

Journeying into the Anthropocene— Scots Pine and Eastern Hemlock Over the Next 400 Years

Duncan Stone

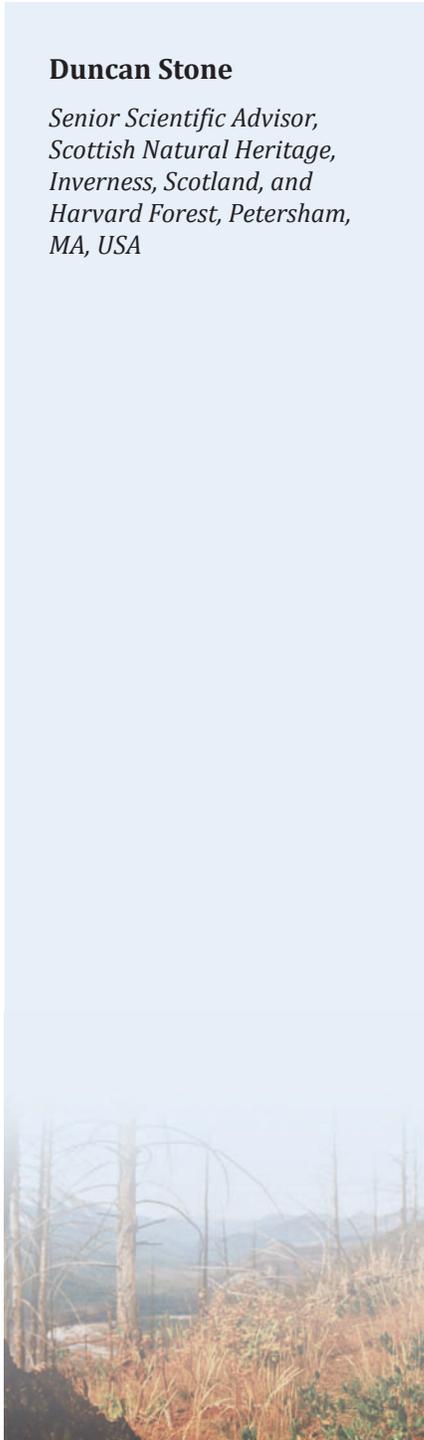
Senior Scientific Advisor,
Scottish Natural Heritage,
Inverness, Scotland, and
Harvard Forest, Petersham,
MA, USA

***Abstract:** Our native trees are much loved and valued components of our forests and fields, towns and cities. For a host of reasons—conservation, landscape, shade, and their sheer visual glory, we want our trees to grow big and old. But it takes time—often several centuries—from planting a tree to the desired outcome. This means that we need to choose trees today, which can grow successfully long into the Anthropocene era. In forest conservation, the standard view is that only locally native trees will deliver the objectives of conservation. The examples of Eastern Hemlock and Scots pine illustrate the challenge of the uncertain Anthropocene future—we cannot guarantee the long-term viability of these (or any) trees. Yet traditional forest conservation approaches do not offer any robust alternative to maintain the functions of those trees. If our aim is to pass on the benefits of big old hemlocks and pines to our descendants, we can no longer place all our eggs in one basket. A key way to reduce the risk of failure is to add diversity and redundancy—to grow a broader range of tree species including non-natives that have similar attributes.*

INTRODUCTION

On 20th April 2013, the Governor of Pennsylvania joined 150 volunteers on a cold, sunny Saturday to plant memorial trees at the Flight 93 National Memorial in Somerset County, Pennsylvania, USA. The first tree to be planted, laden with symbolism and garlanded with history, was a seedling grown from a parent tree living on the Gettysburg Battlefield. It is an Eastern Hemlock (*Tsuga canadensis*), the state tree of Pennsylvania. Earlier in 2013, in Edinburgh, a new ‘State tree’ was being proposed: the Scottish Parliament received a public petition asking that Scots pine (*Pinus sylvestris*) should become the National Tree of Scotland (Macnab 2012).

What links both these actions is a sense that trees can be monuments: predictable in growth, timeless and constant once mature, a well-designed structure reliably delivering the functions we require. Trees can remain relatively unchanged over the short arc of human lives (or attention spans)—our experience up to the beginning of this



century was that trees tended to be robust against natural stresses of weather, pests and diseases, with the example of Dutch Elm Disease (and in some places chestnut blight), being the only example in most people's experiences in either the eastern USA or the UK. As we've moved into a more unstable growing environment, the view of trees as robust, long-lived and highly predictable monuments is being increasingly challenged by the reality of unexpected tree health problems (Allen and others 2010; Anderegg and others 2013; Changhui and others 2011; Cullingham and others 2011; Mantgem and others 2009), and we are only at the beginning of a very long period of unpredictable change. The next few Anthropocene centuries are the future which today's tree seedlings will inhabit, and in choosing to grow long-lived trees in our conservation or multi-use forests, we are choosing paths forward into a wilderness of uncertain and unexpected combinations of opportunity and peril. Given that uncertainty, what trees should we grow?

