 4.2). While methods for spatial resolution enhancement have the potential to provide additional information on sub-pixel scale change, they have not been extensively developed for use in time-series change analysis. Consequently, further investigation is required to identify if spatial resolution enhancement improves the precision of estimates of gradual forest change.

Our capacity to estimate changes in the biomass of montane forests was previously limited by the ability to quantify gradual changes in forest area in mountain ecosystems precisely. While treeline shifts are often gradual, widespread shifts in forest distribution in the Taiwanese Central Mountain Range have led to an estimated 14 % of the study area (587.8 ha \pm 64.4 ha) undergoing forest advance between 1987 and 2017. Consequently, forest advance in high-elevation areas has led to an estimated increase in above-ground woody biomass of 6877.3 \pm 1881.0 t C in the Mt. Hehuan study area suggesting that ongoing forest advance will increase the capacity of montane forests to act as carbon sinks (Devi *et al.*, 2008).

The role that tropical montane forests play in global carbon storage and the importance of range shifts at the elevational treeline have been poorly studied (Greenwood and Jump, 2014; Spracklen and Righelato, 2014). Few studies have quantified changes in forest area or biomass at the elevational treeline compounding the challenge of quantifying the cumulative impact that forest advance at mountain treelines will have on global or regional carbon dynamics. Tropical montane forests represent a significant proportion of forest carbon in tropical regions, accounting for 8.3 % of total tropical forest cover (0.88 million km²) with an average above-ground biomass of 271 t ha⁻¹ (circa. 135 t C ha⁻¹; Spracklen and Righelato, 2014). In the Mt. Hehuan study area forest advance between 1986 and 2017 accounts for 23 % of the area of old growth forest surveyed, equivalent to a gain in forest area of 0.7 % of the old growth forest area per year. While studies that estimate the area of treeline advance are sparse this annual figure of forest advance is similar to other published literature. In the Himalaya, Bharti *et al.* (2012) estimate the increase in forest area dominated by *Betula spp.* is 0.5 % of the old growth forest area per year, while the increase in forest area dominated by *Abies spp.* is 0.1 %

per year. At test sites across Europe, Dinca *et al.* (2017) show considerable variation in forest with the area of forest advance varying from < 0.1 – 2.8 % of the old growth forest per year between study sites. Assuming a gain in forest area of 0.75 % of existing old growth forest area per year and a current forest area of 0.88 million km² in tropical mountains, we could expect an increase in forest area of 6600 km² (660000 ha) per year in tropical mountains which would represent a significant cumulative impact on the capacity of tropical montane forests to act as carbon sinks over decadal periods. However, in order to address the impact of variation in forest range shifts between regions, further studies are needed that quantify the area of forest change and forest biomass in other mountain regions to enable robust estimates of the impacts that forest advance will have on carbon dynamics in tropical mountain regions.

This study has estimated an increase in above-ground woody biomass of 6877.3 ± 1881.0 t C in the Mt. Hehuan study area due to increased forest area. However, above-ground woody biomass accounts for one component of total forest biomass which also includes below-ground biomass, dead wood, forest floor litter and soil organic carbon. In boreal and temperate forests, soil organic carbon is estimated to account for 60 – 85 % of the total terrestrial forest carbon stocks with the proportion of total carbon stored in forest soils increasing with forest age (Dixon *et al.*, 1994; Lal, 2005; Wei *et al.*, 2013). Very little is known about how alpine soils will respond to temperature rises and how forest advance will affect carbon stored in alpine soils (Greenwood and Jump, 2014). In tundra sites beyond the arctic treeline, increased temperatures are resulting in greater rates of soil respiration and causing a release of carbon from the ecosystem as soil organic carbon decomposes (Dorrepaal *et al.*, 2009; Rustad *et al.*, 2001). However, tundra soils have a higher proportion of organic carbon than alpine soils which tend to be thinner with a lower carbon content (Körner, 1998; Michaelson *et al.*, 1996). Consequently, increased deposition of litter into alpine soils could lead to greater carbon accumulation within soils in high-elevation areas and further increase the potential of high-elevation mountain areas to act as carbon sinks as the area of montane forests increase.

Identifying gains and losses in forest biomass across entire mountain ranges is essential to identify how changes in a given direction affect landscape-scale carbon budgets. In the Mt. Hehuan study area most forest loss events were small with a single large forest loss event shown in Figure 4.1. When using Earth observation data to quantify forest loss, Milodowski *et al.* (2017) show that small scale forest disturbance events (2 – 10 ha) are identified with lower accuracy than large-scale clearances despite the areas of forest loss being larger than the spatial resolution of the Earth observation data used. Difficulties identifying small forest loss events are likely to contribute to the low classification accuracy (Table 4.3) and high margin of error

(Table 4.2) associated with the estimated area of forest loss and disturbed forest classes shown here. Inaccuracy in forest loss classification presents a significant challenge to precisely quantifying forest loss in mountain areas where natural disturbances are relatively rare and occur at a small scale. Consequently, the incorporation of sample-based assessment of habitat change using aerial photography is important to improve the precision of area estimates for the forest loss and disturbed forest classes despite the high margin of error.

