

Should tree invasions be used in treeless ecosystems to mitigate climate change?

Martin A Nuñez^{1,2*}, Kimberley T Davis³, Romina D Dimarco⁴, Duane A Peltzer⁵, Juan Paritsis⁶, Bruce D Maxwell⁷, and Aníbal Pauchard^{8,9}

Intentionally allowing or promoting invasion by non-native trees into areas characterized by treeless vegetation could contribute to climate-change mitigation by increasing carbon (C) sequestration. In some areas of the world, incentives exist to retain invasive non-native trees in natural systems as a mechanism for increasing ecosystem C storage and reducing atmospheric carbon dioxide levels. Although this novel opportunity for C sequestration holds appeal, such an approach is problematic for several reasons: (1) invasive trees do not always increase net C sequestration due to greater occurrence of fire or reduced soil C; (2) lower albedo in invaded areas can increase absorption of solar radiation, thereby offsetting potential C sequestration; and (3) tree invasions often also have negative effects on biodiversity, economic opportunities, and water yield. Such drawbacks are sufficient to raise doubts about the widespread use of non-native tree invasions in treeless areas as a tool to ameliorate climate change.

Front Ecol Environ 2021; doi:10.1002/fee.2346

Action is needed to limit the magnitude and rate of climate change, one of the most crucial problems facing humankind (IPCC 2014). Despite their potential negative impacts on biodiversity and human welfare, non-native invasive woody plants have been proposed as a tool for climate-change mitigation through

In a nutshell:

- Non-native tree invasions can increase carbon (C) sequestration in some ecosystems; consequently, unmanaged incursions of introduced tree species are often considered a potential opportunity for climate-change mitigation
- The overall effect of tree invasions on climate-change mitigation is poorly understood, but evidence suggests net negative effects in some instances
- Tree invasions can alter fire regimes, soil C sequestration, and light absorption, all of which influence the impact invaders may have on climate regulation
- Overall, the detrimental impacts of tree invasions on biodiversity, economic opportunities, and water yield may offset any positive effects on C sequestration
- Managers or organizations considering using non-native trees for C sequestration should take into account the diverse problems associated with plant invasions

enhanced carbon (C) sequestration (Liao *et al.* 2008; Pejchar and Mooney 2009). For example, in some countries (eg New Zealand), monetary incentives in the form of C credits are used to discourage the removal of non-native invasive trees (Mason *et al.* 2017). Interest in this approach is growing because C sequestration by trees is a fundamental tool to mitigate climate change (Bastin *et al.* 2019; Griscom *et al.* 2017) and because tree invasions are increasingly common (Richardson *et al.* 2014). In many situations, invasive trees are not at present being retained to mitigate climate change, but employing them as C sinks in the future could undermine broader efforts to control invasives. Allowing tree invasions for the purpose of C sequestration may have limitations and unintended consequences similar to intentional tree planting for C storage (eg Holl and Brancalion 2020), but may also come with unique challenges. Leaving tree invasions intentionally uncontrolled as C sinks could be problematic for at least two primary reasons: tree invasions may not sequester more C long-term compared to the ecosystem they replace, and tree invasions may trigger severe economic and environmental impacts.

Invasive trees often grow faster in areas in which they have been introduced than in their native ranges (Parker *et al.* 2013; Davis *et al.* 2019). Moreover, trees invading treeless ecosystems potentially transform these areas from low aboveground C sequestration to areas of high aboveground C accumulation. Although this factor increases the appeal of using tree invasions as C sinks, maintaining tree invasions as C sinks in treeless ecosystems may generate negative impacts that offset or even outweigh the potential benefits.

■ Understanding how climate can be affected by tree invasions

In forested ecosystems, C sequestration potential by invasive woody species may be low due to the presence of native

¹Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina; ²Department of Biology and Biochemistry, University of Houston, Houston, TX *(nunezm@gmail.com); ³Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT; ⁴Grupo de Ecología de Poblaciones de Insectos, IFAB (INTA-CONICET), San Carlos de Bariloche, Argentina; ⁵Manaaki Whenua Landcare Research, Lincoln, New Zealand; ⁶Laboratorio Ecotono, INIBIOMA, CONICET, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina; ⁷Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT; (continued on last page)