Eastern hemlock in the eastern USA, and Scots pine in Scotland make good illustrations of the difficulties facing us—much loved native trees acting as the foundations of whole ecosystems, threatened by combinations of climate change and novel diseases, and yet valued for their long, long lives. They also make good examples of the way our feelings about our trees have lagged behind the understanding of threats and uncertainty about the future. It's hard to imagine that the Governor and his volunteers planted that memorial tree in the expectation that it will soon be infested with a non-native bug and either die, or survive only through an insecticide life-support recently banned across Europe. Equally, the petitioners at the Scottish Parliament had presumably not selected Scots pine as the national tree because it was showing a novel and worrying susceptibility to a needle fungus, with significant levels of infection in some places.

Designing our forests for their journeys into this uncertain Anthropocene wilderness requires some clear objectives. One approach to tree health and forest adaptation has focussed on preserving populations of tree species through spatial change, moving species or genotypes which are likely to decline to more suitable future destinations. This tactic has stimulated a vigorous debate over the value of assisted migration (AM) and its many synonyms (Hewitt and others 2011; Loss and others 2011). While such action may provide threatened tree species with a new home, we also value them for the functions they provide for us in their current location, including providing habitats for biodiversity as well as cultural, landscape, hydrological and carbon ecosystem functions. For example, an expansion of Scots pine within the boreal forest into higher Arctic latitudes in Norway and Finland (Reich and Oleksyn 2008) is not likely to be seen by Scots as adequate compensation for a decline of Scotland's Caledonian pinewood. Therefore, this paper focusses on how to sustain, in place, the forest functions likely to decline if Scots pine and eastern hemlock decline. This is not to downplay the importance of resolving other threats to these forest systems such as unsustainable logging, development or grazing, but these are comprehensively covered in other work, and are outside the scope of this paper.

Scots pine in the Caledonian pinewoods of Scotland

Scots pine (SP) has an enormous range, from Scotland and Portugal to Greece, Northern Finland, and eastern Siberia. In Scotland it is the primary and defining component of the Caledonian pinewoods, a western, oceanic outlier of the great boreal forests sprawling eastwards from Scandinavia. It is the only large native coniferous tree in Great Britain. SP in the Caledonian pinewoods faces a number of current problems. The overall area of ancient or old growth pinewood is only about 19000 ha (46,950 acres)—1percent of total woodland area, and is somewhat

fragmented (Patterson and others 2014). It has commonly undergone a long period without regeneration, leading to stands dominated by old trees without younger successors (Summers and others 2008). These structural problems have been recently joined by an unexpected increase in infection from *Dothistroma* needle blight (Brown 2012), possibly driven by weather impacts related to climate change (Watt and others 2009). This disease (aka Red Band needle blight) can progressively defoliate a range of pine species, weakening, and in some circumstances killing, SP and other pines in Scotland, especially Lodgepole (*Pinus contorta*) (Forestry Commission 2013). Looking to the future, the forecasts for climate impacts are restricted by the available modelling to the next 70-90 years, and predict a range impacts on SP from moderate (Ray 2008) to large (Reich and Oleksyn 2008). There are no forecasts available for future pest and pathogen impacts. Finally, any threats to SP carry serious consequences to the forest and its functions since it has no natural redundancy—there are no similar native species nearby that could significantly fulfil its functions. Furthermore, there is no possibility of natural range expansion by other similar species because of Britain’s island status.

Eastern Hemlock in Eastern USA

Eastern Hemlock (EH) occupies about a million hectares in eastern North America, distributed in small groves and riparian strips within the generally broadleaved eastern forest, and as a larger component in New England. It has an important foundation role in the wider ecosystem (Ellison and others 2012) with trees living several centuries and when mature providing important functions including the support of stable streamflow in summer. Although it occurs in a more diverse forest than the Caledonian pinewood it has a unique set of characteristics which mean that there is no real redundancy within the system—no similar species can naturally expand to fill its role if it is lost.