Error-adjusted area estimates reveal that $35.3 \text{ ha} \pm 17.2 \text{ ha}$ of forest have been lost in areas above 2400 m a.s.l., leading to an estimated loss in above-ground woody biomass of $2188.6 \pm 374.2 \text{ t C}$ between 1987 and 2017. There was no evidence to suggest that anthropogenic activities caused forest loss or disturbance and so small-scale disturbances and forest loss events are likely to be caused by natural phenomena. In the case of the large forest loss event identified in the Mt. Hehuan area, the complete removal of the substrate indicates that forest loss was caused by a landslide. Landslide events have a strong influence on the spatial distribution of biomass in montane forests, reducing tree biomass and increasing landscape heterogeneity (Dislich and Huth, 2012). However, the destination of carbon losses due to landslides is unclear. It is likely that a proportion of the carbon stored in above-ground woody biomass that is lost due to landslide events will stay within the system as dead wood and transfer to other terrestrial stores (e.g. soil organic matter), while a smaller portion of the forest biomass will be released to the atmosphere (Dislich and Huth, 2012). While landslide events were rare in the Mt. Hehuan area, hotspots of landslide activity exist in Eastern areas of the Taiwanese Central Mountain Range with a further hotspot developing in the Southern areas of the Central Mountain Range since 2008 (Lin *et al.*, 2017). As the strength and frequency of extreme climatic events are expected to increase with ongoing climate change (IPCC, 2013), there is a pressing need to quantify spatial and temporal variation in forest loss as well as forest advance to fully understand the influence that landslides will have on long-term carbon dynamics in montane forests.

4.5 Conclusion

Ongoing shifts in the distribution of montane forests in response to climate and land-use change are expected to increase the capacity of montane forests to act as carbon sinks. However, the capacity to quantify changes in the carbon sequestration potential of montane forests has, in part, been limited by our ability to accurately quantify forest advance in mountain regions and link area changes to forest biomass estimates. Areas undergoing forest advance can be identified using Landsat spectral trends but, high-quality validation data is required for error-adjustment of mapped area estimates in order to improve the utility of Landsat time-series data

for estimating the area of gradual forest change in mountain systems. An estimated 587.8 ha \pm 64.4 ha of the area above 2400 m a.s.l. in the Mt. Hehuan area of the Taiwanese Central Mountain Range is undergoing forest advance, leading to a net increase in above-ground woody biomass of 4688.7 t C between 1987 and 2017. Extension of the research presented here to incorporate changes in below-ground biomass and soil organic carbon as forests expand will enable a quantitative assessment of changes in total forest biomass of these high-elevation mountain ecosystems. The successful integration of Landsat time-series data with high-quality validation and field data, as shown here, offers a unique opportunity to achieve landscape-scale quantification of montane forest distribution shifts, enabling the robust estimation of the impacts that forest advance will have on carbon sequestration potential in mountain regions.

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Appendix 4.1: Topographic Illumination Correction

Differences in terrain orientation can lead to substantial differences in radiance received from the sun resulting in slopes facing away from the sun receiving much less illumination than slopes facing toward the sun. In multispectral satellite imagery slopes that receive less illumination appear darker because the signal received by the sensor is lower than illuminated slopes and this difference can be very pronounced in mountainous regions due to the complexity of the terrain. Illumination differences between different aspects may mean that forest on an illuminated surface need not have the same reflectance value as forest on a non-illuminated surface. Consequently, differences in reflectance values within a vegetation class due to variation in illumination can present a problem in image classification where a key assumption made of the data is that similar surface types will have similar reflectance values.

A simple method to minimise topographic illumination differences is the use of ratio-based spectral indices. Ratio-based indices assume that reflectance changes proportionally in the spectral bands being used to create the spectral index. Therefore, while the absolute reflectance values may vary according to illumination the relative values between the bands will be similar for the same land cover type. While ratio-based indices are effective in some instances, the effects of topographic illumination vary between spectral bands and therefore not all ratio-based indices have the desired effect of normalisation (Galvão *et al.*, 2016). Alternative approaches to topographic illumination correction use a DEM to model surface illumination accounting for the solar geometry at the time of image acquisition and the slope gradient and aspect, subsequently seeking to modify the spectral values according the surface illumination model. In a recent evaluation of different correction methods, Sola *et al.* (2016) show that the C-correction and Sun-Canopy-Sensor + C (SCS + C) correction perform the best of ten different illumination correction algorithms tested. However, the success of illumination correct methods vary between study location and application. Dorren *et al.* (2003) show that the use of the SCS topographic illumination correction with Landsat TM data improved the mapping accuracy of forest types in steep terrain. However, Adhikari *et al.* (2016) found that ratio-based indices were robust against topographic effects in tropical mountain regions when compared against data corrected using the C-correction method and concluded that topographically corrected data did not provide sufficient benefit to warrant the additional processing cost.

