Monitoring and managing responses to climate change at the retreating range edge of forest trees

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Rising temperatures and increasing drought severity linked to global climate change are negatively impacting forest growth and function at the equatorial range edge of species distributions. Rapid dieback and range retractions are predicted to occur in many areas as temperatures continue to rise. Despite widespread negative impacts at the ecosystem level, equatorial range edges are not well studied, and their responses to climate change are poorly understood. Effective monitoring of tree responses to climate in these regions is of critical importance in order to predict and manage threats to populations. Remote sensing of impacts on forests can be combined with ground-based assessment of environmental and ecological changes to identify populations most at risk. Modelling may be useful as a 'first-filter' to identify populations of concern but, together with many remote sensing methods, often lacks adequate resolution for application at the range edge. A multidisciplinary approach, combining remote observation with targeted ground-based monitoring of local susceptible and resistant populations, is therefore required. Once at-risk regions have been identified, management can be adapted to reduce immediate risks in priority populations, and promote long-term adaptation to change. However, management to protect forest ecosystem function may be preferable where the maintenance of historical species assemblages is no longer viable.

Introduction

Anthropogenic emissions of greenhouse gasses have led to significant and ongoing changes in climate, from global to local scales.[1] Climate is a key factor controlling the distribution of plant species,[2] and thus climate change is expected to result in shifts in the distribution of species, from the distribution of biomes to local populations. Such distributional shifts can result from the alteration of mean climatic conditions, climate seasonality, or changes in the magnitude, duration, and frequency of climatic extremes, all of which characterise current climate change to some extent.[1] The impact of climate change on the distribution of species is increasingly well documented, with plant species being driven to higher latitudes and altitudes as the climate warms as a result of population expansion at the expanding edge and extinction at the retreating edge of the species distribution.[3–5]

While the poleward advance of many plant species is limited by minimum temperatures, their limits in the opposite, equatorial direction, are often directly influenced by relatively higher temperatures and lower water availability.[2,6,7] Consequently, widespread species that have a lowland distribution in more poleward regions occur at higher elevations at their equatorial range edge, where the climate to which they are adapted occurs at higher altitude.[8] Topographic variation can, therefore, play a key role in facilitating the local persistence of populations by providing islands of suitable habitat even in regions where the climate is generally unsuitable for the species.[5,9–11] For example, the European beech tree, *Fagus sylvatica*, has a lowland distribution in northern Europe but is confined to mountains approaching its southern (equatorial) range edge.[12] Whilst this drought sensitive species is unable to grow throughout most of the Iberian Peninsula beyond the Pyrenean region, it occurs in isolated upland populations in the volcanic region of La Garrotxa and the mountains of Montseny and Aylión where favourable microclimates persist.

Shifts in the distribution of species result from alterations to juvenile recruitment and adult mortality in range edge populations, due to the exacerbation or alleviation of plant stress.[13,14]

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Environmental impact

Rising temperatures and an increase in drought stress linked to global climate change are likely to trigger widespread dieback and range retractions at the equatorial range edges of trees and other woody plant species. Negative consequences of such changes range from the loss of biodiversity to alteration in ecosystem structure and function and the loss of ecosystem services. Effective monitoring of the responses of tree species to climate change in these regions is, therefore, essential. We discuss the multidisciplinary and comparative approach necessary to allow us to detect and predict likely changes. Ultimately, such information can allow management to be adapted to promote population resilience and maintain ecosystem function.

The reported expansion of many plant species towards higher latitudes and altitudes is evidence of a general improvement of conditions at their poleward range edges. However, the impacts of climate change in the equatorial direction are less clear. At the equatorial range limits, increased temperatures are likely to increase drought stress where these are not matched by increasing precipitation. Yet, much less evidence exists for plant range retractions than range expansions.[9] This paucity of evidence might partly result from methodological difficulties in the study of equatorial range edges, particularly in woody species, which can persist for long periods in apparent disequilibrium with climate, due to their longevity.[9] However, recent research demonstrates that a wide variety of woody plant species are being negatively impacted by rising temperatures over large areas of their distribution,[15,16] suggesting that significant range retractions of woody species should be reported with increasing frequency in the near future.[9,14,16,17]