Since the 1980s EH and the related Carolina Hemlock (*Tsuga caroliniana*) have been seriously affected by the Hemlock Woolly Adelgid (HWA), an insect accidentally imported from Japan. The HWA has rapidly moved through the southern part of the range, where it threatens the almost total loss of the hemlocks (Orwig and others 2002). Its northerly progress has been slowed, probably by winter temperatures, but the predicted warming trend in winter is likely to allow its further impact beyond Massachusetts over the next century (Orwig and others 2012). Even if HWA impacts can be controlled or somehow attenuate to allow EH to persist, its long-term future over the lifespan of today’s seedlings carries the same uncertainty as Scots pine—with forecasts of climate change impacts on eastern United States forests similarly limited to just the next 90 years or so (Rustad and others 2012).

CONSERVATION OBJECTIVES

Timber production is generally dependent on younger trees, harvested in their adolescence or early middle age. For most other functions, especially biodiversity, trees become progressively more valued as they age, with big old trees living through their long natural lives seen as the most valuable of all. Studies also show humans just seem to like big old trees for their visual, landscape and recreational values (Donovan and others 2013; Edwards and others 2012; Gundersen and Frivold 2008; Ribe 1989). A recent analysis (Lutz and others 2012) produced a succinct summary:

Large-diameter trees dominate the structure, dynamics, and function of many temperate and tropical forest ecosystems and are of considerable scientific and social interest... [and] continue to contribute disproportionately to forest ecosystem structure and function after they die.

The functions and values we associate with Caledonian pinewoods and EH within the great eastern forests of North America fit within this general pattern. In the Caledonian forest, SP has a maximum lifespan of around 400 years (Fish and others 2010), with many biodiversity functions dependent on or more abundant in SP stands older than 100 years (Mason 2000) and in large deadwood that develops after mortality from 200 years onwards (Summers 2004). The role of EH in providing shade and reduced evapotranspiration to maintain stream flow and thus aquatic biodiversity and fish populations (Brantley and others 2013; Snyder and others 2002) is dependent on mature EH, as is the production of large dimension deadwood. An analysis from the northern end of its range in Ontario's Boreal-East Forest Region defined *Old Growth* status as having EH at least 180 years old, which are likely to endure for a further 500 years (Uhlir and others 2001).

So, some key functions of these native forests depend on big, old SP and EH. This generally becomes conservation objectives to follow the template of our inherited natural forests by protecting existing big old trees, and to meet our responsibilities to future generations by ensuring the future succession of SP and EH to great age and large sizes. We know little of the environmental conditions looking far into the future; given the vagueness of the few estimates of long-term multi-century climate change (Rogelj and others 2012) and the potential for novel pest or pathogen problems (Aukema and others 2011; Brasier 2008; Levine and D'Antonio 2003), we face considerable difficulties in assessing the viability of today's SP or EH seedlings over their desired lifespan.

Environmental changes have already begun and are causing widespread and significant health problems and mortality for many native trees, including the most valuable large old individuals (Lindenmayer and others 2014, 2012). Even if SP and EH overcome their current threats, we expect these trends to continue, and it seems likely that we will see further tree mortality and decline—indeed potentially on much larger scales as the departure from the 20th century baseline widens, and the cumulative environmental changes approach fundamental species or genotypic limits. A number of authors have pointed out that the effects of climate change on trees go beyond abiotic effects ('climate envelopes') to a range of inter-related biotic impacts (Lindner and others 2010; Sturrock and others 2011). For example, possible impacts of climate on insect pests of trees include changes in insect dispersal, development rates, voltinism, mortality, as well as changes in the resistance of trees through drought, waterlogging or storm stresses, and alterations in the palatability of leaves driven by changes in atmospheric CO₂ concentrations (Netherer and Schopf 2010). The impact of environmental changes on tree growth becomes essentially unknowable beyond the next few decades, because predictions of the drivers of change are too short or too vague—and unravelling the consequences of those changes is extraordinarily difficult. This leads to two troubling conclusions:

- We can neither guarantee nor predict the long-term viability of trees we start to grow today
- Conservation objectives that depend on the long-term viability of any single tree species run the risk of failure, particularly if the intended lifespan is long in relation to environmental change

Delivering our conservation objectives—existing big old trees

Maintaining our existing big old trees includes straightforward conservation tasks like preventing their intentional destruction, for example by avoiding large-scale felling. Reducing the threat from biotic and abiotic health issues could be helped by effective biosecurity and a significant reduction in the pace of greenhouse gas emissions, but these entail greater public motivation than simply forest conservation. For SP and EH, as for many other tree species, improvements in forest condition and the health and vigour of the trees is likely to help them resist damaging health impacts, or at least slow down the rate of spread or mortality. But the recent trends of tree health problems include primary pests and pathogens (including those currently affecting EH and SP) that can kill healthy trees. Faced with such antagonists, improving forest condition may do no more than delay the inevitable, and perhaps not even that. Finally, treatments such as pesticides or biological controls receive initially enthusiastic media coverage, but tend to be ineffective or too costly for forest-scale application (Orwig and others 2002), or are too much of a multi-year commitment to retain public support. Finally, even in the most hopeful scenarios, natural mortality will eventually take our existing big old trees, so sustaining the forest functions provided by these large trees requires us to choose their successors through planting or regeneration management.