The extent of illumination differences between different aspects vary throughout the year due to seasonal differences in sun elevation. Images captured when sun elevation is low have more pronounced illumination differences than when sun elevation is high. This variation in surface illumination is of particular importance when attempting to identify change in a land cover class over time in mountain regions with pronounced seasonal differences in sun elevation. Temporal variation in sun elevation may lead to erroneous identification of change due to seasonal differences in surface illumination rather than changes in land cover type. However, a recent comparison addressing the benefit of using illumination correction in Landsat time-series analysis showed that the use of topographically corrected Landsat data provided no additional benefit over data that had not be corrected for illumination differences when assessing forest change (Chance *et al.*, 2016). In addition, Chance *et al.* (2016) found that the use of illumination corrected data in spectral trend analysis negatively affected the detection of low magnitude changes in the landscape. Therefore, topographic illumination correction is unlikely to improve the accuracy of change assessments when Landsat time-series data are used to quantify gradual ecosystem change.

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Appendix 4.2: Spatial Resolution Enhancement

Changes in forest distribution at mountain treelines can occur within a short distance from the old growth forest (<30 m) and therefore may not be accurately captured in Landsat data with a 30 m pixel size. Inaccurate identification of sub-pixel changes may lead to error in land cover mapping and subsequent miss estimation of the area undergoing forest advance in mountain regions. Enhancing the spatial resolution of Landsat images might offer an opportunity to improve the spatial precision in land cover mapping in order to improve the precision of change estimates at the mountain treeline. Pan-sharpening is a method used to enhance the spatial resolution of medium resolution imagery using a higher resolution panchromatic band. Several methods exist for pan-sharpening that include colour-space transformations that convert spectral Red-Green-Blue (RGB) values into Hue-Saturation-Intensity values and methods that reweight the RGB values according to the panchromatic band such as the Brovey transformation (Ehlers et al., 2010). While pan-sharpening approaches improve the spatial resolution of an image they often lead to colour distortions (Ehlers et al., 2010). Consequently, the interference with reflectance values makes pan-sharpening better suited to image visualisation or visual interpretation rather than in use for time-series change detection where spectral data are required to have high consistency over time.

An alternative method for spatial resolution enhancement is super resolution mapping where the geographic location of land cover class fractions are estimated within a pixel area. Super resolution mapping relies on unmixing the spectral response captured in a pixel to estimate the proportional representation of each land cover class within a mixed pixel (pixels that contain two or more land cover classes) and subsequently estimating the geographic location of each class within the pixel (Boucher and Kyriakidis, 2006; Tatem et al., 2001). Super resolution mapping methods are able to provide land cover representations that are more accurate and more realistic than standard discrete classifications (Muad and Foody, 2012). However, the apparent precise nature with which class proportions are estimated may be misleading in change detection as different combinations of class proportions can share a similar spectral response (Foody and Doan, 2007). The similarity in spectral response between pixels with varying class proportions means that the accuracy of the sub-pixel land cover composition can be low with a large disagreement in the estimated proportion of class composition between predicted and reference data. Consequently, an over reliance on the apparent precision of land cover representations rendered through super resolution mapping may provide misleading estimates of change due to inaccurate estimates of class composition

with a pixel at a given period in change detection (Foody and Doan, 2007). However, if used appropriately, super resolution mapping could lead to a richer data set to base change assessments on by utilising sub pixel information on class proportion and location to identify a range of plausible change scenarios (Foody and Doan, 2007).

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Chapter 5

An integrated approach to assessments of montane forest range
shifts

5.1 Introduction

Changes in global climate and land-use are driving forest range shifts in mountain regions (Améztegui *et al.*, 2016, 2010; Harsch *et al.*, 2009). At the elevational and latitudinal limits of forest distribution, 52 % of treelines show upward or poleward movement of the treeline (Harsch *et al.*, 2009). In areas not showing elevation changes, increases in tree density and forest area below the upper tree limit have been observed (e.g. Bharti *et al.*, 2012; Klasner and Fagre, 2002). Increases in forest density and shifts in montane forest distribution are expected to impact on biodiversity and ecosystem function in mountain regions (Greenwood and Jump, 2014). However, variation in patterns of forest range shifts must be accounted for over large areas to estimate the impacts that forest range shifts will have on biodiversity and ecosystem function accurately.