The detection of 'at risk' populations at the equatorial range edge of a species is particularly important due to their often disproportionate significance for biodiversity. Such populations can be ancient, relict populations, which have persisted throughout multiple Quaternary glaciations, typically where heterogeneous topographic and edaphic factors have allowed them to respond to environmental changes with relatively small migrations.[18,19] Furthermore, the long-term survival of relict populations of forest trees has allowed them to act as refugia for associated biodiversity.[18] Such populations can also be important for intraspecific diversity at the regional scale where isolation has led to elevated genetic divergence between local populations.[18]

Alteration of the competitive balance between species in mixed species stands is predicted in response to climate change, particularly where one or more species exists close to its climatic limits, thereby leading to changes in community composition over time.[20] Gradual changes in community composition have now been observed as a consequence of the interaction between climate change and interspecific competition.[13,21] At the equatorial range edge of beech in the Montseny Mountains in northeast Spain, this species is being replaced by holm oak (*Quercus ilex*) due to declining beech growth and establishment linked to elevated drought.[13] Whilst at a site in the Swiss Alps, downy oak (*Quercus pubescens*) has increased at the expense of Scots pine (*Pinus sylvestris*) during recent decades as a consequence of the differing physiological responses these species show in response to drought.[21] In addition to these more subtle changes in forest composition, sudden, rapid, and long-lasting ecosystem shifts due to loss of forest cover have been predicted as a potential consequence of climate conditions moving beyond the tolerance of all available tree species at a location.[7,9,16,22] Such shifts would result not only in the loss of genetically important populations and a reduction in biodiversity, but would have further negative impacts on ecosystem services such as carbon sequestration and soil stability.[7,9,16,18,21]

Predicting when and where range retractions will occur is difficult. Tree mortality is a non-linear threshold process, and factors such as stand density and interspecific interactions can modify the local response of a species to its environment.[15,16,23] Improving our capacity to predict such changes is, therefore, of prime importance given the pivotal roles that woody species play, from the structure and function of local ecological communities, to global atmospheric composition and hydrological cycles.[15,16,24,25] Here we discuss the monitoring of tree responses to climate-linked environmental changes and the identification and management of populations that are most at risk of imminent decline. We focus primarily on the natural equatorial limits of tree species. However, much of this work is relevant to monitoring the impacts of environmental changes throughout the species range.

Remote sensing

Increased stress on equatorial range edge populations is likely to derive mainly from the direct effects of rising temperatures and drought stress on plant physiology, or their indirect effects in increasing vulnerability to pest and disease outbreaks.[15–17] The ecological consequences of increased stress therefore range from a transitory reduction in stomatal conductance and photosynthetic activity, through phenological changes such as premature leaf fall, to partial dieback or the death of the organism.[26] Increased stress is characterised by symptoms including: increased canopy temperature, due to lower stomatal conductance and reduced transpiration; decreased chlorophyll content, due to limitation of chloroplast synthesis and/or elevated chloroplast degradation; and decreased leaf area index (LAI), resulting from a combination of reduced leaf production and elevated leaf senescence.[27,28] As these symptoms result in alterations to the visible and near-infrared (VNIR), short-wave infrared (SWIR), and thermal infrared (TIR) reflectance properties of the forest canopy, in principle, they should be detectable *via* airborne or spaceborne remote sensing techniques.

The estimation of vegetation biophysical and biochemical properties from remotely sensed data has been classically achieved through the use of simple VNIR reflectance-based vegetation indices, such as the Normalized Difference Vegetation Index (NDVI)[29] or the more recent Enhanced Vegetation Index (EVI),[30] that exploit ratios of reflected red and near-infrared (NIR) light.[27,31,32] NDVI is essentially a 'greenness' index that correlates with the density and/or health of vegetation. It is most widely used vegetation index and has a long history in monitoring change in forest ecosystems.[32] It was designed primarily for use with multispectral satellites, such as National Oceanic and Atmospheric Administration-Advanced Very High-Resolution Radiometer (NOAA-AVHRR), to provide high frequency data (7-day/14-day composites) on vegetation condition at the global scale. The AVHRR-NDVI time-series, together with that provided by more recent follow-on missions such as the Moderate Resolution Imaging Spectroradiometer (MODIS-TERRA), now extends back over three decades, and these archives have been used extensively to study the effects of environmental change on vegetation condition.[33] The crude spatial resolution (0.25–16 km pixels) of these datasets limits their use for studying localised changes in retreating range edge populations,[34] but higher spatial resolution NDVI time-series are available from sensors such as Landsat TM/ETM (30 m pixels).