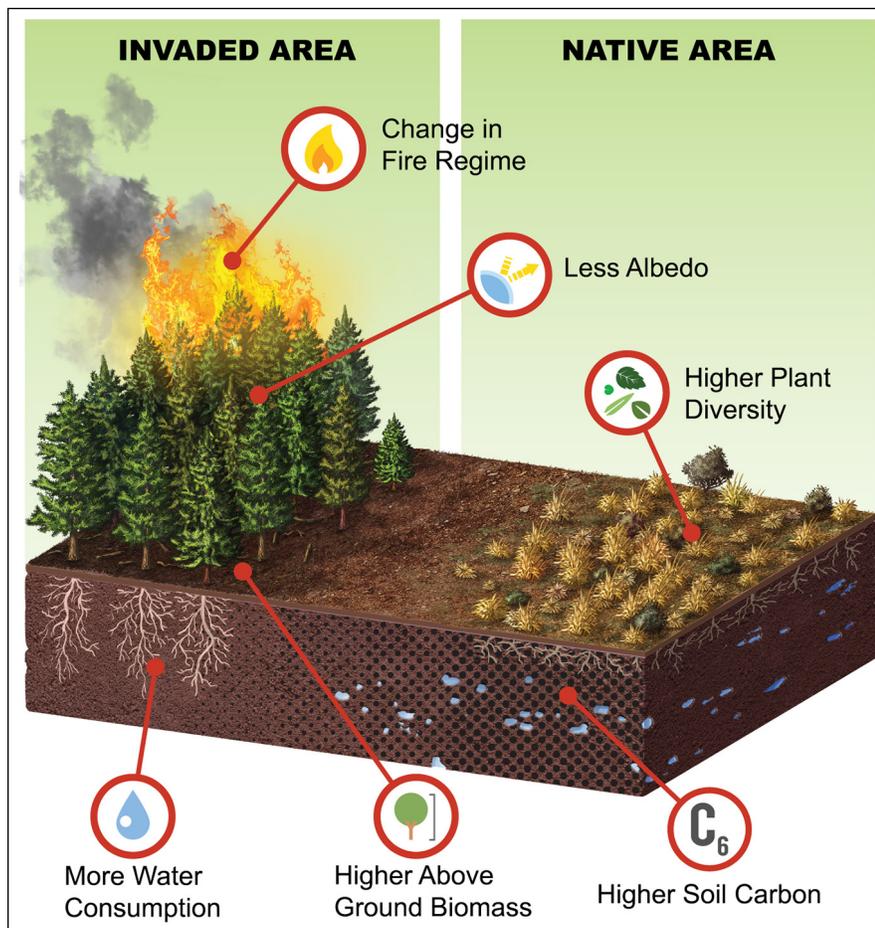


Figure 1. Diagram of the problems and benefits of woody invasions described in the main text, including changes in fire regimes, aboveground and belowground carbon (C) sequestration, water use, species diversity, and albedo.

trees. Tree invasions into treeless ecosystems (eg grasslands, shrublands) are widespread (Rundel *et al.* 2014) but may not enhance C sequestration because of increased fire risk and reduced soil C. In addition, because the overall aim of C credits is to minimize global warming, woody species invasions may result in lower albedo, raising land surface temperatures. Here, we present and discuss the evidence

vegetation to the canopy, thereby increasing the risk of crown fire (Paritsis *et al.* 2018). Fire season length and fire activity are widely projected to increase in many parts of the world due to climate warming (Jolly *et al.* 2015), making stands of invasive trees (particularly flammable species, such as *Pinus* and *Eucalyptus*) more likely to burn and release stored C back into the atmosphere (Panel 1 and Figure 2).

suggesting that invasion of non-native tree species into treeless ecosystems is a less than ideal mechanism for C sequestration, and that it can have detrimental, unintended environmental impacts, even including promotion of positive climate-change feedbacks (Figure 1).

Changes in fire regimes

Aboveground biomass accumulation due to tree invasion increases fuel loads and alters fuel distribution, which in turn modifies fire regimes and enhances fire risk (eg Mandle *et al.* 2011; Souza-Alonso *et al.* 2017; Castro-Díez *et al.* 2019). For example, dense invasions of broad-leaved paperbark (*Melaleuca quinquenervia*) into Florida prairies and wetlands have caused a shift in fire regime from low to high intensity (Mandle *et al.* 2011). In fuel-limited systems like the Patagonian steppe of South America, woody invasions increase both fuel loading and connectivity, leading to increased fire intensity and severity (Taylor *et al.* 2017; Paritsis *et al.* 2018). In contrast, some invasive trees have traits that reduce fire spread in areas with frequent-fire regimes (eg Stevens and Beckage 2009). Plantations of non-native trees are typically managed to improve wood quality (eg by pruning lower branches), which can limit vertical fuel connectivity; however, tree invasions into grasslands or shrublands have lower crown base heights that connect surface vegetation to the canopy, thereby increasing the risk of crown fire (Paritsis *et al.* 2018). Fire season length and fire activity are widely projected to increase in many parts of the world due to climate warming (Jolly *et al.* 2015), making stands of invasive trees (particularly flammable species, such as *Pinus* and *Eucalyptus*) more likely to burn and release stored C back into the atmosphere (Panel 1 and Figure 2).

Panel 1. A worked example of pine invasion, carbon, and fire from the Southern Hemisphere

Native to North America, lodgepole pine (*Pinus contorta*) has been introduced into several regions of the Southern Hemisphere, where it quickly invades open ecosystems and grows faster than in its native range (Taylor *et al.* 2016a), therefore allowing for rapid rates of aboveground carbon (C) sequestration. However, lodgepole pine invasions in Argentina, Chile, and New Zealand were found to greatly increase fuel loads, especially in treeless areas, which is expected to cause more intense fires than in uninvaded stands (Taylor *et al.* 2017; Paritsis *et al.* 2018). To quantify how much C would be released into the atmosphere if invaded and uninvaded grassland and shrubland

sites in New Zealand and Patagonia were burned, we used fuel loads collected across a lodgepole pine invasion gradient (Taylor *et al.* 2017) and the First Order Fire Effects Model (Reinhardt 2003) to simulate C emissions from a wildfire. We found significantly higher simulated C emissions in invaded as compared to uninvaded plots at three of four study sites (two in New Zealand, one each in Argentina and Chile; ANOVA and post-hoc Tukey's tests). Stands of invasive pines that were ~10 years old were found to release much larger amounts of carbon dioxide into the atmosphere under fire simulations than uninvaded plots (Figure 2).