Significant benefits can be gained by integrating remote sensing data into studies of mountain treeline shifts to improve estimates of vegetation change (Chen *et al.*, 2015; Luo and Dai, 2013), characterise forest structure at the treeline (Allen and Walsh, 1996; Hill *et al.*, 2007; Resler *et al.*, 2004) and improve the understanding of pattern-process relationships that control treeline position (Bader and Ruijten, 2008; Weiss *et al.*, 2015). However, methodological inconsistencies and poor reporting of uncertainty in estimates of forest change in the existing literature have limited the effectiveness of integrating remote sensing data into assessments of forest range shifts in mountain systems. Challenges in reconciling trade-offs between different remote sensing data sets and quantifying the degree of structural information that can be identified in remote sensing data sets led to limitations in our ability to scale plot level data on forest range shifts. This limitation combined with challenges obtaining suitable data for validating change assessments in mountain systems introduced the potential to misestimate change and assess the subsequent impacts at the landscape scale.

Given these challenges, this thesis set out to overcome limitations in our ability to characterise variation in patterns of forest range shifts and rates of forest advance at mountain treelines. By addressing these limitations this thesis presents new approaches that deliver revised estimates of change in forest area and elevation, variation in rates of forest advance, and quantifies the impact that forest advance will have on biodiversity and ecosystem function in the Central Mountain Range of Taiwan. The research presented here was structured around three research priorities identified in Chapter one, published as Morley *et al.*, 2018. Specifically, Morley *et al.* (2018) identified needs to address the suitability of remote sensing data, the ecological relevance of maps derived from satellite imagery classifications, and the effectiveness of validation methods to achieve precise estimates of landscape-scale change. By

combining improvements across each of the three research priorities, this thesis aimed to improve the integration of remote sensing data into forest range shifts to enable estimates of the impact forest advance has on biodiversity and ecosystem function in mountain regions.

5.2 Suitability of remote sensing data

Inconsistencies in the methodologies used to map and quantify changes in montane forest distribution in previous work that uses remote sensing data to study mountain treelines left uncertainty in the ability of different passive optical remote sensing data sets to resolve structural variation at the mountain treeline. There are trade-offs between the spatial resolution, temporal resolution and geographic coverage of individual data sets that must be considered when using remote sensing data to estimate changes in montane forest area. It is often perceived that imagery with a high spatial resolution will lead to an improved characterisation of habitat heterogeneity due to the ability to identify small objects, e.g. individual trees. Consequently, in studies that use remotely sensed data to study mountain treelines, a majority used high-resolution aerial photography or satellite imagery (< 10 m pixel size) rather than open-access Landsat data (30 m pixel size) (Morley *et al.*, 2018). The apparent preference for high-resolution remote sensing data led to uncertainty in the ability of Landsat data to adequately characterise heterogeneity in forest structure that occurs over short distances at the mountain treeline. However, a quantitative assessment of the ability of sensors with different spatial resolutions to resolve variation in forest structure at the treeline had not been carried out. Consequently, two key priorities were set out in Morley *et al.* (2018); the first to identify the appropriate compromise between spatial resolution and increasing cost that allows for sufficient ecological and biogeographical information to be extracted; and the second to identify the most appropriate method or combination of methods that allow for accurate assessments of landscape-scale shifts in montane forest distribution.

In order to adequately characterise treeline shifts, change in forest cover must be quantified over decadal periods due to the gradual nature of forest advance at mountain treelines. Aerial photographic survey data is often the earliest form of remote sensing data available, yet prior uncertainty in the use of repeat aerial photography arose due to mapping by manual image interpretation and a lack of quantitative measures of uncertainty reported in the literature. However, when implemented with a probability-based sampling design, manual interpretation of aerial photography provides precise estimates of forest change (Chapter 3). Despite the high precision of change estimates, repeat aerial photography is a geographically limited resource, restricting the use of aerial photography as a sole source of data in large-area estimates of forest change. Therefore, it is important to assess the ability of satellite-borne

Earth observation data to capture structural variation at the mountain treeline that would enable the characterisation of spatial patterns of forest structural heterogeneity across large areas and to track change over decadal periods using archived satellite imagery. Despite prior concerns raised over the ability of Landsat data to adequately identify fine-scale heterogeneity in vegetation structure at the treeline (Bharti *et al.*, 2012; Buchanan *et al.*, 2015; Chen *et al.*, 2015), there is little quantitative difference between the relationships defined between discrete descriptors of vegetation structure and spectral measures from Landsat-8 and spectral measures from higher resolution sensors (GeoEye, SPOT-7 and Sentinel-2; Chapter 2 published as Morley *et al.* 2019). Consequently, there is an opportunity to exploit the long-term open-access Landsat archive to quantify gradual changes in montane forest position over large areas (Vogelmann *et al.*, 2016, 2012).