NDVI and other related ratio-based indices have been widely used for sensing vegetation condition because of their ability to reduce noise caused by variations in illumination, shadow, topography and atmospheric conditions. NDVI time-series are, therefore, generally sufficiently robust to allow comparisons of forest growth at seasonal and/or inter-annual scales. NDVI-based algorithms have been developed to estimate biophysical parameters such as total (green) biomass,[35] LAI,[36] canopy gap fraction and clumping,[37] and the fraction of absorbed photosynthetically active radiation (*f*APAR).[38] The effects of stressors such as drought on forest ecosystems can be assessed through the detection of long-term change in the biophysical properties of forest canopies,[39] but this may be of limited use for the early detection of vulnerable populations.

The NDVI has also be used to assess shorter-term seasonal changes in vegetation phenology through the development of metrics based on factors such as the onset and rate of NDVI increase (*i.e.*, start and fastness of green-up);[40] the timing of the annual NDVI maximum;[41] and the length of the 'green' season.[42] These methods have been used to assess seasonal changes in climatic factors including rainfall.[43] The ability to assess changes in forest phenology using remote sensing would seem to be particularly relevant to studies of climate-related range retractions, particularly if such changes could be detected in advance of longer-term modifications to canopy structure. However, the use of remote sensing for studying climate-related changes in vegetation phenology has so far been generally limited to continental scale studies.

Although the NDVI is easy to derive from remote sensed imagery, and standard composite products are available for a range of sensors, the data must be interpreted critically. NDVI has been shown to respond differently to drought not only in different forest types, but also in populations differing in both drought history and species richness within forest types.[26] Further ambiguity of NDVI is related to its integration of both the abundance of green vegetation and its greenness.[26] NDVI can be less sensitive to changes in canopy condition in low-density stands, while effects related to disturbance of the forest canopy can be compensated for by green-up of understory vegetation.[32,44] Moreover, since the NDVI averages over broad bandwidths and effectively reduces three-dimensional vegetation to two dimensions, this metric saturates, and thus becomes insensitive, in highly multilayered (high LAI) canopies,[26,31] particularly when used with high spatial resolution imagery.[45] NDVI cannot, therefore, be used to assess subtle changes in moist tropical forests.[31] Despite these limitations, NDVI remains a vital tool in remote sensing of changes in forest extent and condition in response to climatic and other environmental changes. While it is beyond the scope of this perspective to review the literature in this area, the utility of the index is demonstrated by recent examples of the monitoring of forest response to, and recovery from, drought and other stressors.[24,26,32,44]

There has been a rapid advancement in remote sensing technologies over recent years. The development of hyperspectral imagers capable of measuring reflectance in hundreds of narrow contiguous bands has, in particular, led to significant improvements in the retrieval of vegetation biophysical and biochemical properties. The key advantage of hyperspectral imaging is that it provides fine-scale spectral information and can therefore be used to assess subtle changes in vegetation that might not be detectable in broadband multispectral imagery. There are now a number of airborne hyperspectral imagers, such as the Compact Airborne Spectrographic Imager (CASI) and the Airborne Prism Experiment (APEX), that are capable of acquiring imagery at spatial resolutions (metres) suited to fine-scale studies of forest range edges. The geographic coverage attainable using airborne systems is obviously limited, and the cost of data acquisition restricts their use for long-term monitoring. However, the extension of these imaging capabilities to new high spatial resolution polar-orbiting satellites (*e.g.* EnMap, German Aerospace Center, 30 m pixels) will greatly enhance our ability to study the effects of environmental change on forest ecosystems.