Reductions in soil C

Although increased aboveground C storage following woody species invasion is well documented, much less is known about belowground storage. This is surprising because soil C storage is the primary component of global C sequestration, with two- to threefold more C stored in soils than in terrestrial vegetation (Houghton 2007). A meta-analysis across invasive species and ecosystems revealed that soil C can increase slightly following invasion (Liao *et al.* 2008), but recent experimental evidence suggests that non-native species reduce soil C through interactions with herbivores and soil biota (Waller *et al.* 2020). Other studies focused on woody species suggest that soil C can either increase or decline after invasions (Jackson *et al.* 2002) due to changes in rooting depth, associated soil biota, or lower C inputs from resident species. For instance, co-invasion of ectomycorrhizal tree species, which are globally important invaders (eg all Pinaceae and *Eucalyptus*, and species in the Salicaceae and *Acacia*), and their symbionts can increase rates of nutrient cycling and oxidation of C pools compared to native mycorrhizal forms, thereby reducing soil C in comparison to native vegetation (Farley *et al.* 2004; Dickie *et al.* 2014).

C accumulation in soils is driven by numerous and complex processes that are both directly and indirectly influenced by invasive trees (Sapsford *et al.* 2020) through, for example, differences in biomass allocation or accretion of the invader itself, longevity of the non-native species, or alteration of litter quality and quantity to the soil subsystem and therefore C and nutrient cycling (eg Castro-Díez *et al.* 2014). The relatively rapid increase in aboveground biomass of invaders (Liao *et al.* 2008) commonly exerts important indirect effects on ecosystem C by altering the composition, diversity, and function of resident vegetation (Wardle and Peltzer 2017; Davis *et al.* 2019). Overall, the assumption that tree invasions will promote soil C levels may not be true in all cases, underscoring the need for more comprehensive species- and system-specific information.

Reduction in albedo

Increased forest cover in the temperate and cold regions of the world can produce a net warming of the atmosphere even under scenarios of C accumulation due to altered surface albedo (Arora and Montenegro 2011; Davies-Barnard *et al.* 2014; Kreidenweis *et al.* 2016). Changes in albedo are fundamental to understanding the net effect of tree invasions on global warming, especially in treeless areas. Because of the vast extents of the planet's terrestrial surface that could potentially be occupied by non-native tree species, changes in reflection could undermine the overall goal of using invasive woody species as a tool to mitigate climate change. To illustrate, we observed a 20% reduction in albedo in a native steppe in Chile within ~10 years of pine invasion (Figure 3); if unmanaged, it is likely that the invaded area will eventually attain albedo levels similar to those of nearby plantations (or possibly even lower, given the higher tree density in invaded versus

