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Opportunities and limitations of thinning to increase resistance and resilience of trees and forests to global change

Guillaume Moreau[1,2], Catherine Chagnon[1], Alexis Achim[1], John Caspersen[2], Loïc D'Orangeville[3], Martina Sánchez-Pinillos[3,4] and Nelson Thiffault[5,*]

[1]*Département des sciences du bois et de la forêt, Université Laval, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada*
[2]*Daniels Institute of Forestry and Conservation, University of Toronto, 33 Willcocks St., Toronto, ON M5S 3B3, Canada*
[3]*Faculty of Forestry and Environmental Management, University of New Brunswick, 28 Dineen Drive, Fredericton, NB E3B 5A3, Canada*
[4]*Centre for Forest Research, Université du Québec à Montréal, Université du Québec à Montréal, P.O. Box 8888, Stn. Centre-Ville, Montreal, QC H3C 3P8, Canada*
[5]*Canadian Wood Fibre Centre, Natural Resources Canada, 1055 du P.E.P.S., P.O. Box 10380, Sainte-Foy Stn., Québec, QC G1V 4C7, Canada*

*Corresponding author. E-mail: nelson.thiffault@nrcan-rncan.gc.ca

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We reviewed recent literature to identify the positive and negative effects of thinning on both stand- and tree-level resistance and resilience to four stressors that are expected to increase in frequency and/or severity due to global change: (1) drought, (2) fire, (3) insects and pathogens, and (4) wind. There is strong evidence that thinning, particularly heavy thinning, reduces the impact of drought and also the risk and severity of fire when harvest slash is burned or removed. Thinning also increases the growth and vigor of residual trees, making them less susceptible to eruptive insects and pathogens, while targeted removal of host species, susceptible individuals and infected trees can slow the spread of outbreaks. However, the evidence that thinning has consistent positive effects is limited to a few insects and pathogens, and negative effects on root rot infection severity were also reported. At this point, our review reveals insufficient evidence from rigorous experiments to draw general conclusions. Although thinning initially increases the risk of windthrow, there is good evidence that thinning young stands reduces the long-term risk by promoting the development of structural roots and favouring the acclimation of trees to high wind loads. While our review suggests that thinning should not be promoted as a tool that will universally increase the resistance and resilience of forests, current evidence suggests that thinning could still be an effective tool to reduce forest vulnerability to several stressors, creating a window of opportunity to implement longer term adaptive management strategies such as assisted migration. We highlight knowledge gaps that should be targeted by future research to assess the potential contribution of thinning to adaptive forest management. One of these gaps is that studies from boreal and tropical regions are drastically underrepresented, with almost no studies conducted in Asia and the southern hemisphere. Empirical evidence from these regions is urgently needed to allow broader-scale conclusions.

Introduction

In addition to anthropogenic disturbances, forest ecosystems are shaped by abiotic stressors such as drought, fire and wind, as well as biotic stressors such as insects, and pathogens. While natural disturbances help maintain the natural equilibria of forests by creating heterogeneous landscapes and promoting species diversity (Thom and Seidl, 2016; Buma and Schultz, 2020), global change is accelerating many of these disturbances and threatening the provision of forest ecosystem services (Millar and Stephenson, 2015; Trumbore *et al.,* 2015; Wingfield *et al.,* 2015; Anderegg *et al.,* 2020). An increase in the frequency and severity of droughts has accelerated tree mortality in many regions of the world, resulting in broad-scale forest die-off (Dai, 2012; Allen *et al.,* 2015). Climate and land-use changes are altering fire regimes in many forest ecosystems, leading to a generalized increase in the frequency and severity of wildfires and of burned area (Hood and Kimberley, 2009; Andela *et al.,* 2017; Príncipe *et al.,* 2017; Piqué and Domènech, 2018). Recent research also suggests that wind damage will increase in many forest ecosystems due to increases in the frequency and severity of windstorms, as well as shifts in storm tracks towards forests that are not adapted to strong winds (Bengtsson *et al.,* 2006; Kamimura *et al.,* 2017). Global warming is also amplifying the outbreaks of eruptive insects and pathogens and allowing them to extend their ranges into forests poorly adapted to them (Battisti *et al.,* 2005; Robinet and Roques, 2010; Klapwijk *et al.,* 2012; Wingfield *et al.,* 2017).

Positive feedback between stressors often compounds the impact of multiple disturbances. Examples of interactions

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between drought, fire, wind, and eruptive insects are numerous and diverse. For example, drought conditions reduce tree vigour, which in turn increases the vulnerability of trees to invasive insect outbreaks (Scheller *et al.*, 2018). Drought-induced mortality is also known to increase the risks of severe fire by increasing the accumulation of dry and dead fuels (Jactel *et al.*, 2009). Similarly, wind damage can increase fire risks (Woodall and Nagel, 2007) and trigger severe insect outbreaks by providing suitable breeding environments (Stadelmann *et al.*, 2013; Kärvemo *et al.*, 2014). Conversely, stand degradation by severe fires may subsequently exacerbate wind damage in tropical forests (Silvério *et al.*, 2019).

Many uncertainties exist when predicting the influence of climate change on forest ecosystems, ranging from the future extent of climate change to the geographical and temporal variability of expected impacts. In this context, most adaptation models for ecosystem management advise for applying a portfolio of choices (Aplet and McKinley, 2017; Dudney *et al.*, 2018; Royer-Tardif *et al.*, 2021). Notably, the intensification and interaction of disturbances call for the development of forest management strategies that increase resistance (the ability to resist change; Millar *et al.*, 2007) and resilience (the ability to both accommodate change and return to prior conditions; Millar *et al.*, 2007) to multiple stressors, with a focus on finding opportunities to manage them as one global threat (Jactel *et al.*, 2017; Scheller *et al.*, 2018; Roberts *et al.*, 2020). One such strategy is thinning, which is commonly used to control the density, structure and species composition of stands. By removing a portion of the wood volume, and pre-empting natural mortality (Curtis *et al.*, 1997; Zeide, 2001; Thiffault *et al.*, 2021), thinning alters the competitive environment of the stand and redistributes access to site resources (light, nutrients and water) among the residual trees (Bréda *et al.*, 1995; Medhurst *et al.*, 2002; Moreau *et al.*, 2020). In terms of wood production, the objectives of thinning are diverse but may be summarized as maintaining stand yield while improving the growth and vigour of individual stems, which can increase the value of processed products at maturity and/or reduce rotation age. Thinning can be carried out in different ways that have been described in detail in silvicultural textbooks (Daniel *et al.*, 1979; Smith *et al.*, 1997; Nyland *et al.*, 2016). Based on these descriptions and on the thinning types mentioned in the studies included in this review, we may broadly classify thinning as follows: thinning from above (high thinning) removes the largest trees in the diameter distribution; thinning from below (low thinning) removes the smallest trees in the diameter distribution; and sanitation thinning (improvement thinning) in which the objective is to remove trees affected by insects and diseases and/or defects to improve both the vigour and timber quality of the residual stand. Selective thinning (crown thinning, crop tree thinning, which removes the strongest competitors of the dominant crop trees) and systematic thinning (or row thinning, consists of removing whole rows of trees, without specifically favouring large or small trees) have also been defined in textbooks but were not mentioned in any of the studies included in this review. It is also recognized that high, low, and selective thinnings can be combined with systematic thinning; this allows cost savings associated with systematic thinning to be combined with the selection for vigorous trees with good form.