Narrow band hyperspectral vegetation indices have been shown to be less prone to saturation in heavily foliated forest canopies and often show stronger and more robust relations with biophysical and biochemical variables.[46] Hyperspectral data also allow for the use of more advanced approaches to the retrieval of vegetation biophysical and biochemical properties, including the use of indices based upon red-edge characteristic.[47] Increasingly, physically based methods such as radiative transfer (RT) and geometric optical (GO) models (and their hybrids) are being coupled with hyperspectral imagery to develop and refine methodologies for the retrieval of forest biophysical and biochemical parameters.[48] RT and GO models attempt to explain absorption and scattering processes as a function of the biophysical and biochemical attributes of the canopy; the inversion of the forward model can then be used to develop algorithms for parameter retrieval. Physically based models thus provide a more explicit link between canopy reflectance and canopy biophysical and biochemical properties; consequently, algorithms derived from physical-based model generally have far greater power for generalisation.

In addition to 'greenness' indices that can be used to assess drought stress in forests through the effect on parameters such as canopy chlorophyll or LAI, drought-induced stress in vegetation can be estimated more directly by exploiting the sensitivity of the SWIR region to changes in vegetation moisture content. The normalized water difference index (NDWI) uses a similar formulation to the NDVI but exploits reflectance ratios in the NIR and SWIR.[49] The NDWI has, for example, been used to detect drought-related decline in oak forests.[50] In comparison to greenness indices, NDWI is less prone to saturation, and is consequently better at capturing climate-driven variations in canopy properties.[51] NDWI can also be used to study climate-related changes in forest phenology.[52] NDWI was initially developed for broadband multispectral sensors such as Landsat, but more recently comparable indices have also been published for hyperspectral sensors,[53] but have yet to be widely tested in forest ecosystems. This includes for example the spectroscopic water absorption metric (SWAM) specifically designed to overcome problems associated with NDVI saturation in heavily foliated tropical forests.[31]

Whereas changes to reflectance-based indices can only be observed when damage has already occurred, other remote sensing methods might be used to detect or predict elevated stress before this point. Passive microwave radiation can be analysed to monitor soil moisture, with the potential to use these data to predict likely plant responses.[39] Likewise, a pre-damage decline in photosynthesis can be detected from a reduction in chlorophyll fluorescence, the process by which excess light energy absorbed by chlorophyll is re-emitted at a different wavelength.[54]

Increases in the frequency in fluorescence reduction events might be employed to warn of increasing levels of tree stress in sensitive sites if sensor revisits were of sufficient frequency. Both methods are appealing and, in principle, can be employed based on airborne or spaceborne sensing, but so far application at the field scale in forest ecosystems has been limited by the need for further technological and theoretical advances.[28,54]

Adverse environmental conditions that result in reduced stomatal conductance lead to elevated leaf temperatures due to a reduction in the cooling effect of transpiration. These changes have been exploited in the thermographic remote sensing of plant water relations and stress responses to airborne pollutants and pathogen outbreaks.[27,55] However, leaf temperature shows a complex relationship with air temperature, air humidity, wind speed and absorbed net radiation. All of these environmental variables vary on a small scale both spatially and temporally across the forest canopy[27,55] so far limiting the use of thermography to identify and monitor effects of environmental changes on forests.

Impacts of climate change on forests range from gradual to sudden, step-wise changes in condition and vary in their extent from individual trees to the regional level.[9,16,56] Widespread and sudden step-wise changes, such as rapid, regional dieback and storm damage, are much easier to detect and quantify than the impacts of stresses that result in gradual and progressive decline.[39] Whilst sudden changes might be detected in medium to low-resolution imagery, gradual decline requires the frequent capture of high-resolution images over long time-series, and its detection may, therefore, often be limited by poor data availability. Detection of gradual decline by remote sensing is a particular challenge where it is limited in areal extent.[39] Monitoring of decline at the equatorial range limits of tree species in mountain regions thus presents a particular problem, since due to the altitudinal compression of species distributions, decline may be limited in its areal extent, despite occurring over a significant proportion of the species distribution.[9] Marked topographic variations across altitudinal gradients also pose problems for the interpretation of satellite observations because of the effect on the bidirectional reflectance function of forest canopies.