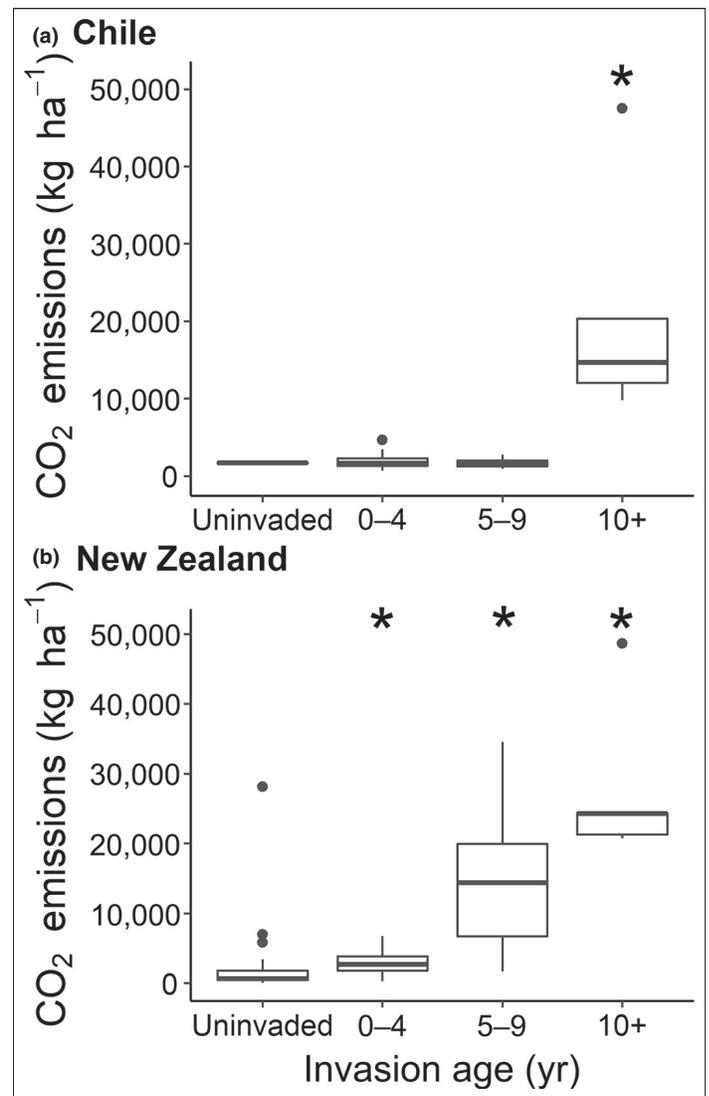


Figure 2. Simulated carbon dioxide emissions as a function of time since lodgepole pine (*Pinus contorta*) invasion (years) and in comparison to uninvaded plots in grassland systems, at sites in Chile (a) and New Zealand (b). Horizontal lines within boxes depict median values, boxes represent the interquartile range (25th–75th percentiles), whiskers (vertical lines) represent 1.5×interquartile range, and solid circles depict outliers. Asterisks highlight groups that were significantly higher ($P < 0.05$) than the uninvaded plots based on post-hoc Tukey's tests.

managed stands). Other studies have reported even greater differences; for instance, evergreen plantations and grasslands were characterized by albedos of 0.12 and 0.19, respectively (that is, 88% and 81% of the sunlight received by these land-cover types would be absorbed) (Schaeffer *et al.* 2006). It was beyond the scope of this article to calculate temperature increases that could result from such invasions, but these findings illustrate that changes in albedo of this magnitude could contribute to shifts in global temperature if they occur over large spatial scales, possibly producing a net rise in temperature even under a scenario of high C accumulation (Davies-Barnard *et al.* 2014; Kreidenweis *et al.* 2016). Although albedo can be affected by complex factors (eg cloud cover), a change in albedo of

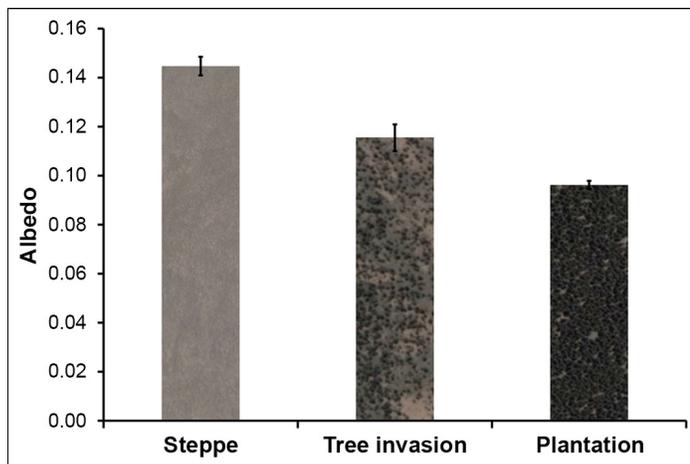


Figure 3. Total shortwave albedo (mean \pm standard deviation) obtained from Landsat 7 products for the Coyhaique area, Chile, for a Patagonian steppe, a dense but recent (~10-year-old) lodgepole pine (*P. contorta*) invasion in the steppe, and a lodgepole pine plantation in an adjacent area. Albedo was calculated based on 20 points for each vegetation type using equations described in Liang (2001).

0.01 at a global scale would have a warming effect equal to that generated by a doubling of the current amount of carbon dioxide in the atmosphere (Wielicki *et al.* 2005).

■ Impacts of tree species invasion beyond climate-change mitigation

Tree species invasions into treeless areas may have multiple ecosystem-scale effects, many of which – such as altering C

sequestration – can be pervasive (Panel 2 and Figure 4). First, these invasions often lower the abundance and diversity of native species (Pyšek *et al.* 2012; Davis *et al.* 2019) and induce shifts in soil biotic communities and nutrient cycling (Le Maitre *et al.* 2011; Castro-Díez *et al.* 2019), resulting in fundamental and persistent changes to ecosystems. Second, greater aboveground C sequestration is associated with increased water use and consequently lower water yield in catchments. Global studies show afforestation of grasslands or shrublands reduces streamflow and runoff by 40–75% (Farley *et al.* 2005; Jackson *et al.* 2005), which can restrict water availability to urban areas (Pejchar and Mooney 2009) and exacerbate problems of surface and groundwater availability in dry regions (Le Maitre *et al.* 1996, 2000). In addition, decreased soil organic matter beneath invasive pines can reduce soil water retention relative to native grasslands (Farley *et al.* 2004). Greater water use can also interact with other factors, for example, by increasing fire risk. Third, woody species invasions can have severe negative social and economic impacts across diverse sectors, such as plantation forestry, tourism, and sheep and cattle ranching (Ledgard 2001; Le Maitre *et al.* 2011; van Wilgen and Richardson 2012; Castro-Díez *et al.* 2019). Heavily invaded areas cannot be used for other activities without the removal of trees, which is often unaffordable for landowners (Nuñez *et al.* 2017). For example, at sites in New Zealand, the cost of removing invasive pines ranges from NZ\$1–50 per hectare for sparse invasions to more than NZ\$2500 per hectare for dense invasions, and management is often repeated within a site before a different land use is feasible. Other major economic impacts include the reduction of surface streamflow,