In addition to achieving production objectives, thinning has also been reported to reduce the negative impacts of drought, as stand density reduction can increase water availability to residual trees (Sohn *et al.*, 2016). By removing trees likely to suffer from competition-induced mortality, thinning treatments may also reduce fuel accumulation rate and reduce fire hazard (Kalies and Yocom Kent, 2016). In stands affected by organisms with invasive behaviour, thinning may increase the growth rate and vigour of residual trees, thereby limiting losses of productivity and increasing resilience (Hood and Sala, 2016). However, thinned stands may also be more susceptible to root rot infections (Piri and Korhonen, 2008; Hood and Kimberley, 2009), some defoliator insects (Fajvan *et al.*, 2008) or wind damage (Gardiner *et al.*, 2013). These findings suggest the existence of potential trade-offs, whereby the reduction of risk from one stressor may increase vulnerability to another stressor. Despite this, recent reviews on adaptive management options have mainly focused on a single stressor (e.g. Sohn *et al.* (2016) for drought; Kalies and Yocom Kent (2016) for fire hazard; Roberts *et al.* (2020) for invasive organisms and Gardiner (2021) for wind risks). Consequently, it is difficult to draw general conclusions from the literature about the potential of thinning to increase the overall resistance and resilience of forests to global change.

In this study, our objective was to review recent research on the efficacy and limitations of thinning as a means of increasing resistance and resilience to multiple stressors, with a view to facilitating the adaptation of forests to global change. We aimed to identify publications that directly assessed the positive or negative effects of thinning on both stand- and tree-level resistance and resilience to four main stressors that are expected to increase in frequency and/or severity in a near future. This process highlighted both recent progress and gaps in current knowledge that should be targeted by future research to assess the potential of thinning to enable existing stands to better persist under global change, in support of the broader effort to develop adaptive forest management practices.

Methods

We have structured our review around the following four main stressors: (1) drought, (2) fire, (3) insects and pathogens, and (4) wind. Because our work aimed to bring up-to-date information on the topic by emphasizing interesting and important new findings, we mainly concentrated our research on the recent literature published in the last decade. Major and pioneering works published before 2010 were also included in the review to provide a longer term perspective to our synthesis. To be included in this review, studies had to meet the following criteria: (1) they permitted a comparison between thinned and un-thinned stands (included a control treatment); and (2) the effects of thinning on forest resistance and/or resilience was directly assessed through quantitative indices, such as growth indices and mortality rate, damage severity and frequency, or vulnerability indices. Results from empirical studies carried out under field conditions and for which stressors had taken place during the study period were prioritized and considered as providing the strongest evidence. In accordance with these criteria, we used the following keywords to identify relevant peer-reviewed literature: 'thinning' + 'resistance' and/or 'resilience' + each of the main stressors. Our research was complemented by a combination of additional relevant keywords specific to each stressor of interest, such as ‘growth’, ‘mortality’ and ‘water use efficiency’ for drought, ‘severity’, ‘damage’, ‘risk’ and ‘hazard’ for fire and wind, and ‘infestation’ for insects and pathogens. Google Scholar was used as our main search engine and Web of Science (Clarivate, London, UK) was also used to check and complement our literature research. Once the queries were completed, an initial check of the title and abstract of several hundred papers allowed us to exclude irrelevant studies. Overall, we identified about 100 recent publications that directly assessed the positive or negative effects of thinning on both stand- and tree-level resistance and resilience to the four stressors of interest.

Results

Drought

There is considerable evidence that reducing stand density by thinning is effective at increasing growth and reducing mortality under drought conditions (Table 1). Positive effects have been observed in a wide range of biomes (Figure 1): for example in temperate (Wang *et al.,* 2019), subtropical (Bottero *et al.,* 2017a; Navarro-Cerrillo *et al.,* 2019) and tropical (Sinacore *et al.,* 2019); in xeric and hydric sites (Elkin *et al.,* 2015; Trouvé *et al.,* 2017; van Mantgem *et al.,* 2020); in different stand structures (Jones *et al.,* 2019), with trees of different sizes (Calev *et al.,* 2016; Trouvé *et al.,* 2017; Vernon *et al.,* 2018; Wang *et al.,* 2019); and in a wide range of stand compositions (Dănescu *et al.,* 2018), with broadleaf and coniferous species varying in shade tolerance (Sohn *et al.,* 2016; Wang *et al.,* 2019; Low *et al.,* 2021). Overall, the positive effects increase with thinning intensity, with heavy thinning (removing more than 40 per cent of basal area (BA)) being most effective (Calev *et al.,* 2016; Sohn *et al.,* 2016; Aldea *et al.,* 2017; Trouvé *et al.,* 2017; Cabon *et al.,* 2018; Navarro-Cerrillo *et al.,* 2019; Steckel *et al.,* 2020; Zamora-Pereira *et al.,* 2021). In some cases, removing less than 30 per cent of BA appears to have no measurable effect on the response of trees to drought (Cabon *et al.,* 2018; Bello *et al.,* 2019).

The positive effects of a single thinning treatment tend to decrease over time, becoming negligible within 20–40 years (Elkin *et al.,* 2015; Ameztegui *et al.,* 2017; Cabon *et al.,* 2018). At these time scales, initially positive effects can even be reversed as stands mature, resulting in higher vulnerability for thinned stands (D’Amato *et al.,* 2013; Mausolf *et al.,* 2018; Bottero *et al.,* 2021). Such a reversal of effect has been attributed to long-term responses of crown architecture to thinning, resulting in higher leaf/sapwood area ratios for trees released from competition (D’Amato *et al.,* 2013; Mausolf *et al.,* 2018). Higher leaf area in larger trees often results in increased water demand, which can increase the vulnerability of the released trees to later drought events (D’Amato *et al.,* 2013; Mausolf *et al.,* 2018; Bottero *et al.,* 2021). These results are in line with those of Seidl *et al.* (2017) and Sohn *et al.* (2016) that reported a general decreasing benefit of thinning with increasing stand age.

While numerous studies have shown that thinning was effective at reducing the short-term impacts of drought, the factors and processes responsible for its success remain unclear and are often contradictory among recent studies. At the regional scale, studies from boreal and tropical regions were drastically underrepresented in the recent literature (Sohn *et al.,* 2016). This is particularly true for tropical regions, where density reduction through thinning showed only weak effects on forest resistance and resilience (Shenkin *et al.,* 2018; Sinacore *et al.,* 2019). Thus, the lack of studies prevents us from reaching any general conclusion on the potential effect of thinning on the response of tropical forests to drought.