Satellite-based time-series of vegetation ‘greenness’ and ‘wetness’ indices compiled by broadband sensors such as Landsat TM/ETM, and follow-on sensors such as the Advanced Land Imager (ALI), are clearly invaluable to large-scale assessments of change in forest ecosystems. However, accurate detection of climate-induced stress in fragmented and compressed range edge populations will require imagery that can resolve down to a much finer spatial scale. High-resolution multispectral data (*ca.* 2 m) are now commercially available from satellites such as QuickBird, IKONOS and WorldView-2. However, significant progress towards the development of robust models for the retrieval of canopy biophysical and biochemical parameters at the retreating edge of forests might only be realised with the use of high-resolution hyperspectral imagery. These imaging capabilities are largely limited to airborne systems at present, but the forthcoming generation of satellite-based hyperspectral imagers will offer previously unparalleled opportunities for spaceborne monitoring of forest responses to climate change.

Ground-based assessment

Combined approaches, integrating information from different remote sensing methods and at different spatial resolutions, might improve our ability to detect gradual changes at small spatial scales and also to differentiate between different potential causes.[39,55] However, ground-based assessment remains an essential component of forest monitoring. Ground-based data are needed to ground-truth parameter estimates and models derived from remotely sensed data. Additionally, such data provide point source data for integration into forest productivity and bioclimatic models and for independent ecological assessments.[13,28,39] Within Europe, a coordinated network for monitoring forest condition exists as a part of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP-Forests: http://www.icp-forests.org/). ICP-Forests data include assessments ranging from tree growth and crown condition to stand structure and measurements of soil and atmospheric chemistry. Where compatible, such data might be integrated with productivity and demographic data derived from national forest inventory programmes and data from individual research project networks. However, as with remote sensing data, a trade-off typically exists between the total area covered by an ecological monitoring network and its local resolution. Consequently, similar limitations of ground-based and remote sensing data exist for monitoring range retractions in woody species, particularly in topographically complex regions where microclimate and tree growth can vary over short distances.[11]

The observation that climate change is driving changes in species distributions[4] is not surprising, given the general sensitivity of species range margins to climate.[2] However, we still lack the necessary understanding of how and where changes in climate are impacting equatorial range edges, in part due to a substantial bias in data availability, which favours the poleward and upper limits of species distributions.[9,18] Whilst lower resolution data, whether from remote sensing or ground-based monitoring, can inform on widespread regional changes in forest condition, these data are often not adequate for monitoring changes occurring at equatorial range margins owing to their complex distribution and/or topographical variability.[11] In such regions, targeted collection of high-resolution data is necessary in order to identify currently occurring changes and predict the magnitude and spatial distribution of future decline.

Modelling techniques can be used as a ‘first-filter’ to identify where species are most vulnerable to growth decline or dieback caused by current environmental changes and biotic interactions. However, a major challenge for distribution modelling is identifying how the basic demographic parameters necessary for modelling population persistence or extinction respond to environmental changes over small spatial scales.[23] Most models are, therefore, unable to fully exploit their potential for monitoring changes at the equatorial range edge due to a lack of ecological realism required for them to adequately represent complex local distributions in this region of a species distribution.[23,57] Targeted collection of ground-based data referred to above in the context of ground-truthing remote sensing data would also enable an increase in the resolution of bioclimatic models by providing better data on the factors causing the extinction or persistence of populations at the equatorial range edge.[23] Such increased spatial resolution from distribution models would allow us to predict locally resistant and vulnerable stands, thereby improving the targeting of remote sensing assessment and identifying local control stands against which to measure more subtle changes in forest condition. In effect, this might allow us to trade space for time, detecting decline from spatial as well as temporal comparisons.

The pre-identification of vulnerable sites would also improve our ability to detect the onset of decline at an earlier stage. Monitoring at the plot level should exploit and enhance datasets already collected under international programmes such as ICP-Forests, for example, assessing crown condition, stand structure, tree growth and phenology.[13,14,56,58,59] The lack of historical data for such a monitoring network might be partly circumvented by integrating dendroecological analyses to identify past extreme growth anomalies and, where possible, the responsible climatic factors, together with changes in current and historical climate–growth relationships.[60] Changes in tree growth might be reconstructed by using measures such as tree basal area increment (BAI) derived from tree ring width measurements and current tree diameter. Such data provide not only the historical context for current levels of tree growth in monitoring plots, but can also indicate the trajectory of current growth changes.[56,59] However, further research is required to fully understand the implications of BAI changes over time.[59] As with remote sensing, the value of ground-based monitoring will be increased by comparing neighbouring sensitive and resistant sites. Whilst such local comparisons have been employed at specific sites at the equatorial range edge of tree species,[13,56] a more systematic approach is needed across the range edge of a variety of representative species. By doing so, we would be in a better position to make both fine-scale species-specific predictions of range retractions and predict more general patterns of decline, thereby enabling us to identify species, populations and associated communities that are most at risk.