Panel 2. A practical example of the potential conflicts and concerns of using tree invasions for C sequestration in New Zealand

Species of Pinaceae underpin the plantation forestry industry in New Zealand but are also widely naturalized biological invaders. For example, wood exports from pines comprise ~99% of total log volume exports and are the fourth largest industry nationally (NZMPI 2019). On the other hand, at least 14 species of Pinaceae are considered to constitute a serious weed problem on ~1.8 million ha (Froude 2011; Hulme 2020). As a consequence, government agencies, land managers, and communities currently spend in excess of NZ\$15 million annually on management. Overall, there are nontrivial costs and benefits of non-native pines in New Zealand that have generated much debate over their management, both as a resource and as invaders. One of these issues is whether invasive pines should be retained in some areas for C sequestration. There is active debate on the pros and cons of using invasive trees for C sequestration. This debate spills over directly into C sequestration policy through New Zealand's Emissions Trading Scheme (ETS; www.mfe.govt.nz/ets), which is intended to promote more environmentally sustainable management by C emitters paying for C credits from entities that remove greenhouse gases. At present, New Zealand is the only country so far to include plantation forests as full participants in an ETS (Evison 2017). A large number of plantations that were

established in the 1980s through afforestation incentives are now due for harvest, and this has created an urgent need to replace forests that can rapidly sequester C to meet international climate obligations, such as the 2015 Paris Agreement. Post-1989 forests registered in the ETS can be liable for deforestation by removing invasive trees; likewise, pre-1990 forests require a “tree weed” exemption if subject to the ETS. The 1989/1990 cutoff in managing forests for C sequestration means that, in some instances, there are ~30 years of potential invasion that either can be partially claimed under ETS or require exemption to allow for weed management. Although tree invasions can be considered under some circumstances to provide benefits for C sequestration, the trade-offs involved with ongoing invasion and negative impacts mean that retaining invasive trees is not generally considered acceptable practice over the long term (Edwards *et al.* 2020). However, invasive trees are retained in some long-invaded or remote areas where management is considered intractable or unaffordable, but these are not included in the ETS. Ultimately, this example highlights that the interplay between management of biological invaders, policy, and practice underpins decisions for when and where tree invaders are removed or retained (Hulme 2020).

for instance after the introduction of acacias in South Africa, which resulted in losses equivalent to over US\$200 million and exacerbated social conflicts in the region (De Wit *et al.* 2001; Shackleton *et al.* 2018). Tree invasions can also alter landscapes and their aesthetics, driving shifts in intrinsic, tourism-based, and recreational values (Castro-Díez *et al.* 2019). Collectively, these impacts and the shifts they produce (eg in fire regimes or water cycles) suggest that tree invasions can cause major environmental and social problems (Kull *et al.* 2018). How the total economic costs or benefits of biological invaders can be quantified adequately across their multiple effects on environmental, social, and economic factors remains unresolved (Bartkowski *et al.* 2015).

■ When would it be justified to use tree invasions as a climate-change mitigation effort?

Although leaving woody species invasions unmanaged to act as C sinks has several disadvantages, this approach may be a viable option for species that have a net positive effect on C sequestration over the long term but only minor adverse impacts on biodiversity and ecosystem services. Some non-native woody species are more invasive than others, which can be explained by their characteristics. For example, lodgepole pine (*Pinus contorta*) is highly invasive in the Southern Hemisphere due in part to its relatively small seed size and early age of reproduction (Richardson and Rejmánek 2004), making removal of this species essential regardless of its value to C sequestration because it can quickly spread into areas where it is unwanted; in addition, large-scale removal is costly and can produce negative soil legacy effects (Nuñez *et al.* 2017; Dickie *et al.* 2014). Similarly, invasions by some *Acacia* spp have negative ecological or economic impacts (Souza-Alonso *et al.* 2017) that far exceed the benefits of their C sequestration, such as reductions in water availability for crops and urban areas (De Wit *et al.* 2001). In contrast, other types of conifers (eg cypress [*Cupressus* spp]) do not readily spread in some areas (Richardson and Rejmánek 2004), and therefore may be preferable to more invasive species.

Retaining invasive tree species may also be considered if populations can be contained or managed within specific sites. Some woody species only become invasive in specific environments (eg degraded pastures) and may be passive bystanders as opposed to active drivers of ecological change (MacDougall and Turkington 2005); spread of these species may be more easily controlled, making them better suited for C sequestration purposes. At present, however, few management options exist for the efficient removal of invasive woody species, and containment requires ongoing management of buffers and surveillance to confirm effectiveness (Panetta 2012). Furthermore, removal of woody non-natives will not necessarily restore the ecosystem to its previous state (Sapsford *et al.* 2020) but instead may induce shifts toward different community compositions and ecosystem



Figure 4. Pine invasions create landscape-level changes in both fire regimes and ecosystem properties, including C sequestration. This image shows lodgepole pine (*P. contorta*) and Austrian pine (*Pinus nigra*) invading native tussock grasslands in the Southern Alps of New Zealand. Any C sequestration driven by pine invasion may be short-lived due to increased fire disturbance or large-scale management to remove these invasive trees.

processes, and in some cases additional invasions by other non-native species (Nuñez *et al.* 2017). Overall, the management costs of retaining invasive tree species can be considerable, and these costs must be balanced against the benefits for climate mitigation or other services. Yet invasions should still be used with caution and continuously monitored given the ongoing and long-term potential for non-native species to both invade and, in some cases, fundamentally alter ecosystems (eg Strayer *et al.* 2006; Hulme 2020).