Positive, long-term greening trends have been identified in alpine grasslands, old-growth montane forests and across the treeline ecotone using Landsat time-series data that indicate increases in vegetation productivity and woody biomass across the mountain treeline ecotone (Bolton *et al.*, 2018; Carlson *et al.*, 2017; Gartzia *et al.*, 2016). Changes in forest position and structure at the mountain treeline have been investigated using images from the Landsat archive analysed over time (e.g. Allen and Walsh, 1996; Bharti *et al.*, 2012; Dinca *et al.*, 2017; Mihai *et al.*, 2017). However, there is often a lack of reference data to validate estimates of change in forest area derived from satellite imagery. Consequently, the ability to distinguish between changes in spectral signatures identified in the Landsat archive that occur due to increases in woody biomass across the treeline and those that occur due to increased productivity in alpine vegetation above the treeline or in montane forests below the treeline was unknown. The classification of spectral trends, defined from a time-series of Landsat data, resolves a realistic spatial pattern of forest advance and stasis at the mountain treeline (Chapter 4). However, when used to estimate changes in forest area, the classification of spectral trends shows a strong bias that underestimates the area of forest advance (Chapter 4). The ability to make precise estimates of change in montane forest distribution at a landscape-scale using time-series Landsat data is improved by combining time-series analysis of Landsat imagery with precise estimates of change from repeat aerial photography analysed using a sample-based assessment (Chapter 4). The ability of repeat aerial photography to obtain precise estimates of area change is vital to validate area estimates derived from Landsat time-series data and adjust for classification errors. Consequently, this combined approach to change assessment allows sufficient ecological and biogeographical information to be extracted and changes in treeline position that occur over decadal periods to be quantified, thereby enabling estimates of the

impacts of forest advance on biodiversity and ecosystem services in areas where access to field locations is challenging.

5.3 Ecological relevance of classifications

Two needs were identified to improve the current ecological and biogeographic understanding of mountain treelines; the need for theoretically and methodologically consistent approaches to better define geographic variation in pattern-process relationships at the treeline (Malanson *et al.*, 2011) and to monitor the impacts treeline shifts will have on biodiversity and ecosystem function across mountain ranges (Greenwood and Jump, 2014). Within the previous studies that use remote sensing data to study treeline shifts, there is often an over-simplification of structural diversity in forest vegetation that limits the interpretation of pattern-process relationships and the impacts that treeline shifts will have on biodiversity and ecosystem function.

Harsh and Bader (2011) have suggested treeline forms (discrete classes that separate forested areas at the treeline according to variation in forest/tree structure and growth form) as a method to improve the consistency of treeline definitions within the ecological and biogeographic literature. In Taiwan's Central Mountain Range, Greenwood *et al.* (2015, 2014) have shown that similar treeline forms that describe areas of old-growth forest, areas of low-density establishment and areas of high-density establishment, are important for understanding the processes that drive variation in response to environmental change with topography, microclimate and local sheltering all influencing the treeline form. Furthermore, community assemblage varies between treeline form and therefore, forest advance and changes in forest structure are likely to lead to changes in community composition and reductions in biodiversity (Greenwood *et al.*, 2016). The ability to identify structural forms similar to those identified by Greenwood *et al.* (2014) across large areas would represent a significant contribution to addressing the two needs identified above. However, few studies that use remote sensing data to study mountain treelines have attempted to resolve variation in forest structure at the treeline using definitions of forest structure based on the treeline forms suggested by Harsch and Bader (2011).

At the mountain treeline, the spectral similarity between areas of differing forest structure across the treeline ecotone presents a challenge to resolving structural classes identified by Greenwood *et al.* (2014) at the treeline in the Central Mountain Range of Taiwan (defined in Morley *et al.* 2019 as full structural classes). At the mountain treeline, saturation of the spectral signature occurs when the forest reaches an above-ground woody biomass value

around 25 t C ha⁻¹. Consequently, resolving differences in forest structure between areas with above-ground woody biomass values greater than 25 t C ha⁻¹ is problematic and fine-scale differences in forest structure described in the full structural classes cannot be resolved in multispectral satellite remote sensing data (Morley *et al.*, 2019). Simplifying the structural classes to distinguish between areas of old-growth forest, establishing forest and non-forest allows for areas indicative of forest advance to be distinguished from areas of forest stasis in single date imagery (Morley *et al.*, 2019). Furthermore, tracking changes in the simplified class structure over time using repeat aerial photography returns precise estimates of forest advance, thereby improving the understanding of mechanisms that drive variation in forest range shifts and enabling estimation of the impacts that forest ranges shifts will have in mountain systems (Chapter 3).