Management of vulnerable populations

Attempts to protect and promote resilience to change at the equatorial range edge face challenges in conservation resource allocation, which can only be solved if data resolution and availability for monitoring and bioclimatic forecasting are improved. Currently, overly targeted resource use runs the risk of directing resources to the wrong places, whilst a 'catch all' strategy would spread resources too thinly to be effective. Therefore, broad-scale surveys to identify areas where populations of particular conservation concern and risk of degradation coincide are vital.[18,61] An approach based on the integration of plant phylogeographical studies with known areas of important biodiversity in the Mediterranean basin has demonstrated the potential for identifying areas potentially rich in key relict populations, some 25% of which are severely threatened due to human population pressure.[61] Work integrating predicted climate shifts with the current distribution of genetic diversity within *F. sylvatica* demonstrates the risk of losing substantial genetic diversity from the equatorial range edge of this species in Europe as the climate warms.[62] Future work should seek to further integrate paleoecological studies with molecular genetics and bioclimatic modelling to identify and prioritise populations of significant conservation importance.[61,62]

Once populations of particular conservation concern have been identified, management plans can be adapted to promote resistance and resilience of the population to environmental change, or to manage alteration of community composition as environmental change progresses.[63] The overarching aim of adapting management is to promote the long-term viability of populations through the avoidance of short-term risks, and through the promotion of long-term adaptability to changing climate. Where continuing population decline is unavoidable, management strategies should aim to slow the process, thereby providing an opportunity for change to occur in a managed way and protecting, where possible, associated biodiversity and the continuity of ecosystem goods and services. Attempts to preserve populations through intensive management must be weighed against the risk of sudden and severe impacts on the ecosystem if management stops at a later date.[64] In such cases, the maintenance of forest ecosystem function and services such as soil stabilisation and carbon sequestration may need to be the core goal, rather than conservation of particular suites of species.[65]

Uncertainty is a defining feature of biodiversity management relating to climate change, both in predicting climate effects and in evaluating the significance and risks to individual populations. Management must be flexible enough to be able to change direction and re-evaluate as time progresses[64] and must also take into account the intrinsic variability of ecosystems over time. Attempting to manage for a static habitat based on conditions at a site through recent history will be impractical in the face of rapid environmental change.[66] Forest management should be prepared to re-evaluate the utility of management applications as change develops, considering a broad range of actions on a case specific basis, such as those outlined below.

Destruction of competitors

Loss of tree populations at the equatorial range edge can be exacerbated by reduced competitive ability when species better adapted to new environmental conditions are present.[13,14] Competitors can be invasive exotics, other species normally found in the community, or newly colonising neo-natives. Vegetation management prescriptions are a common recommendation to delay climate impacts.[65,67] For example, encroaching shrubland coupled with competition from maritime pine (*Pinus pinaster*) has been implicated in the reduction of recruitment of cork oak (*Quercus suber*) in marginal populations. A management regime of shrub clearance and selective logging of *P. pinaster* has been recommended to prevent the decline of these populations.[68] Where populations are threatened by invasive species, detection of and removal of invasives at key immigration points can proactively remove the threat before intensive restoration effort becomes necessary.[63]

Modification of fire regime

Rising temperatures and reductions in precipitation will impact upon natural fire regimes and are expected to lead to an increase in wildfire frequency and duration as the climate warms.[66,69]

Altering the structure and amount of dead wood and forest litter can manage the risk of fire disturbance, as can controlled burning.[67] For the highest conservation value sites, fuel breaks in the surrounding area could be used in conjunction with fuel removal to avoid catastrophic destruction.[63] However, a less frequent fire regime itself represents a change in the normal disturbance pattern for a population and is, therefore, likely to alter natural forest development.