■ Are there more sustainable alternatives to using invasions?

Native species that spread into new ecosystems can also be used for C sequestration (Simberloff *et al.* 2011). Expansion of native tree species is a widespread phenomenon and may have fewer negative consequences for the environment than non-native invasive species given their coevolutionary history with the invaded community. However, invasion of native species into adjacent areas (that is, woody encroachment) can also result in loss of biodiversity (Jackson *et al.* 2002; Taylor *et al.* 2016b), shifts in fire regime (Ratajczak *et al.* 2014), and possibly lower C sequestration. Evaluation of leaving native invaders uncontrolled to serve as C sinks must therefore also take ecosystem impacts into account.

Native and non-native tree species in planted forests with clear commercial value and defined management plans may

be a viable option for use as C sinks. Commercial value may derive from firewood, timber, or a non-wood forest product used in the food, chemical, or pharmaceutical industries (Rodrigues-Corrêa *et al.* 2012; Hulme 2020). In these cases, it is important to assess how invasive the commercial tree species is, given that it could escape into areas where it cannot be harvested commercially (Nuñez *et al.* 2012). Management plans of plantations should thus consider the control of all individuals that spread beyond the original plantation stands (eg through inclusion into Forest Stewardship Council standards).

Restoration of areas previously occupied by trees has been promoted as a key tool to increase C sequestration at a global scale (Griscom *et al.* 2017; Bastin *et al.* 2019). This alternative is ideal if the species included in the restoration were present historically (ie native). Large amounts of C can be stored through forest restoration, and this should be a priority given the combined benefit of C sequestration and the restoration of natural ecosystems.

■ How can management decisions be improved?

Economic and technical resources for controlling invasive species are often limited. In these instances, a detailed analysis of C sequestration and other impacts – taking into account soil C, fire activity, albedo, biodiversity, and water use – should be considered before the decision whether to retain an invasive species is made. Although invasions may provide net C accumulation, there are still no effective management options available, as with pine invasions in different parts of the world (Nuñez *et al.* 2017). In these scenarios, available methods for evaluating impacts (eg economic impact classification of alien taxa [EICAT], socioeconomic impact classification of alien taxa [SEICAT]; Bacher *et al.* 2018) should be used to produce objective impact assessments, which can then be used to determine the costs and benefits of different management options.

In cases where effective management options are available, net C sequestration and positive impacts on mitigating climate warming should be determined; these positive effects of C sequestration must be considered along with negative effects, such as impacts on local economies or biodiversity, when deciding whether the affected area should be prioritized for management. For example, funds available for climate-change mitigation can be allocated toward removal of invasive species that promote climate warming due to a reduction in long-term C sequestration or in albedo. As an example, several areas in New Zealand that are managed for pine invasions under a national wilding conifer control program are now being considered for subsequent afforestation under a different national initiative, the One Billion Trees Programme (Te Uru Rākau 2018), which uses both native trees and non-native tree species with low risk of invasion. Such an approach both reduces the current and future risks

of tree invasion and supports a shift toward afforestation for climate mitigation.

When contemplating whether to remove or retain invasive trees it will be crucial to apply objective decision-making tools. The decisions might be similar to those made when considering managed relocation (or assisted migration), for which multicriteria decision frameworks have been developed (eg Richardson *et al.* 2009). In this regard, there are important scientific, regulatory, and ethical challenges that must be taken into account (see Schwartz *et al.* 2012). Experimental evidence concerning impacts and C accumulation is frequently lacking, yet such information is fundamental for decision making and adaptive management under global change scenarios.

■ Conclusions

Determining whether an invasive species can and should be retained as a C sink to help mitigate climate change involves consideration of aspects beyond its aboveground C storage capacity. Many factors play a role in decision making concerning the use of invasive woody species as climate-change ameliorators. Climate change and biological invasions are complex problems requiring solutions that incorporate scientific, economic, and social considerations. The objective of this review was to show that woody species invasions are rarely effective or desirable in mitigating climate change because their effects on C sequestration are not always positive, and they can have a range of detrimental impacts on ecosystems.

■ Acknowledgements

We thank P Kardol and C Iversen for helpful comments on early versions of the manuscript. MAN was supported by PICT 2016-1412 and PICT 2018 329; DAP was supported by the Winning Against Wildings research program funded by the New Zealand Ministry of Business Innovation and Employment; AP was funded by CONICYT PIA AFB170008; and MAN and AP were funded by NERC NE/S011641/1.