At the site scale, aridity due to soil water availability or microtopography was commonly examined as a factor contributing to the resistance and resilience to drought (e.g. Sohn *et al.,* 2016; Ameztegui *et al.,* 2017; Diaconu *et al.,* 2017). While several studies have described a decreasing positive effect of thinning with increasing site aridity (Elkin *et al.,* 2015; Ruzicka Jr. *et al.,* 2017; Restaino *et al.,* 2019), others found the inverse relationship (Ameztegui *et al.,* 2017; Diaconu *et al.,* 2017; Trouvé *et al.,* 2017; Steckel *et al.,* 2020). Here, two processes appear to be involved: on the one hand, species that are currently near their physiological limits on dry sites may be highly vulnerable to increasing water limitations, and thinning may not be sufficient to enhance their resistance and resilience during severe droughts (Elkin *et al.,* 2015); on the other hand, individual acclimation and cross-generation adaptation of trees to water limitations may imply that trees growing in drier conditions are less vulnerable to severe drought events, which allows them to respond positively to reduced neighbourhood competition (Trouvé *et al.,* 2017). Again, further research is needed to clarify the mechanisms involved in the response of the residual trees to thinning when affected by drought (Trouvé *et al.,* 2017).

At the stand scale, density reduction proved to be effective at mitigating drought impacts on growth, but very few studies have looked at how changes in structural and species diversity created by different thinning methods influence forest growth responses to drought (Dănescu *et al.,* 2018; Jones *et al.,* 2019; Comeau, 2021). While increasing structural diversity through thinning was related to an increasing stand resistance and resilience in a red pine (*Pinus resinosa* Ait.) monoculture (Jones *et al.,* 2019), the effect of both structural and species diversity was weak and inconclusive in both mixed *Picea-Abies* stands (Dănescu *et al.,* 2018) and mixed *Quercus-Pinus* stands (Bello *et al.,* 2019). Indeed, thinning offers the opportunity to shift species composition of mixed stands towards more drought-adapted species to improve overall stand resistance and resilience. However, more results from experimental studies are needed to confirm the benefits of such approaches.

At the tree scale, growth responses to drought following thinning appear to be largely species-specific (Sohn *et al.,* 2016; Aldea *et al.,* 2017; Cardil *et al.,* 2018; Vernon *et al.,* 2018; Steckel *et al.,* 2020). A meta-analysis has concluded that the adaptation potential of thinning differs between conifers and broadleaves, where thinning enhances the resistance of broadleaves and the resilience of conifers (Sohn *et al.,* 2016). Since then, recent studies tend to suggest that thinning may or may not increase the resistance and the resilience of both conifers and broadleaves (e.g. Aldea *et al.,* 2017; Diaconu *et al.,* 2017; Lechuga *et al.,* 2017; Cardil *et al.,* 2018; Dănescu *et al.,* 2018; Ogaya *et al.,* 2019; Steckel *et al.,* 2020; van Mantgem *et al.,* 2020) and that the magnitude of the effect might be partly explained by the species-specific sensitivity to local climate, in such way that higher climate sensitivity increases the potential to reduce drought susceptibility

Table 1 Summary of the effect of thinning on tree responses to drought events or low soil water availability. The effect is reported as growth resistance (R_T; growth response during the event), growth resilience (R_L; ratio of the growth before and after the event), water use efficiency (WUE; evaluated through stable carbon isotope (δ13C) or sap flow), mortality (M) and general long-term effect (>20 years since thinning).

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Short-term effect				Long-term effect	Remarks
					R_T	R_L	WUE	M		
*Sohn *et al.* (2016)	Temperate; subtropical (mostly Europe and North America)	Several conifers and broadleaves	Commercial (1–5)	0; <40; >40	+	+				Increased resistance for broadleaves, resilience for conifers
Wang *et al.* (2019)	Temperate (British Columbia, Canada)	*Pinus contorta*	Precommercial (1)	0; 85; 95	+		+			
Bottero *et al.* (2017b)	Temperate and subtropical (Minnesota, South Dakota, Arizona, USA)	*P. ponderosa; P. resinosa*	Commercial (3–5)	0–80	+	+				
Navarro-Cerrillo *et al.* (2019)	Subtropical (southern Spain)	*P. nigra; P. sylvestris*	Commercial - below (1)	0; 30; 60	+	+	0			Increased growth recovery
Sinacore *et al.* (2019)	Tropical (Panama)	*Tectona grandis*	Commercial (1)	0; 50	0		+			
Elkin *et al.* (2015)	Temperate (Switzerland)	Several conifers and broadleaves	Commercial (3)	0; 20; 55; 75				–	0	Site-specific effect
**van Mantgem *et al.* (2020)	Subtropical (mostly Arizona, USA)	Mostly *P. ponderosa*	Thinning or thinning and burning (1–6)		+	+				Species- and site-specific responses
Jones *et al.* (2019)	Temperate (northern Minnesota, USA)	*P. resinosa*	Commercial - above and below (6)	0; 30–40	+	+				Only for above treatment
Calev *et al.* (2016)	Mediterranean (Israel)	*P. halepensis*	Precommercial (2) + commercial (1)	0; 45; 80	+			–		Reduced drought stress
Vernon *et al.* (2018)	Temperate (northern California, USA)	*Pseudotsuga menziesii; P. ponderosa*	Commercial - below (1)	0; 30	+					
Dănescu *et al.* (2018)	Temperate (southwestern Germany)	*Abies alba; Picea abies*	Commercial (multiple)	Variable	+	+				
Low *et al.* (2021)	Temperate (California)	*A. magnifica; A. concolor; Calocedrus decurrens; P. contorta; P. jeffreyii; P. lambertiana*	Commercial - below (1)	10–70	+			–		

(Continued)