Sample-based estimates of change at the mountain treeline in the Central Mountain Range of Taiwan using repeat aerial photography show that forest advance has led to a 29 % reduction in the area of non-forest habitats and an increase in the mean elevation of the establishing forest class at a rate of 2.17 m yr⁻¹ between 1963 and 2016 (Chapter 3). However, the rate of forest advance varies according to slope gradient and aspect. Variation in patterns of forest advance will likely lead to variation in the impacts that forest range shifts will have on biodiversity and ecosystem function (Greenwood *et al.*, 2016; Greenwood and Jump, 2014). In the Central Mountain Range of Taiwan west facing slopes and slopes with a gradient > 46° show negligible increases in forest area between 1963 and 2016 (Chapter 3). Consequently, as forest advances, some areas may remain open and act as refugia that allow the persistence of alpine species below the upper limit of forest distribution. However, continued upward advance of establishing forest and increases in forest area will lead to a reduction in non-forest habitat, risking a reduction in alpine biodiversity and population loss at high elevations. Using forest structural classes as a basis for the classification of spectral trends identified in Landsat time-series data, areas of old-growth forest, areas of treeline stasis and areas of forest advance can be identified at a landscape-scale (Chapter 4). The classification of spectral trends enables landscape-scale estimates of the impacts of forest range shifts, revealing that forest advance has led to a net increase in above-ground woody biomass of 4688.7 t C in areas above 2400 m a.s.l. in the Mt Hehuan study area (4070.8 ha) of the Central Mountain Range (Chapter 4).

The ability to quantify changes in forest area accurately and estimate the impacts forest advance will have on biodiversity and ecosystem function at the landscape-scale, relies on the ability to resolve variation in forest structural characteristics from remotely sensed data. Assessments of forest change such as those based on the FAO (2018) definition used for the

Global Forest Resource Assessment rarely comment on areas that do not meet pre-defined criteria for forest cover. However, ecological and biogeographical literature use a much broader interpretation to characterise the treeline ecotone, describing the treeline as the uppermost areas where trees reach 3 m in height and the species limit as the location at the extremes of distribution irrespective of tree size (Harsch and Bader, 2011; Holtmeier and Broll, 2005). Identifying areas of establishing forest as a separate vegetation class ensures a greater area of the forest-grassland transition is represented than a simpler forest / non-forest vegetation classification. Differences between areas that meet the criteria of a forest as defined by the FAO (2018) and those defined as establishing forest in response to environmental change as shown in this thesis highlight the importance of accounting for differences in forest structure and growth stage when quantifying forest ranges shifts in mountain systems. While no change in the mean elevation of the forest class was identified, a substantial increase in the area occupied by the forest class was reported (Chapter 3). However, when considering the establishing forest class, a 115.1 m increase in mean elevation is identified but there was a negligible increase in the area occupied by the establishing forest class between 1963 and 2016 (Chapter 3). By considering changes in the forest class separately from changes in the establishing forest class, as used here, ensures that the results presented in this thesis are comparable to literature from both the ecological and biogeographic fields and forest resource assessments. Consequently, the results presented here offer a consistent approach to identifying variation in forest response to environmental change in multispectral remote sensing data, allowing for pattern-process responses to be better understood and for robust estimates of the implications forest advance will have on biodiversity and ecosystem function in mountain systems.

5.4 Effectiveness of training and validation procedures

Few studies that use remote sensing data to quantify treeline change report quantitative assessments of the precision of the change estimates reported or accuracy of classified maps. Field surveys provide the most accurate assessment of forest advance and interpretation of the subsequent impacts on biodiversity and ecosystem function. However, obtaining field data for validation of remote sensing data in mountain areas is challenging because complex terrain limits the collection of field data to accessible areas. Consequently, many studies that seek to identify changes in forest area or elevation do so without high-quality validation data that provide precise estimates of change and rates of change (Morley *et al.*, 2018).

In areas where extensive fieldwork is not possible, repeat aerial photography analysed with a sample-based change assessment provide precise estimates of forest change and high-

quality training and validation data that could not be achieved in the field (Chapter 3 & 4). Using sample data collected from repeat aerial photography to classify Landsat spectral trends offers an opportunity to improve the mapping and consistency of estimates of forest range shifts in mountain regions. However, it is necessary to adjust for errors that occur during the classification of spectral trends from Landsat time-series data in order to minimise map bias and calculate estimates of change in forest area reliably (Olofsson *et al.*, 2013; Stehman, 2013). The process of error-adjustment requires high-quality sample-based assessments of forest change and so sample-based estimates of change should be a pre-requisite to using coarser resolution remote sensing data in forest change assessments. Consequently, complimenting field data with photointerpretation of high-resolution remote sensing data offers a compelling method to improve the reliability of change assessments and return quantitative measures of uncertainty in area estimates.