■ References

- Arora VK and Montenegro A. 2011. Small temperature benefits provided by realistic afforestation efforts. *Nat Geosci* **4**: 514–18.
- Bacher S, Blackburn TM, Essl F, *et al.* 2018. Socio-economic impact classification of alien taxa (SEICAT). *Methods Ecol Evol* **9**: 159–68.
- Bartkowski B, Lienhoop N, and Hansjürgens B. 2015. Capturing the complexity of biodiversity: a critical review of economic valuation studies of biological diversity. *Ecol Econ* **113**: 1–14.
- Bastin JF, Finegold Y, Garcia C, *et al.* 2019. The global tree restoration potential. *Science* **365**: 76–79.
- Castro-Díez P, Godoy O, Alonso A, *et al.* 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol Lett* **17**: 1–12.

- Castro-Díez P, Vaz AS, Silva JS, *et al.* 2019. Global effects of non-native tree species on multiple ecosystem services. *Biol Rev* **94**: 1477–501.
- Davies-Barnard T, Valdes PJ, Singarayer JS, *et al.* 2014. Full effects of land use change in the representative concentration pathways. *Environ Res Lett* **9**: 114014.
- Davis KT, Callaway RM, Fajardo A, *et al.* 2019. Severity of impacts of an introduced species corresponds with regional eco-evolutionary experience. *Ecography* **42**: 12–22.
- De Wit M, Crookes D, and Van Wilgen B. 2001. Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biol Invasions* **3**: 167–78.
- Dickie IA, St John MG, Yeates GW, *et al.* 2014. Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB Plants* **6**: plu056.
- Edwards P, Stahlmann-Brown P, and Thomas S. 2020. Pernicious pests and public perceptions: wilding conifers in Aotearoa New Zealand. *Land Use Policy* **97**: 104759.
- Evison D. 2017. The New Zealand forestry sector's experience in providing carbon sequestration services under the New Zealand Emissions Trading Scheme, 2008 to 2012. *Forest Policy Econ* **75**: 89–94.
- Farley K, Kelly E, and Hofstede R. 2004. Soil organic carbon and water retention following conversion of grasslands to pine plantations in the Ecuadorian Andes. *Ecosystems* **7**: 729–39.
- Farley KA, Jobbagy EG, and Jackson RB. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. *Glob Change Biol* **11**: 1565–76.
- Froude VA. 2011. Wilding conifers in New Zealand: status report. Bay of Islands, New Zealand: Pacific Eco-Logic Ltd.
- Griscom BW, Adams J, Ellis PW, *et al.* 2017. Natural climate solutions. *P Natl Acad Sci USA* **114**: 11645–50.
- Holl KD and Brancalion HS. 2020. Tree planting is not a simple solution. *Science* **368**: 580–81.
- Houghton R. 2007. Balancing the global carbon budget. *Annu Rev Earth Pl Sc* **35**: 313–47.
- Hulme PE. 2020. Plant invasions in New Zealand: global lessons in prevention, eradication and control. *Biol Invasions* **22**: 1539–62.
- IPCC (Intergovernmental Panel on Climate Change). 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- Jackson RB, Banner JL, Jobbagy EG, *et al.* 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**: 623–26.
- Jackson RB, Jobbagy EG, Avissar R, *et al.* 2005. Trading water for carbon with biological sequestration. *Science* **310**: 1944–47.
- Jolly WM, Cochrane MA, Freeborn PH, *et al.* 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat Commun* **6**: 7537.
- Kreidenweis U, Humpenöder F, Stevanović M, *et al.* 2016. Afforestation to mitigate climate change: impacts on food prices under consideration of albedo effects. *Environ Res Lett* **11**: 085001.
- Kull CA, Kueffer C, Richardson DM, *et al.* 2018. Using the “regime shift” concept in addressing social–ecological change. *Geogr Res* **56**: 26–41.
- Le Maitre DC, Gaertner M, Marchante E, *et al.* 2011. Impacts of invasive Australian acacias: implications for management and restoration. *Divers Distrib* **17**: 1015–29.
- Le Maitre DC, van Wilgen BW, Chapman RA, and McKelly DH. 1996. Invasive plants and water resources in the Western Cape province, South Africa: modeling the consequences of a lack of management. *J Appl Ecol* **33**: 161–72.
- Le Maitre DC, Versfeld DB, and Chapman RA. 2000. The impact of invading alien plants on surface water resources in South Africa: a preliminary assessment. *Water SA* **26**: 397–408.
- Ledgard N. 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl) in New Zealand. *Forest Ecol Manag* **141**: 43–57.
- Liang S. 2001. Narrowband to broadband conversions of land surface albedo I: algorithms. *Remote Sens Environ* **76**: 213–38.
- Liao C, Peng R, Luo Y, *et al.* 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* **177**: 706–14.
- MacDougall AS and Turkington R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**: 42–55.
- Mandle L, Bufford JL, Schmidt IB, and Daehler CC. 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biol Invasions* **13**: 1815–27.
- Mason NWH, Palmer DJ, Vetrova V, *et al.* 2017. Accentuating the positive while eliminating the negative of alien tree invasions: a multiple ecosystem services approach to prioritising control efforts. *Biol Invasions* **19**: 1181–95.
- Núñez MA, Chiuffo MC, Torres A, *et al.* 2017. Ecology and management of invasive Pinaceae around the world: progress and challenges. *Biol Invasions* **19**: 3099–120.
- Núñez MA, Kuebbing S, Dimarco RD, and Simberloff D. 2012. Invasive species: to eat or not to eat, that is the question. *Conserv Lett* **5**: 334–41.
- NZMPI (New Zealand Ministry for Primary Industry). 2019. Situation and outlook for primary industries: June 2019. Wellington, New Zealand: NZMPI.
- Panetta FD. 2012. Evaluating the performance of weed containment programmes. *Divers Distrib* **18**: 1024–32.
- Paritsis J, Landesmann JB, Kitzberger T, *et al.* 2018. Pine plantations and invasion alter fuel structure and potential fire behavior in a Patagonian forest–steppe ecotone. *Forests* **9**: 117.
- Parker JD, Torchin ME, Hufbauer RA, *et al.* 2013. Do invasive species perform better in their new ranges? *Ecology* **94**: 985–94.
- Pejchar L and Mooney HA. 2009. Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* **24**: 497–504.
- Pyšek P, Jarošík V, Hulme PE, *et al.* 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Change Biol* **18**: 1725–37.
- Ratajczak Z, Nippert JB, Briggs JM, and Blair JM. 2014. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the central Great Plains of North America. *J Ecol* **102**: 1374–85.
- Reinhardt E. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. Presentation at the Second International Wildland Fire Ecology and Fire Management Congress; 16–20 Nov 2003; Orlando, FL. Boston, MA: American Meteorological Society.