Table 1 Continued

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Short-term effect				Long-term effect	Remarks
					R_T	R_L	WUE	M		
Aldea *et al.* (2017)	Temperate (Spain)	*Quercus-Pinus* mixed stands	Commercial - below (1)	0; 25; 40	+					
Cabon *et al.* (2018)	Mediterranean (southern France)	*Quercus ilex*	Commercial - below (1)	0; 25; 45; 60; 80	+					Through a delayed drought-induced growth cessation
Steckel *et al.* (2020)	Temperate (Germany); Temperate (Arizona, USA)	*P. sylvestris; Q. petrae; P. ponderosa*		Three stand densities	+	+				Increased recovery
Bello *et al.* (2019)	Temperate (France)	*Q. petrae; P. sylvestris*	Commercial (1)	0; 40; 70	0/+					Species-specific; only for *Q. petrae*
Ameztegui *et al.* (2017)	Mediterranean (northeastern Spain)	*P. sylvestris*	Commercial - below (1)	0–70	+				0	Reduced drought stress; tested with different soil water availability
D'Amato *et al.* (2013)	Temperate (Minnesota, USA)	*P. resinosa*	Commercial - above, below and proportional (7)	0–90	+	+			–	
Mausolf *et al.* (2018)	Temperate (northwestern Germany)	*Fagus sylvatica*	Commercial	0; 40	–				–	
Shenkin *et al.* (2018)	Tropical (Bolivia)	Semi-deciduous forest	Commercial (1)	0–10				0/–		Depending on tree height
Diaconu *et al.* (2017)	Temperate (southwestern Germany)	*F. sylvatica*	Commercial (1)	0; 30–40; 60	+	+				No effect on growth recovery
Restaino *et al.* (2019)	Temperate (California, USA)	*A. magnifica; C. decurrens; A. concolor; P. menziesii; Q. kelloggii*	Commercial - below and burning (multiple)	Variable				0/–		Species-specific; especially for *P. ponderosa*

(Continued)

Table 1 Continued

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Short-term effect				Long-term effect	Remarks
					R_T	R_L	WUE	M		
Ruzicka Jr. *et al.* (2017)	Temperate (Oregon, USA)	*P. menziesii*	Commercial - below (1)	0; two thinning intensities	+		+			Tested with different soil water availability
Cardil *et al.* (2018)	Temperate (Spain)	*P. sylvestris* *F. sylvatica*	Commercial (2)	0; 20; 30–40	+					Greater effects for *F. sylvatica*
Ogaya *et al.* (2019)	Mediterranean (northeastern Spain)	*Q. ilex; Phillyrea latifolia; Arbutus unedo*	Commercial (1)	0; 20	+			–		Only for *Q. ilex*
Lechuga *et al.* (2017)	Mediterranean (southern Spain)	*A. pinsapo*	Commercial (1)	0; 50			+			
Comeau (2021)	Boreal (Canada)	*Populus tremuloides; P. glauca*	Pre-commercial (2)	Variable	+	+			+	Only for *P. glauca*
Bottero *et al.* (2021)	Temperate (southwest Germany)	*A. alba; P. abies*	Commercial	0; 25	+	+			–	Positive effect during mild drought, but negative effect during severe drought
Zamora-Pereira *et al.* (2021)	Temperate (southwest Germany)	*P. abies; A. alba; F. sylvatica*	Commercial	0; 50		+				
Bosela *et al.* (2021)	Temperate (Slovakia)	*F. sylvatica*	Commercial	Variable					0	Thinning did not impact long-term climate sensitivity in beech
Knapp *et al.* (2021)	Mediterranean (California, USA)	*A. concolor; P. lambertiana; C. decurrens; P. ponderosa; P. jeffreyi*	Commercial	0; 75	+			+		

Resistance and resilience are used as described by Millar *et al.* (2007). Positive and negative effects are indicated by + and –, respectively; 0 indicates no effect; empty cells represent non-available data. Authors of meta-analyses and reviews are marked with * and **, respectively.

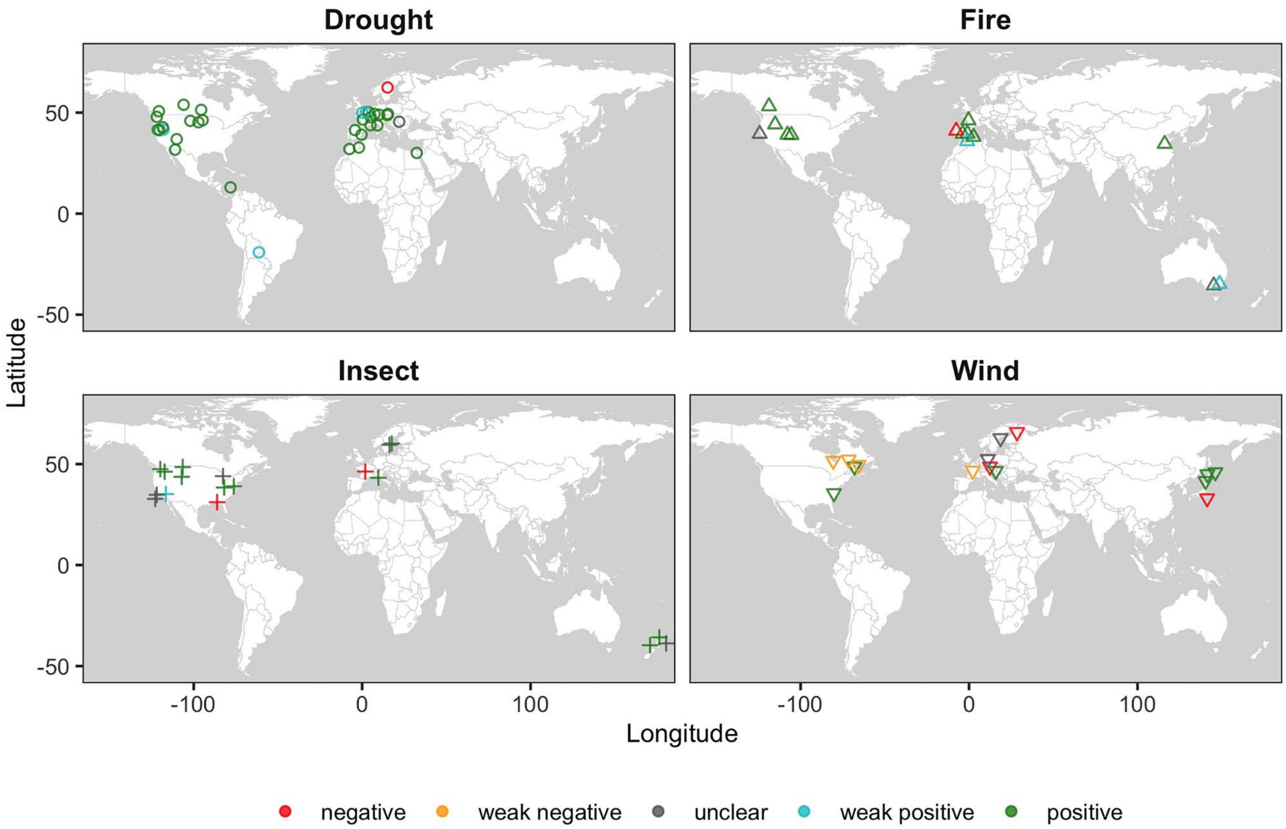

Figure 1 Effect of thinning on the response of forest stands to different stressors. See Tables 1–4 for detailed information for each study. Weak negative and positive effects refer to no effect to negative response (0/− in the Tables) or no effect to positive response (0/+), while unclear responses refer to null (0) or inconclusive effect (+/−). Reviews and meta-analyses with broad geographical extent are not included in the maps.