5.5 An integrated approach to change assessments in montane forests

Successful advances made in each of the three research priorities improves the platform for monitoring changes in forest extent, helps to characterise treeline structure and reduces the uncertainty in reported changes in forest range shifts at mountain treelines. The integration of advances across these three research priorities is essential to enable landscape-scale monitoring of forest range shifts at mountain treelines that will lead to improvements in our understanding of pattern-process relationships at the mountain treeline and improve estimates of the impacts that montane forest range shifts will have on biodiversity and ecosystem function.

Forest advance in the Mt. Hehuan area of the Central Mountain Range, Taiwan has led to a 29 % reduction in area of non-forest habitats present in 1963 (Chapter 3). However, topography alters patterns of forest advance in the Mt. Hehuan area, resulting in east and south facing slopes experiencing the greatest increases in forest area while slopes facing west or with gradients of $>46^\circ$ show negligible increases in forest area (Chapter 3). The role of topography in mediating patterns of forest advance shown in chapter 3 is consistent with the findings of Greenwood *et al.* (2014) in the same study area. Greenwood *et al.* (2014) showed forest advance in the Central Mountain Range of Taiwan predominantly displays infilling below the upper tree limit and estimated an elevation shift in treeline position of 27-33 m over 53 years in a subset of the study area considered in this thesis. While change in the mean elevation of the forest class and the role of topographic drivers of change found here are consistent with the findings of Greenwood *et al.* (2014), this thesis delivers a substantial advance beyond the work of Greenwood *et al.* (2014) by delivering precise estimates of forest area change and rates

of forest advance split between forest growth stages that improve our ability to characterise variation in forest range shifts. By considering different growth stages it is possible to identify that the mean elevation of the establishing forest class has increased by 115.1 m between 1963 and 2016 (equivalent to 2.17 m yr^{-1}) lagging 0.5 m yr^{-1} behind estimated changes in the isotherm position (Chapter 3). Accurate quantification of forest range shifts using repeat aerial photography analysed with a sample-based change assessment provide a foundation for Landsat based time-series classification, that enable the precise estimation of forest advance at a landscape-scale (Chapter 4). In the Mt. Hehuan area of the Central Mountain Range, an estimated $587.8 \text{ ha} \pm 64.4 \text{ ha}$ of the 4070.8 ha study area has undergone forest advance between 1987 and 2017 leading to an estimated net increase in above-ground woody biomass of 4688.7 t C in areas above 2400 m a.s.l. (Chapter 4). Incorporating detailed field data on forest biomass with precise estimates of forest range shifts derived from remote sensing data improves our understanding of the capacity of montane forests to act as carbon sinks, highlighting the significant increase in woody-biomass associated with forest advance in high-elevation areas.

In combination, the advances presented here deliver revised estimates of non-forest habitat loss, identify variation in patterns of forest advance attributable to topography and growth stage, and enable estimates of changes in above-ground woody biomass at the mountain treeline in the Central Mountain Range of Taiwan. By bringing together methods from multiple fields of research, the results presented in this thesis demonstrate the benefit of integrating different sources of remote sensing data for assessing forest range shifts in mountainous areas. The methods used here can easily be adapted and implemented in other areas to improve the methodological consistency of change assessments in montane forests. Consequently, the framework provided in this thesis for estimating forest range shifts in mountain areas presents a major opportunity to improve the ecological understanding of forest range shifts and quantify the impacts that forest advance will have on biodiversity and ecosystem function in mountain systems.

5.6 Future directions

The work presented in this thesis offers a platform to improve our understanding of pattern-process relationships at the mountain treeline, enabling research into the factors that give rise to variable patterns of forest advance and stasis. Bader and Ruijten (2008) identified the position of the treeline in Landsat data and subsequently modelled the role that topographic variables have in controlling the present day position of the treeline. Similarly, Weiss *et al.* (2015) identified the treeline in Landsat data then characterised scale dependencies of the

patterns and controls on current treeline position. Both Bader and Ruijten (2008) and Weiss *et al.* (2015) use Landsat data to identify the mountain treeline allowing for environmental factors that explain the current position of the treeline to be identified at a landscape-scale. However, their work can be advanced by identifying landscape-scale variation in patterns of forest advance using remote sensing data. A detailed understanding of the controls that cause variation in patterns of forest advance or stasis is essential to predict how mountain treelines will respond to ongoing climate change. Therefore, by integrating assessments of forest change with environmental data to test hypothesised drivers of forest change at mountain treelines, predictions of future forest ranges shifts can be made with greater confidence.