- Richardson DM, Hellmann JJ, McLachlan JS, et al. 2009. Multidimensional evaluation of managed relocation. *P Natl Acad Sci USA* **106**: 9721–24.
- Richardson DM, Hui C, Nuñez MA, and Pauchard A. 2014. Tree invasions: patterns, processes, challenges and opportunities. *Biol Invasions* **16**: 473–81.
- Richardson DM and Rejmánek M. 2004. Conifers as invasive aliens: a global survey and predictive framework. *Divers Distrib* **10**: 321–31.
- Rodrigues-Corrêa KCDS, de Lima JC, and Fett-Neto AG. 2012. Pine oleoresin: tapping green chemicals, biofuels, food protection, and carbon sequestration from multipurpose trees. *Food and Energy Security* **1**: 81–93.
- Rundel PW, Dickie IA, and Richardson DM. 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biol Invasions* **16**: 663–75.
- Sapsford SJ, Brandt AJ, Davis KT, et al. 2020. Towards a framework for understanding the context-dependencies of the impacts of non-native tree species. *Funct Ecol* **34**: 944–55.
- Schaeffer M, Eickhout B, Hoogwijk M, et al. 2006. CO₂ and albedo climate impacts of extratropical carbon and biomass plantations. *Global Biogeochem Cy* **20**: GB2020.
- Schwartz MH, Hellmann JJ, McLachlan JM, et al. 2012. Integrating the scientific, regulatory and ethical challenges posed by managed relocation. *BioScience* **62**: 732–43.
- Shackleton RT, Biggs R, Richardson DM, and Larson BMH. 2018. Social–ecological drivers and impacts of invasion-related regime shifts: consequences for ecosystem services and human wellbeing. *Environ Sci Policy* **89**: 300–14.
- Simberloff D, Souza L, Nuñez MA, et al. 2011. The natives are restless, but not often and mostly when disturbed. *Ecology* **93**: 598–607.
- Souza-Alonso P, Rodríguez J, González L, and Lorenzo P. 2017. Here to stay. Recent advances and perspectives about *Acacia* invasion in Mediterranean areas. *Ann For Sci* **74**: 55.
- Stevens JT and Beckage B. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytol* **184**: 365–75.
- Strayer DL, Eviner VT, Jeschke JM, and Pace ML. 2006. Understanding the long-term effects of species invasions. *Trends Ecol Evol* **21**: 645–51.
- Taylor KT, Maxwell BD, McWethy DB, et al. 2017. *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. *Ecology* **98**: 678–87.
- Taylor KT, Maxwell BD, Pauchard A, et al. 2016a. Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. *Global Ecol Biogeogr* **25**: 96–106.
- Taylor KT, Maxwell BD, Pauchard A, et al. 2016b. Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Divers Distrib* **22**: 578–88.
- Te Uru Rākau. 2018. The One Billion Trees Programme: our future, our billion trees. Wellington, New Zealand: Ministry of Primary Industry.
- van Wilgen BW and Richardson DM. 2012. Three centuries of managing introduced conifers in South Africa: benefits, impacts, changing perceptions and conflict resolution. *J Environ Manage* **106**: 56–68.
- Waller LP, Allen WJ, Barratt BIP, et al. 2020. Biotic interactions drive ecosystem responses to exotic plant invaders. *Science* **368**: 967–72.
- Wardle DA and Peltzer DA. 2017. Impacts of invasive biota in forest ecosystems from an aboveground–belowground context. *Biol Invasions* **19**: 3301–16.
- Wielicki BA, Wong T, Loeb N, et al. 2005. Changes in Earth's albedo measured by satellite. *Science* **308**: 825.

⁸Laboratorio de Invasiones Biológicas, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile; ⁹Institute of Ecology and Biodiversity, Santiago, Chile