Delivering our conservation objectives—growing the future big old trees

Since the early days of forest conservation the question of what trees should be grown generally meets the same answer—locally native genotypes and species, using the template derived from post-glacial or pre-settlement eras. In the Caledonian pinewoods for example, strenuous efforts have been made to ensure that only Scots pine of local origin is grown. In order to define ‘local’, 7 seed zones have been established across Northern Scotland (the smallest being only a few miles across), and only SP grown from seed collected within that zone should be planted there (Forestry Commission Scotland 2006). Such rules are designed to maintain the genetic and compositional status quo for a future of stable environmental conditions. Given we expect substantial, unpredictable and chaotic changes in the growing environment, it isn’t easy to make a new justification for this exclusive approach that explicitly incorporates the changes we foresee. So, what are the options for improving our chances of successfully passing on viable trees to become the big old trees for future generations?

Doing nothing is always an option. Beyond a simple panglossian view—‘it will probably all work out OK’—is a more thoughtful argument that we know that tree species decline and recover, and perhaps we should simply accept our current difficulties as cyclic processes. Both our example species have suffered substantial declines in prehistory, with EH declining precipitously 5000 years ago, probably through a pest or pathogen impact combined with changing climatic conditions (Foster and others 2006). The recovery to pre-decline levels, measured by pollen records, took some 1900 years (Allison and others 2013). SP experienced a significant decline around 4400 years ago, principally driven by a climate which became cooler and wetter, leading to the formation of extensive peat deposits (Bennett 1995), and has never recovered the lost ground. A wider perspective perhaps should consider that the vast majority of all species that ever lived are extinct, and an assumption of likely eventual recovery is little more than a guess. Even if recovery does occur, the species in decline will not be providing their forest functions for long periods—so long that they may be functionally lost in terms of human objectives. In forest

systems where the declining species have significant redundancy—where their functions can be delivered by other species that fill the vacated space—then perhaps a non-intervention approach has a stronger justification. However, for our examples that backup role is not available, because there are no species that can provide this redundancy—so any decline means their forest functions decline as well.

A variation on doing little requires the adoption of a luckily-timed and affordable future technological fix. This allows us to continue with the status quo (perhaps using short term or unsustainable measures to buy time), and rely on currently unavailable technologies that may allow us to protect our native forests. This might include defanging specific pests or pathogens, modifying the tolerances of individual trees, or reversing the momentum of climate change. But just as the continual postponement of nuclear fusion power shows the limits of technological promises, placing all our hopes on such a *deus ex machina* requires accepting the decline of tree species and their functions if the technological fix does not become available.

Numerous forest climate change adaptation strategies focus on actions that fit within conservation's native-ness and natural processes principles (Anonymous 2009; National Fish and Partnership 2012). These commonly include: improving forest condition by reducing stresses; encouraging range adjustments and the removal of migration barriers and forest fragmentation; and relying on future natural selection or tree breeding to produce trees successively well adapted to future environments. However, as noted in the section above, the current health problems of SP and EH are, like many other recent examples, caused by primary pests and pathogens capable of killing healthy trees. For this reason, improving the condition of our conservation forests cannot provide the basis of an effective strategy. In terms of range changes, the maximum natural rate of tree migration is too slow to track climate change (Aitken and others 2008), and for SP and EH there are in any case no candidates with similar functions which are near enough or without insurmountable barriers. Finally, a strategy based on growing successively different genotypes each adapted to the conditions of the time can only deliver big, old trees if the rate of environmental change is slow compared to the time required to grow such trees. Such a strategy is reasonable in timber plantations, where the trees are felled and replanted quickly (often <50 years)—but a poor strategy where we want to grow individual trees for 150-400 years.