Selective thinning

Competition amongst trees can influence the occurrence and severity of drought-induced mortality and pest and pathogen damage.[16,24,70] Thinning and the selective removal of individual diseased or poorly growing trees might benefit those that remain, by increasing the availability of resources such as water, nutrients and light.[67] Thinning can, therefore, promote resilience to disturbance, while increased tree vigour can help reduce the impact of disease and insect attack.[65] In addition to increased stability of adult trees, gap creation provides an opportunity for recruitment and reduces competition for water between seedlings and adult trees,[71,72] thereby facilitating sapling establishment during periods when conditions for recruitment are favourable.

Many forests develop uniform age structures due to the abandonment of traditional management practices and recovery from widespread disturbance events.[24,73] By promoting asynchrony in forest age structure, deleterious density dependent effects could be reduced, whist maximising potential for recruitment of the canopy forming species.[63,72,74–76] However, although thinning can benefit remaining trees, dead and decaying wood provides an important range of habitats for taxa including insects and fungi and their predators,[76,77] therefore, its removal is likely to have negative impact on biodiversity. Variable density thinning might be an effective compromise, reducing stem density in some areas more than others and maintaining a proportion of dead and decaying wood in order to increase vigour and encourage reproduction whilst maintaining habitat diversity.[76]

Although thinning can be beneficial, gap creation can also increase the risk of colonisation by invasive species.[78] Furthermore, if gap size is too large, alteration of the microclimate of the forest floor can increase climatic extremes and reduce tree recruitment and establishment probability.[75,79] This latter process will be exacerbated as the climate warms, which is a particular risk if contemplating thinning to maintain equatorial range edge populations given the alterations to recruitment patterns already reported in this region of a species distribution.[13,14,72]

Traditional management techniques

Low impact traditional management techniques have some significant advantages for managing forests in a changing climate. Practices such as pollarding, coppicing and woodland grazing have often played a key role in the development and maintenance of forest structure and biodiversity,[13,64,80] and their abandonment can lead to habitat degradation.[80,81] Adapting forest management to a changing climate might exploit some of the characteristics of these traditional techniques. For example, selection coppicing could be used to create multi-age and structurally complex woodlands. In this practice, stems of differing ages are left on stools thus maintaining canopy cover whilst allowing harvesting to continue. When combined with the retention of standards for seed production, such techniques might significantly increase structural and age diversity in equatorial range edge populations by combining vegetative regeneration with rare seedling recruitment. Continuing canopy cover would protect soil from erosion and litter mineralisation[82] and reduce large gap formation. However, significant problems exist. Traditional management systems have lapsed in many countries due to their poor financial rewards, which are likely to be even lower in equatorial range edge populations.[82] Additionally, many practices have been out of favour for long enough to create a skills gap, which would complicate any drive to re-establish them.

Reduction of non-climate related stresses

The final cause of tree mortality is often due to pest or pathogen injury once other stresses have reduced an individual's defences.[16] Climatic stresses can be expected to combine synergistically with other anthropogenic stresses such as land use change, nutrient enrichment and atmospheric pollution, thereby exacerbating tree mortality. The identification and minimisation of non-climate change stresses should help reduce mortality in equatorial range edge populations.[63,65,83] By reducing the combined stresses impacting populations, the likelihood of exceeding the threshold for individual tree mortality[15,16] would, therefore, be reduced.

Conclusions

Given their disproportionate significance for biodiversity and the imminent threats posed by changes in climate, the identification and conservation of the most at-risk equatorial range edge populations is a pressing concern. Active monitoring is essential, both to pre-emptively identify populations that may suffer decline, and to assess the rate of decline currently occurring. A problem shared by remote sensing, ground-based assessment and modelling is the lack of fine-scale resolution needed to identify, monitor and predict climate impacts on populations. This is especially apparent in equatorial range-edge populations, which often exist in highly topographically varied landscapes. Progress in meeting these challenges would enable more focused and, therefore, more efficient use of conservation resources and the tailoring of management strategies to better adapt to and mitigate the impacts of climate change.

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