Greenwood *et al.* (2016) highlighted the importance that fine-scale differences in forest structure have in altering community composition, and the potential for ongoing changes in forest structure to cause community disassembly in alpine communities. Furthering the research presented in this thesis by improving the characterisation of forest structure would advance our understanding and the quantification of the impacts that forest range shifts will have on biodiversity in mountain systems. Incorporating satellite imagery with a finer spatial resolution into Landsat time-series based change assessments may improve the ability to quantify fine-scale changes in montane forest distribution. Sentinel-2 data show a better ability to resolve variation in forest structure at mountain treelines than Landsat-8 data when using above-ground woody biomass to define variation in forest structure (Morley *et al.* 2019). Consequently, it is likely that the 10-20 m pixel size of Sentinel-2 imagery would improve the spatial precision of change assessments in areas with complex patterns of forest advance. While Sentinel-2 data have been used to validate maps of forest change in mountain areas (Mihai *et al.*, 2017), the integration of Sentinel-2 and Landsat data into time-series change detection methods is challenging due to slight differences in the position and width of each spectral band between the sensors that limits the direct comparison of spectral data between sensors (Claverie *et al.*, 2018). Ongoing improvements in the harmonisation of Sentinel-2 and Landsat data are likely to reduce the data processing burden and make the integration of different data products easier (Claverie *et al.*, 2018). Consequently, there is an opportunity to improve the spatial precision of mapped areas of forest change in ongoing monitoring efforts by integrating the long-term Landsat archive with recent high spatial resolution data from Sentinel-2.

Despite improvements in the spatial precision that may be gained by integrating data from Sentinel-2, improved characterisation of forest structure may not be possible by using multispectral imagery alone due to the spectral similarities between structural classes. LiDAR data collected from airborne platforms have been used to describe vegetation structure within

the treeline ecotone (Coops *et al.*, 2013), have been integrated with multispectral satellite imagery to produce maps of vegetation cover types over large areas (Ørka *et al.*, 2012) and have helped improve the interpretation of spectral trends identified in time-series Landsat data (Bolton *et al.*, 2018). Despite these benefits, LiDAR data are not widely available in many mountainous areas and the acquisition of new data sets can be prohibitively expensive. However, data from the Global Ecosystem Dynamics Investigation (GEDI) LiDAR sensor (Coyle *et al.* 2015; Dubayah *et al.* 2014), currently mounted on the International Space Station, is due to be released in 2019. While the above-ground biomass estimates from the GEDI LiDAR sensor will be delivered at a 1 km grid cell size and therefore unlikely to improve the characterisation of treeline structure, processed data characterising tree height and canopy cover from the laser footprint will be available with a 25 m diameter. The ability of the GEDI LiDAR sensor to provide high-resolution estimates of forest height and canopy cover offers a valuable data source for characterising 3-dimensional forest structure at the treeline enabling variation in forest structure to be quantified in remote mountain areas. Therefore, investigating the use of data quantifying tree height and canopy cover from the GEDI LiDAR sensor should be a priority when data becomes available. The successful unification of estimates of forest advance with detailed information on 3-dimensional forest structure would represent a significant improvement in the capacity of ecologists, biogeographers and resource managers to quantify variation in forest structure and estimate the impacts that forest ranges shifts will have on biodiversity, ecosystem function and carbon sequestration potential in mountain systems.

5.7 Conclusion

In this thesis, the close integration of field data, repeat aerial photography and Landsat time-series data has enabled precise estimation of changes in forest area and elevation, the quantification of variable patterns of forest range shifts and estimates of the impacts forest range shifts will have on biodiversity and ecosystem function. In the Central Mountain Range of Taiwan, there has been a 29 % reduction in the area of non-forest habitats due to increases in forest area and uphill advance of forest establishment. Declines in the area and contraction in the range of non-forest habitats risk the loss of alpine populations, as such ongoing increases in forest area are a severe threat to alpine biodiversity. Variation in the rate of forest advance means that some areas might experience sufficiently small gains in forest area or tree growth limitation that will lead to the persistence of refugial areas that will likely reduce, but not eliminate the risk of local extinctions. While increased forest area is likely to have negative consequences for alpine biodiversity, increased forest area has resulted in a net increase in above-ground woody biomass at high elevations. Ongoing monitoring of changes in forest

extent in mountain regions is vital given that further increases in forest area are expected with continuing changes in global climate and land-use. Therefore, embedding remote sensing data future assessments of species ranges shifts is essential to enable the robust estimation of the impacts that forest advance will have on biodiversity and ecosystem function in mountain systems globally.

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