(Steckel *et al.,* 2020). A better understanding of the physiological process responsible for species-specific adaptive potential following thinning should be a research priority in the near future. Lastly, due to the scarcity of long-term monitoring of thinning experiments, the potential reversal from positive to negative as stands age remains insufficiently documented, and the factors responsible for this reversal effect are poorly understood. Because of the important management implication of such reversal effects, additional monitoring of drought vulnerability over long-periods following thinning is urgently needed.

Fire

There is strong evidence that thinning reduces the risk and severity of fire when harvest slash is burned or removed and also that thinning is also effective even if harvest slash is left in place (Table 2). These positive effects increase with the intensity of thinning (Collins *et al.,* 2014; Palmero-Iniesta *et al.,* 2017; Hevia *et al.,* 2018; Tardós *et al.,* 2019), and particularly, when it is applied to suppressed and subdominant individuals (i.e. thinning from below rather than thinning from above) (Collins *et al.,* 2014). Overall, in the long-term, thinning reduces the risk and severity of fire by reducing fuel loads and disrupting fuel continuity in the stand (Safford *et al.,* 2012; Prichard and Kennedy, 2014; Thomas and Waring, 2015). In contrast, the accumulation of harvest slash and the quick colonization by shade-intolerant species may increase surface fuels and, therefore, the risk and severity of fire in the short-term (Kalies and Yocom Kent, 2016; Madrigal *et al.,* 2017; Arellano-Pérez *et al.,* 2020; Banerjee, 2020; Taylor *et al.,* 2021). Thus, harvest slash is often burned or removed, and thinning is generally considered to be most effective when combined with short-term fuel treatments (Safford *et al.,* 2012; Collins *et al.,* 2014; Kalies and Yocom Kent, 2016; Piqué and Domènech, 2018; Volkova and Weston, 2019; Stoddard *et al.,* 2021). The benefits of thinning to promote forest resistance to fire have been documented in a large amount of recent research and corroborated by previous syntheses (e.g. Martinson and Omi, 2013; Collins *et al.,* 2014; Kalies and Yocom Kent, 2016). Studies are, however, restricted to temperate and subtropical biomes (Figure 1). Besides the direct effects on stand structure, thinning can be used to promote the abundance of fire-resistant species, which improves the magnitude and longevity of the treatment effects (Jain *et al.,* 2020). Moreover, treatments appear to be more effective in coniferous than broadleaved forests, which is mostly explained by the difference in fuel accumulation rates (Martinson and Omi, 2013; Kalies and Yocom Kent, 2016). Indeed, a key factor determining the duration of the effect is the fuel decomposition and accumulation rates in the years following treatment, which is directly related to forest productivity and local climate (Barnett *et al.,* 2016; Palmero-Iniesta *et al.,* 2017).

Generally, treatment effects only last 20–30 years, even in conifer forests composed of fire-resistant species (Barnett *et al.,* 2016; Jain *et al.,* 2020).

While recent simulation-based studies provide important insights into the potential effect of fuel treatment on fire behaviour and severity, more experimental studies are needed to confirm these results, particularly regarding the long-term effects of fuel treatments and the relationship between dead fuel dynamics and fire behaviour (Palmero-Iniesta *et al.,* 2017). Process-based models should also be designed to simulate the effect of thinning on the micrometeorological conditions that limit fire (Banerjee, 2020). It is generally recognized that canopy opening increases windflow, solar radiation, and near-surface temperature (Russell *et al.,* 2018), potentially reducing canopy fuel moisture and influencing fire behaviour (Banerjee, 2020). However, it remains poorly understood how fuel moisture is influenced by the micrometeorological changes brought on by thinning. Lastly, fuel properties and accumulation rates are directly affected by local climate, which could evolve rapidly as climate change continues to accelerate. A future research priority should be to better understand the impact of climate on fuel properties and accumulation rates following thinning. Such knowledge could constitute a first step towards improving future fire behaviour under projected climatic scenarios.

Insect and pathogen outbreaks

Thinning can mitigate the impact of insect and pathogen outbreaks (Table 3) by (1) increasing the overall diversity and evenness of species while reducing the density of host species, (2) reducing connectivity by ensuring that the residual host trees are dispersed among other species and/or separated by other barriers to spread, and (3) reducing host susceptibility by retaining vigorous trees with favourable traits and growing conditions, and maintaining genetic diversity where possible (see Figure 1 in Prospero and Cleary, 2017). Furthermore, canopy opening may allow for beneficial change in the microclimate such as increased air movement, lower humidity, and higher light penetration, all of which have been shown to reduce the development of some eruptive organisms (Ellis *et al.,* 2010; Ferchaw *et al.,* 2013; Brantley *et al.,* 2017). However, the effectiveness of these approaches remains mostly theoretical, as they have not been sufficiently tested to draw solid conclusions.

Yet, a few rigorous experiments have been conducted in recent years, showing that thinning significantly reduced the negative effects of different insect outbreaks, such as bark beetles (Stadelmann *et al.,* 2013; Hood and Sala, 2016; Negrón *et al.,* 2017; Scheller *et al.,* 2018; Steel *et al.,* 2021; Morris *et al.,* 2022), woodwasps (Dodds *et al.,* 2014) and gypsy moths (Fajvan and Gottschalk, 2012). Thinning was also effective in mitigating the spread of diseases and infections, such as the Dutch elm disease caused by the fungus *Ophiostoma ulmi* (Ganley and Bulman, 2016; Menkis *et al.,* 2016), Dothistroma needle blight caused by the fungus *Dothistroma septosporum* (Bulman *et al.,* 2013; Bulman *et al.,* 2016), western gall rust caused by the fungus *Endocronartium harknessii* (Roach *et al.,* 2015) and to improve overall forest growth of pine plantations affected by armillaria root disease caused by the fungus *Armillaria mellea* (Hood and Kimberley, 2009). However, other experiments have reported inconclusive evidence for effects on various defoliators (Fajvan *et al.,* 2008; Régolini *et al.,* 2014). More importantly, a significant effect of thinning on root rot infection severity was reported, which was mainly attributed to resulting stumps and mechanical damage on the stems and roots of residual trees (Oliva *et al.,* 2010). In the case of root rot infections, complementary stump chemical or biological treatments or direct stump removal showed great potential to reduce pathogen incidence (Oliva *et al.,* 2010).

Overall, even if recent work is scarce and provides incomplete information, there is growing evidence that thinning is a potential solution to promote forest resistance and resilience to some eruptive organisms by increasing growth rate and vigour of potential hosts (Muzika, 2017; Roberts *et al.,* 2020). Over the long-term, repeated thinning treatments may have positive legacy effects in shaping post-outbreak successional trajectories (Morris *et al.,* 2022). Current knowledge also suggests that the direct removal of infested trees through thinning may contribute to slowing spread and development in infected stands (Roberts *et al.,* 2020), although the magnitude of the effects and the processes responsible for its success are still poorly understood.