Sustaining forest function through adding diversity and redundancy

The electricity supply for a major hospital is a perhaps a better model for the kind of resilience we need in our forests. Few such hospitals rely only on the external electricity supply. Instead, they will commonly have backup generation systems to maintain at least their key functions during a power outage. Such a backup system requires *diversity*—i.e., separate systems that can work independently, and *redundancy*—i.e., systems that provide at least the critical functions—i.e., continuing electrical power. For forests, a resilience strategy following this approach (formally 'robustness', see Morecroft and others 2012) aims to ensure the continuity of the ecosystem functions that depend on big old trees, by ensuring that sufficient big old trees are continuously present. It essentially pre-empts tree health crises by making changes now (i.e., developing backup systems) that reduce the future impacts of environmental stresses to acceptable levels.

Both our forest examples lack natural redundancy—they have functions that other nearby species cannot replicate. Even if they shrug off their current health issues they remain highly

vulnerable to future health threats over their long slow lives because they have no backup systems. Therefore any diversity added for resilience can only come as non-native genotypes and species. This approach thus becomes a direct challenge to the ubiquitous conservation view that promotes the exclusive use of locally native species.

A native tree in a natural forest is a package of functions and relationships that is unlikely to be replaceable as a single unit, and some of our forest functions may be exclusively reliant on a unique characteristic only found in a single tree species or genotype. But other functions we value depend on characteristics which can also be found in non-native species, suggesting that partial functional analogues can be found (Mascaro and others 2012; Schlaepfer and others 2011). For example, crested tits (*Parus cristatus*), naturally nest in cavities in larger SP—but will readily breed in nestboxes (Summers and others 1993), implying no strong obligate relationship to SP. Red squirrels (*Sciurus vulgaris*) in the Caledonian pinewoods will readily eat—and even thrive—on a wider range of conifer seeds (Bryce and others 2002) than just those of SP including Norway Spruce (*Picea abies*). In terms of the landscape and visual function of SP, the characteristic orange upper bark and growth habit has a striking similarity with that of Ponderosa pine (*Pinus ponderosa*). For EH, both Chinese hemlock (*Tsuga chinensis*) and hybrids between EH and Chinese hemlock have been seen positive early results in terms of growth and adelgid resistance (Evans 2012). Another candidate might be Norway spruce, planted and present in New England for many years and having some structural and shade qualities similar to EH.

A core part of forest research has been the exploration of the characteristics of different genotypes within tree species, and provenance trials (see Persson and Beuker 1997; Schmidting 1994) have been used to consider the impact of anticipated climate change on those genotype. In terms of the conservation concepts of native-ness, using a non-native genotype of a native tree is an unresolved issue—to do so might offer some adaptation benefits but at the cost of the likely permanent loss of local genotype through gene flow from the non-natives. Perhaps more importantly, using such trials to match species or genotypes to future projected climates requires both reasonably accurate knowledge of those future climates (which is, as previously noted, not available on the multi-century timescales needed for big old SP and EH) and an assumption that pests and pathogens will not intervene. A striking example of this issue was noted in (Aitken and others 2008), ‘...Lodgepole pine should be one of the species least affected by climate change. However, the recent climate-associated population explosion of the mountain pine beetle and the resulting decimation of vast tracts of Lodgepole pine forest...underscore the difficulty of predicting complex ecological interactions and the limitations of the models described herein.’

Finally, there may be a trade-off between redundancy and diversity: using non-native genotypes of native species is likely to provide very good redundancy, and can be used to anticipate some near-term climatic changes, but they may not provide effective diversity and share vulnerabilities with their native cousins.

The use of non-native species, genotypes, or novel hybrid constructs carries potential disadvantages and risks. Backup genotypes and species will inevitably take space from the natives. Any single such backup may not be viable in the longer term and fail to provide our desired functions—thus requiring multiple backup genotypes and species. They may deliver those functions less well than the natives, and introductions may carry some risk of invasive consequences or, more commonly, the simultaneous introduction of ‘passenger’ pests and pathogens (Ricciardi

and Simberloff 2009). While good research and carefully controlled actions should minimise unintended consequences, there are probably unavoidable costs—perhaps best considered in the same way as insurance premiums, or the cost of maintaining a backup generator system—i.e., the price of resilience. Also, to consider the risks and costs of a diversity/redundancy approach without including risks to the viability of native species is to make an unfair comparison. Over coming decades and centuries we expect rapid change which may eliminate or diminish native tree species, or uncouple their mutualistic relationships. The status quo is no longer likely to sustain the same conservation value as the ecosystem loses species, continuity and complexity or may only do so through repeated interventions which implicitly erode a claim to native or natural status. Essentially, the future may allow us no native or natural forest—our choice is whether we seek changes that help to sustain the functions we like—or to accept unpredictable changes that are less likely to include big old trees.

CONCLUSION

This problem—selecting trees that will be viable through the unpredictable conditions of the next centuries—is as challenging as any conservation dilemma. The long development time of big old trees means we have to take decisions well before we can be certain of the nature and timing of any threats. Many of the proposed adaptation strategies carry significant risks, and no approach guarantees success.

We can and should use what we know—our understanding of trees and the factors that cause them to grow or die—to create a framework for our decisions. We can and should build in risk assessments and assumptions based on our experience and the predictions available. However, the complexity of forest ecosystems, and our difficulty in projecting knowledge forward by many decades or centuries suggests that this framework is inadequate for a mechanistic decision-making process. Our recent experience of ‘black swan’ type events (like the abrupt spread in 2009 of *Phytophthora ramorum* from *Rhododendron* species to Japanese larch (*Larix kaempferi*) (Brasier and Webber 2010) supports this view. Can we remedy the inadequacy of our knowledge and risk framework to the point where we can plant a long-lived tree with confidence? This is an important question worthy of deeper consideration, but it seems very challenging given the tree growth timescales involved, the long residence time of CO₂ in the atmosphere, the lag between changes in emissions and climatic effects and the influence of politics, trade and technology. When even the IPCC offers predictions on the basis of a series of very different climate scenarios, the chances of a clear understanding of the consequences to individual trees seem small. As an example of the difficulty, provenance trials have been very useful in illustrating the characteristics of different tree genotypes, and we should certainly use this in thinking about our choices. But without reliable information on climate, weather extremes or pests and pathogens occurring in (say) 100 years’ time, that genotypic knowledge is hard to apply with precision or certainty. A related issue to the difficulty of predicting tree viability centuries into the future is that any assessment of the reliability of such predictions is rather hard, and likely to offer a range of answers subject to differing assumptions used in the frameworks or models.

If we can’t rely on a knowledge and risk framework to give us unequivocal answers, then we have to supplement these with values and judgements of risk. A confidence in technological advancement might prompt leaving problems to some future technological fix, whilst a focus on today’s values of native-ness might regard future species losses and functional breakdowns as a

gamble worth taking. An expectation of damaging impacts of environmental change on native trees, or a view that we would have only a weak ability to predict the viability of tree genotypes more strongly suggests a diversity/redundancy approach—as a necessary backup for a system facing much uncertainty and an intolerance of functional breakdown.

Since all approaches carry uncertainty, and are influenced by individual values and judgements, we probably should not settle for *any* single approach. A reasonable set of approaches spread across our landscapes might include:

- a suite of reference native stands and forests, allowing species losses such as EH and SP to occur without excessive interference
- investing in modest assisted migration-style genotype movements within existing ranges, for example, perhaps making better use of the enormous natural range of SP
- native forests with varying proportions and numbers of additional non-native species, to provide backup diversity and redundancy

It also seems wise to continue development of better technologies to respond to tree diseases—especially ways to buy time to develop and implement responses.

Unless we can quickly improve our knowledge and risk framework (or develop a consensus on its limitations) we run a risk of an extended period of debate where fundamental uncertainties mean that no resolution is available, and no action is taken other than the status quo. The discussions over AM perhaps provide an example of this. Perhaps we can make faster progress by acknowledging that none of the perspectives or approaches are flawless—and seeking to match each approach to the different perceptions of decision-makers to create ‘coalitions of the willing’ to implement the range of actions described above across our forest landscapes. Within this uncertainty-driven approach there will be much work for researchers to populate and extend the framework of our understanding, and a need for an adaptive management approach incorporating regular review of our priorities and techniques. Maybe from this composite approach comes an energising sense that forest conservation can do more than despairingly watch the loss of our big old trees—that we have more options to deliver conservation objectives if we can re-define these more positively as sustaining forest functions rather than simply avoiding any non-native species.

REFERENCES

- Aitken, S.N.; Yeaman, S.; Holliday, J.A. [and others]. S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*. 1: 95-111.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660-684.
- Allison, T.D.; Moeller, R.E.; Davis, M.B. 2013. Pollen in Laminated Sediments Provides Evidence For a Mid-Holocene Forest Pathogen Outbreak. *Ecology*. 67: 1101-1105.
- Anderegg, W.; Kane, J.; Anderegg, L. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature: Climate Change*. 3: 30.
- Anonymous. 2009. Climate change action plan 2009-2011. Forestry Commission Scotland.