Our review of the recently published literature revealed insufficient evidence from rigorous experiments to draw general conclusions about the potential of thinning to reduce forest vulnerability to eruptive organisms. Moreover, while a few reviews have investigated the potential of thinning in that context from a worldwide perspective (Bulman *et al.,* 2016; Muzika, 2017; Roberts *et al.,* 2020), the majority have been conducted in the temperate or subtropical biomes with one exception found in the boreal forest (Figure 1; Table 3). The limited number of studies that reported a consistent positive effect of the treatment were specific to a few insects (i.e. mostly bark beetle outbreaks) or diseases (i.e. mostly red band needle blight). Because failures are often not reported in the scientific literature, general trends from such a limited number of experiments must be interpreted carefully (Six *et al.,* 2014). Further research on a wider range of insects, pathogens and hosts is needed to assess the effects of increasing host diversity, connectivity, and susceptibility on forest resilience. The life history and population dynamics of eruptive organisms vary tremendously, so the efficacy of thinning will surely vary just as much. Yet, a refined understanding of the effects of host abundance, diversity, and connectivity on eruption dynamics should help identify thresholds to be targeted by thinning, such as maintaining a given proportion of non-host or less susceptible tree species in threatened stands (Prospero and Cleary, 2017). Still, exacerbated invasions of exotic pests (insects and pathogens) driven by future climate conditions and globalization are difficult to predict and anticipate, leading to great uncertainty to define adequate management practices.

Wind

The effect of thinning on the risk of wind damage (i.e. stem breakage or tree uprooting) (Table 4) is the result of complex interactions, mostly driven by stand age, tree height, the timing of thinning and its intensity (Gardiner *et al.,* 2013). By removing a part of the canopy, thinning immediately reduces stand stability by increasing the wind load on residual trees, which in turn increases their vulnerability to wind and storm damage

Table 2 Summary of the effect of thinning treatment on fire risk (evaluated though factors enhancing fire risk, e.g. crown bulk density, canopy base height, surface fuels), fire severity (crown scorch, scorch height and volume or rate of spread), stand regeneration (Reg), stand mortality (M) and general long-term effect (>20 years since thinning).

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Short-term effect				Long-term effect	Remarks
					Risk	Severity	Reg	M		
Piqué and Domènech (2018)	Mediterranean (northeast Spain)	*P. nigra* sbsp. *Salzamanni*	Commercial and/or burning (1)	0; 25; 40–50	–					Thinning + burning was most efficient
Safford *et al.* (2012)	Mediterranean (California)	*A. concolor, C. decurrens, Juniperus californica, P. jeffreyi, lambertiana and ponderosa, Q. chrysolepis and kelloggii.*	Pre-commercial and/or burning + Commercial and/or burning	Variable		+		+		Thinning + burning was most efficient
Prichard and Kennedy (2014)	Temparate (Washington, USA)	*P. ponderosa, P. menziesii*	Commercial and/or burning			+				
**Kalies and Yocom Kent (2016)	Temperate; subtropical (western USA)	*P. ponderosa; P. jeffreyi; Pinus-Quercus* stands; *Quercus spp.*	Thinning and/or burning (1)			+/–	+	–		General positive effect most consistent for thinning + burning treatment; thinning alone may increase fire severity
Collins *et al.* (2014)	Temperate (California, USA)	Mixed conifer forests	Commercial – below – and/or burning (1)					–		Through a vulnerability index; thinning alone decreased vulnerability; thinning + burning increased vulnerability
Hevia *et al.* (2018)	Temperate (northwestern Spain)	*P. pinaster*	Precommercial and pruning (1)	0–60	–					
Palmero-Iniesta *et al.* (2017)	Mediterranean (northeast Spain)	*P. halepensis*	Commercial (1)	0; 90		–				

(Continued)

Table 2 Continued

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Short-term effect				Long-term effect	Remarks
					Risk	Severity	Reg	M		
Tardós *et al.* (2019)	Subtropical (northeast Spain)	*P. nigra* sbsp. *Salzmannii*	Commercial – below + burning or understory clearing (1)	0; 10; 50			+			Thinning + burning was most effective
Thomas and Waring (2015)	Temperate (New Mexico, USA)	*P. ponderosa*	Commercial – below – or commercial + burning (1)	0; two thinning intensities	0/−		+			Thinning + burning was most effective
Arellano-Pérez *et al.* (2020)	Temperate (northwestern Spain)	*P. pinaster; P. radiata*	Commercial (3–4)	0; 20; 40	+	+		+		
Banerjee (2020)	Temperate (USA process-based model)	*P. ponderosa*	Commercial (1)	0; 25; 50; 75		+/−				Complex non-linear response; high degree of thinning may be effective
Madrigal *et al.* (2017)	Mediterranean (eastern Spain)	*P. halepensis*	Commercial (1)		0/−	0/−				Efficient with understory cleaning
Taylor *et al.* (2021)	Temperate (southeastern Australia)	*Eucalyptus regnans; E. delegatensis*	Commercial (1)		+/−	0/+				Depending on stand type and stand age
Volkova and Weston (2019)	Temperate (southeastern Australia)	*E. sieberi*	Commercial – above – and/or burning (1)	0; 50	0/−					Thinning + burning treatment only
*Martinson and Omi (2013)	Temperate; subtropical (mostly western USA)		Canopy thinning and/or burning (1)			0/−				Thinning + burning as most efficient
Jain *et al.* (2020)	Xeric Shrubland (western USA)	Dry mixed conifer forests	Commercial – below – and improvement cut (1)		−			−	0	Effect lasted a maximum 20–30 years
Stoddard *et al.* (2021)	Xeric Shrubland (western USA)	*P. ponderosa*	Commercial	Variable	+			+		

Positive and negative effects are indicated by + and –, respectively; 0 indicates no effect; empty cells represent non available data. Authors of meta-analyses and reviews are marked with * and **, respectively.

Table 3 Summary of the effect of thinning treatment on insect and pathogens infestation levels (Inf; usually as the percentage of tree attacked), tree growth response (Growth; mainly in term of growth recovery following the infestation), stand mortality (M) and general long-term effect (>10 years since thinning).