- Aukema, J.E.; Leung, B.; Kovacs, K. [and others]. 2011. Economic Impacts of Non-Native Forest Insects in the Continental United States. *PLoS ONE*. 6: e24587.
- Bennett, K.D. 1995. Post-glacial dynamics of pine (*Pinus sylvestris* L.) and pinewoods in Scotland, in: Aldhous, J.R. (Ed.), *Our Pinewood Heritage*. Bell and Bain, Glasgow, UK. 23 p.
- Brantley, S.; Ford, C.; Vose, J. 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. *Ecological Applications*. 23: 777-790.
- Brasier, C.; Webber, J. 2010. Plant pathology: Sudden larch death. *Nature*. 466: 824-825.
- Brasier, C.M. 2008. The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology*. 57: 792-808.
- Brown, A. 2012. Time for action: *Dothistroma* (red band) needle blight in Scotland. *Journal of Forestry*. 18: 16.
- Bryce, J.; Johnson, P.J.; Macdonald, D.W. 2002. Can niche use in red and grey squirrels offer clues for their apparent coexistence? *Journal of Applied Ecology*. 39: 875-887.
- Changhui, P.; Zhihai, M.; Xiangdong, L. [and others]. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature: Climate Change*. 1(9): 467-471.
- Cullingham, C.I.; Cooke, J.; Dang, S. [and others]. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology*. 20: 2157-2171.
- Donovan, G.H.; Butry, D.T.; Michael, Y.L. [and others]. 2013. The Relationship Between Trees and Human Health: Evidence from the Spread of the Emerald Ash Borer. *American Journal of Preventative Medicine*. 44: 139-145.
- Edwards, D.M.; Jay, M.; Jensen, F.S. [and others]. 2012. Public preferences across Europe for different forest stand types as sites for recreation. *Ecology and Society*. 17: 27.
- Ellison, A.M.; Bank, M.S.; Clinton, B.D. [and others]. 2012. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and Environment*. 3: 479-486.
- Evans, A.M. 2012. Growth and Infestation by Hemlock Woolly Adelgid of Two Exotic Hemlock Species in a New England Forest. *Journal of Sustainable Forestry*. 26: 223-240.
- Fish, T.; Wilson, R.; Edwards, C. [and others]. 2010. Exploring for senescence signals in native scots pine (*Pinus sylvestris* L.) in the Scottish Highlands. *Forest Ecology and Management*. 260: 321-330.
- Forestry Commission, G.B. 2013. *Pests & Diseases—Dothistroma needle blight* [WWW Document]. URL <http://www.forestry.gov.uk/dothistromaneedleblight> (accessed 2.5.14).
- Forestry Commission Scotland. 2006. *Seed Sources for Planting Native Trees and Shrubs in Scotland (Guidance)*. Forestry Commission Scotland, Edinburgh.
- Foster, D.R.; Oswald, W.W.; Faison, E.K. [and others]. 2006. A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. *Ecology*. 87: 2959-2966.
- Gundersen, V.S.; Frivold, L.H. 2008. Public preferences for forest structures: A review of quantitative surveys from Finland, Norway and Sweden. *Urban Forestry and Urban Greening*. 7: 241-258.
- Hewitt, N.; Klenk, N.; Smith, A.L. [and others]. 2011. Taking stock of the assisted migration debate. *Biological Conservation*. 144: 2560-2572.
- Levine, J.M.; D'Antonio, C.M. 2003. Forecasting Biological Invasions with Increasing International Trade. *Conservation Biology*. 17: 322-326.
- Lindenmayer, D.B.; Laurance, W.F.; Franklin, J.F. 2012. Global Decline in Large Old Trees. *Science*. 338, 1305-1306.