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Insect/Pathogen	Thinning treatment (repetitions)	% BA removed	Short-term effect			Long-term effect	Remarks
						Inf	Growth	M		
Hood and Kimberley (2009)	Subtropical (New Zealand)	*P. radiata*	Armilla root disease (*Armillaria novae-zelandiae*)	Precommercial (stand age = 7 and 13.5 years) (1 or 2)	0; 70	+	+		0	
Scheller *et al.* (2018)	Temperate (California and Nevada, USA)	*P. jeffreyi; A. concolor*	Bark beetles (*Dendroctonus jeffreyi; D. ponderosae; Scolytus ventralis*)	Commercial – below – + burning (1)				0/–	0	Ineffective at the landscape-scale
Stadelmann *et al.* (2013)	Temperate (Switzerland)	*P. abies*	Bark beetle (*Ips typographus*)	Sanitation cut (1)		–				Windstorm increased risk of infestation
**Roberts *et al.* (2020)	Worldwide	Several conifers and broadleaves	Fungi and oomycetes	Commercial			+	+/–		Mostly North America (59% of papers); Europe (29%)
Hood and Sala (2016)	Temperate (Montana, USA)	*P. ponderosa; P. menziesii*	Bark beetle (*D. ponderosae*)	Commercial and/or burning (1)	0; 50–60		+	–	+	Prevent species dominance shift
Fajvan *et al.* (2008)	Temperate (Pennsylvania, USA)	*Quercus spp.*	Gypsy moth (*Lymantria dispar*)	Commercial – below (1)	0; 33; 34		0			No effect on tree growth resistance; thinning conducted in the first year of the outbreak.
Brantley *et al.* (2017)	Temperate (North Carolina, USA)	*Tsuga canadensis*	Hemlock woolly adelgid (*Adelges tsugae*)	Shade treatment: 0–90% light attenuation (1)	None	+				Shade treatment increased infestation

(Continued)

Table 3 Continued

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Insect/Pathogen	Thinning treatment (repetitions)	% BA removed	Short-term effect			Long-term effect	Remarks
						Inf	Growth	M		
Ferchaw *et al.* (2013)	Temperate (California, USA)	*P. radiata*	Pitch cancer desease (*Fusarium circinatum*)	Canopy gap and/or slash treatment (1)	Three gap sizes	+/−		0/−		On seedlings; no effect of canopy gap size alone; infestation rate increased in medium-sized gap
Negrón *et al.* (2017)	Temperate (South Dakota; Wyoming, USA)	*P. ponderosa*	Mountain pine beetle (*D. ponderosae*)	Commercial – below (1)				−		
Steel *et al.* (2021)	Mediterranean (California, USA)	*A. concolor; A. magnifica; C. decurrens; P. jeffreyi; P. lambertiana*	Bark beeltes (*D. jeffreyi; D. ponderosae; D. valens; S. ventralis*)	Commercial – below and above – and commercial + burning (1)	0; two thinning intensities	+/−		0/−		Burning increased beetle infestation probability and mortality; species- and size-specific
Dodds *et al.* (2014)	Temperate (NY, USA)	*P. resinosa, P. strobus and P. sylvestris*	Woodwasp (*Sirex noctilio*)	Sanitation/non-commercial (1)	0; 20–40; 30–60	−	0			
Fajvan and Gottschalk (2012)	Temperate (Pennsylvania, USA)	*Quercus spp.*	Gypsy moth (*L. dispar*)	Commercial – below (1)	0; 33–34		+	0		
**Ganley and Bulman (2016)	Subtropical (New Zealand)	*Ulmus* spp.	Dutch elm disease (*Ophiostoma novo-ulmi*)	Sanitation cut (1)		−		−		
Menkis *et al.* (2016)	Temperate (Sweden)	*Ulmus minor*	Dutch elm disease (*Ophiostoma* spp.)	Sanitation cut + herbicide (1)		−				Effect of sanitation cut alone not investigated; always combined with herbicide
**Bulman *et al.* (2016)	Worldwide		Dothistroma needle blight (*D. septosporu; D. pini*)			−		−	0	Effect weakening over time

(Continued)

Table 3 Continued

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Insect/Pathogen	Thinning treatment (repetitions)	% BA removed	Short-term effect			Long-term effect	Remarks
						Inf	Growth	M		
Bulman *et al.* (2013)	Subtropical (New Zealand)	*P. radiata*	Dothistroma needle blight (*D. septosporu; D. pini*)	Precommercial (1)		–				
Roach *et al.* (2015)	Temperate (southeastern British Columbia, Canada)	*P. contorta var. latifolia*	Western gall rust (*Endocronartium harknessii*)	Precommercial (1)		–				Perhaps because stand criteria for thinning included low infection rates and/or damaged trees were preferentially removed
Régolini *et al.* (2014)	Temperate (France)	*P. pinaster*	Pine processionary moth (*Thaumetopoea pityocampa*)		variable stand density	+				Effect of tree size and edge
Oliva *et al.* (2010)	Boreal (Sweden)	*P. abies*	Root and butt rot (*Heterobasidion annosum*)	Commercial and commercial + stump treatment (1–2)	0; 33–50	0				Stump treatment should be applied
**Muzika (2017)	Worldwide	Mostly conifers; also broadleaves	*S. noctilio; L. diapar; Agrilus planipennis*	Commercial or precommercial (variable)		0/–	0/+			Potential positive effect of thinning on reducing pest; limited direct experimental evidence
**Six *et al.* (2014)	Temperate and Subtropical (USA)		Mountain pine beetle (*D. ponderosae*)	Commercial				0/–		Generally reduced mortality but few studies investigated the impact on thinning during an outbreak
Morris *et al.* (2022)	Temperate (USA)	*P. contorta var. latifolia; P. engelmannii; A. lasiocarpa*	Mountain pine beetle (*D. ponderosae*)	Commercial	variable stand density				+	Minimal effect on resistance, but leave persistent effects on post outbreak successional trajectories

Positive and negative effects are indicated by + and –, respectively; 0 indicates no effect; empty cells represent non available data. Authors of meta-analyses and reviews are marked with * and **, respectively.

(Gardiner *et al.,* 2013). The period of higher vulnerability is estimated to last from 2 to 10 years after thinning, before tree stems and root systems have adapted to the new wind regime and before crown growth leads to complete canopy closure (Albrecht *et al.,* 2012; Hanewinkel *et al.,* 2014; Pukkala *et al.,* 2016). The negative effect of thinning on the short-term vulnerability to wind damage increases with stand age and tree height, with heavy thinning performed in the late stages of a rotation leading to the highest increase in risk (Gardiner *et al.,* 2013; Pukkala *et al.,* 2016). In dense, mature stands composed of trees with high height-to-diameter ratios or low stem taper, even light to moderate thinning can increase the risk of storm and wind damage (Albrecht *et al.,* 2012; Albrecht *et al.,* 2015). Conversely, there is good evidence that pre-commercial and commercial thinning performed at an early stand age reduces vulnerability to wind damage by promoting the development of structural roots and more tapered stems (Achim *et al.,* 2005; Subramanian *et al.,* 2016; Kamimura *et al.,* 2017; Novák *et al.,* 2017; Torita and Masaka, 2020). In young stands, moderate to heavy thinning only slightly affects the overall risk of wind damage over a short period so that the subsequent gain in stability may ultimately lead to a reduction of stand vulnerability over the full lifetime of the stand (Gardiner *et al.,* 2013).