- Lindenmayer, D.B.; Laurance, W.F.; Franklin, J.F. [and others]. 2014. New Policies for Old Trees: Averting a Global Crisis in a Keystone Ecological Structure. *Conservation Letters*. 7: 61-69.
- Lindner, M.; Maroschek, M.; Netherer, S. [and others]. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest and Ecology Management*. 259: 698-709.
- Loss, S.R.; Terwilliger, L.A.; Peterson, A.C. 2011. Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation*. 144: 92-100.
- Lutz, J.A.; Larson, A.J.; Swanson, M.E.; Freund, J.A. 2012. Ecological Importance of Large-Diameter Trees in a Temperate Mixed-Conifer Forest. *PLoS ONE*. 7: 1-15.
- Macnab, S. 2012. Campaigners pine for Scottish national tree. *The Scotsman*, Oct. 12, 2012 [<http://www.scotsman.com>]
- Mantgem, P.J.; van Stephenson, N.L.; Byrne, J.C. [and others]. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science*. 323: 521-524.
- Mascaro, J.; Hughes, R.F.; Schnitzer, S.A. 2012. Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs*. 82: 221-238.
- Mason, W.L. 2000. Silviculture and stand dynamics in Scots pine forests in Great Britain; implications for biodiversity. *Investig. Agrar. Sist. Recur. For.* 9, 175.
- Morecroft, M.D.; Crick, H.Q.P.; Duffield, S.J.; Macgregor, N.A. 2012. Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*. 49: 547-551.
- National Fish, W. Partnership, P.C.A. 2012. National Fish, Wildlife and Plants Climate Adaptation Strategy. Association of Fish and Wildlife Agencies, Council on Environmental Quality, Great Lakes Indian Fish and Wildlife Commission, National Oceanic and Atmospheric Administration, and U.S. Fish and Wildlife Service.
- Netherer, S.; Schopf, A. 2010. Potential effects of climate change on insect herbivores in European forests—General aspects and the pine processionary moth as specific example. *Forest and Ecological Management*. 259: 831-838.
- Orwig, D.A.; Foster, D.R.; Mausel, D.L. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography*. 29: 1475-1487.
- Orwig, D.A.; Thompson, J.R.; Povak, N.A. [and others]. 2012. A foundation tree at the precipice: *Tsuga canadensis* health after the arrival of *Adelges tsugae* in central New England. *Ecosphere*. 3: 10.
- Patterson, G.; Nelson, D.; Tullis, J. 2014. Scotland's Native Woodlands Results from the Native Woodland Survey of Scotland. Forestry Commission Scotland, Edinburgh.
- Persson, B.; Beuker, E. 1997. Distinguishing between the effects of changes in temperature and light climate using provenance trials with *Pinus sylvestris* in Sweden. *Canadian Journal of Forest Resources*. 27: 572-579.
- Ray, D. 2008. Impacts of climate change on forestry in Scotland—a synopsis of spatial modelling research, Forestry Commission Research Note 101. ed. Forestry Commission Scotland.
- Reich, P.B.; Oleksyn, J. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters*. 11: 588-597.
- Ribe, R.G. 1989. The aesthetics of forestry: What has empirical preference research taught us? *Environmental Management*. 13: 55.
- Ricciardi, A.; Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology and Evolution*. 24: 248-253.
- Rogelj, J.; Meinshausen, M.; Knutti, R. 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. *Nature: Climate Change*. 2: 248.

- Rustad, L.; Campbell, J.; Dukes, J.S. [and others]. 2012. Changing climate, changing forests: The impacts of climate change on forests of the northeastern United States and eastern Canada, Gen. Tech. Rep. NRS-99. ed. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.
- Schlaepfer, M.A.; Sax, D.F.; Olden, J.D. 2011. The Potential Conservation Value of Non-Native Species. *Conservation Biology*. 25: 428-437.
- Schmidting, R.C. 1994. Use of provenance tests to predict response to climate change: loblolly pine and Norway spruce. *Tree Physiology*. 14: 805-817.
- Snyder, C.; Young, J.; Lemarié, D.; Smith, D. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 59: 262.
- Sturrock, R.N.; Frankel, S.J.; Brown, A.V. [and others]. 2011. Climate change and forest diseases. *Plant Pathology*. 60: 133-149.
- Summers, R.W. 2004. Use of pine snags by birds in different stand types of Scots Pine *Pinus sylvestris*: Capsule Hole-nesting birds tended to breed in the largest pine snags (standing dead trees) predominating in ancient native pinewood and scarce in plantations. *Bird Study*. 51: 212.
- Summers, R.W.; Taylor, W.; Underhill, L.G. 1993. Nesting Habitat Selection by Crested Tits *Parus cristatus* in a Pine Plantation. *Forestry*. 66: 147-151.
- Summers, R.W.; Wilkinson, N.I.; Wilson, E.R. 2008. Age structure and history of stand types of *Pinus sylvestris* in Abernethy Forest, Scotland. *Scandinavian Journal of Forest Research*. 23: 28-37.
- Uhlig, P.; Harris, A.; Craig, G. [and others]. 2001. Old growth forest definitions for Ontario. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, Toronto, ON, Canada.
- Watt, M.S.; Kriticos, D.J.; Alcaraz, S. [and others]. 2009. The hosts and potential geographic range of *Dothistroma* needle blight. *Forest and Ecology Management*. 257: 1505-1519.

This paper received peer technical review. The content of the paper reflects the views of the authors, who are responsible for the facts and accuracy of the information herein.