In recent years, research has focused on post-storm empirical studies, which have the disadvantage of being specific to a single event. Moreover, they are mostly restricted to the temperate and boreal biomes (Figure 1). To obtain a broader understanding of the underlying processes involved in this disturbance, key research efforts have been dedicated to the development of process-based models of wind and tree interactions. This allows for simulations of the impacts of different types of treatments on the risk of wind damage for different types of forests. While there are still several limitations that affect model accuracy and the capacity to extrapolate results (Byrne and Mitchell, 2013; Kamimura *et al.,* 2017; Díaz-Yáñez *et al.,* 2019; Torita and Masaka, 2020; Duperat *et al.,* 2021), these simulation-based studies have brought important insights on the critical factors related to wind damage after thinning. Among these, an improved understanding of the factors facilitating the acclimation of trees to their wind loading situation is key (Hale *et al.,* 2010; Bonnesoeur *et al.,* 2016; Dèfossez *et al.,* 2022). In general, dominant trees are known to be better acclimated to high wind loading than the more slender subdominant or oppressed stems (Kamimura *et al.,* 2008; Novák *et al.,* 2017). Thinning is therefore likely to induce a larger difference in wind loading for the residual subdominant or oppressed trees. Because of their smaller crowns, the adaptive growth response to the new conditions may also be delayed, which could have the consequence of increasing their risk of wind damage. No clear empirical evidence is available, however, to confirm such an increased risk of wind damage among the most slender residual stems immediately thinning.

Both modelling and empirical results have suggested that the presence of understory vegetation could reduce the vulnerability of wind damage in dominant trees (Lavoie *et al.,* 2012). During a windstorm, the absence of understory vegetation may increase the subcanopy windflow, which would concentrate momentum absorption in the canopy and increase the wind loading on the taller trees. Avoiding the removal of subcanopy vegetation during thinning operations may thus help mitigate the initial negative effect of the treatment on stand stability, although no empirical evidence is yet available to confirm this. Because maintaining subcanopy vegetation may also have negative consequences with respect to fire risk, such an approach should be avoided in regions where fire is also an important stressor.

Another important factor determining how thinning may affect stand risk to wind damage is its effect on species composition. Indeed, characteristics that influence resistance to wind forces such as average crown size and density, root system architecture and anchorage, wood stiffness and strength all vary among tree species (Hanewinkel *et al.,* 2014; Albrecht *et al.,* 2015; Morimoto *et al.,* 2019). In general, conifers are considered to be more vulnerable than broadleaves, but some exceptions exist (see Table 1 in Gardiner *et al.,* 2013). While thinning could be used as a tool to shift species composition of mixed stands towards more wind-adapted species to improve stand resistance and resilience, recent findings show that changes in structural and species diversity created by different thinning treatments only have a weak and marginal effect on tree damage in mixed longleaf pine-hardwoods stands (Bigelow *et al.,* 2021). Thus, further results from experimental studies are still needed to confirm the benefits of such an approach. Lastly, to a lesser extent, site-specific characteristics such as stand exposition to dominant winds and the slope of the terrain have been shown to potentially alter the relationship between thinning and the vulnerability to wind damage (Kamimura *et al.,* 2008; Hanewinkel *et al.,* 2014).

Perspectives and concluding remarks

Drawing general conclusions to best inform forest management in the face of a diversity of (and likely, increasing pressure from) future stressors is challenging. In this context, we have reviewed the recent research pertaining to the opportunities and limitations offered by stand density management through thinning—one of the most common silvicultural treatments applied worldwide—to enhance forest resistance and resilience to multiple stressors associated with global change. Climate-smart adaptive forest management should address disturbances not as independent agents of change, but rather as synergistic modifying-agents to be managed concomitantly while focusing on opportunities to achieve multiple goals (Scheller *et al.,* 2018). However, to date, studies on the effects of thinning have mostly considered either single or a small number of disturbances. Our literature survey also revealed that studies from boreal and tropical regions are drastically underrepresented, with almost no studies conducted in Asia or the southern hemisphere. Therefore, in many regions, forest managers lack strong evidence to identify practices that will promote forest resilience against multiple expected and unexpected threats in the future (Roberts *et al.,* 2020).

For temperate, mediterranean, and subtropical ecosystems, our work revealed strong evidence that thinning may promote forest resistance and resilience to multiple individual disturbances by altering forest structure to favour the growth and vigour of the residual trees and promoting the abundance of species well adapted to future perturbations (Table 5). More particularly, heavy thinning (removing more than 40 per cent of BA) can be effective at mitigating the impact of drought

Table 4 Summary of the effect of thinning treatment on windthrow resistance (assessed through windthrow probability, wind damage, critical wind speed, mortality and general long-term effect (>20 years since thinning).

Authors	Biome (Region) (Dinerstein et al. 2017)	Species	Thinning treatment (repetitions)	% BA removed	Resistance	Long-term effect	Remarks
Kamimura *et al.* (2017)	Temperate (northern Japan)	*Larix kaempferi*	Precommercial (1)	Three thinning intensities	+		Based on observed damage
**Gardiner *et al.* (2013)	Europe	Several conifers and broadleaves	Commercial; Precommercial		+/–	+	Late moderate/heavy thinning increase vulnerability, precommercial/light thinning wind resistance ~5–10 years following thinning
Albrecht *et al.* (2012)	Temperate (southwestern Germany)	Mostly *P. abies; P. menziesii*	Commercial – above and below	0–50	–		Thinning from above destabilized stands
Hanewinkel *et al.* (2014)	Temperate (western Switzerland)	*A. alba;* *P. abies;* *F. sylvatica*	Commercial	Variable	0/–		No effect of thinning intensity; risk decreased with time since thinning (measured up to 8 years)
Pukkala *et al.* (2016)	Boreal (Finland)	*P. abies*	Precommercial + Commercial – below or above (3–4)	Variable intensities	–	+	Thinning from below increased wind damage probability; effect weakening over time
Achim *et al.* (2005)	Boreal (Quebec, Canada)	*A. balsamea*	Precommercial (1) + commercial (1)	0; 30		+	Increased critical wind speed with lower stand density 25 years after treatment
Novák *et al.* (2017)	Temperate (Czech Republic)	*P. abies;* *F. sylvatica*	Commercal – above and below (2)	0; 20; 60	+		Reduced mortality
Torita and Masaka (2020)	Temperate (northern Japan)	*L. kaempferi*	Precommercial (1–5)	Three thinning intensities	+		Critical wind speed increases with stand density
Kamimura *et al.* (2008)	Temperate (Japan)	*Cryptomeria japonica*	Commercial (variable)	0; two thinning intensities	–		Heavy thinning increased risk; risk increased with stand age
Lavoie *et al.* (2012)	Boreal (Quebec, Canada)	*P. mariana; A. balsamea; P. tremuloides;* *P. banksiana*	Dispersed retention; Group retention		0/–		Site-specific effect on risk; higher mortality in treated than untreated stands
Morimoto *et al.* (2019)	Temperate (northern Japan)	*A. sachalinensis, Tilia japonica;* *Q. crispula*	None – plantation with different stand densities		+		Natural forest less prone to windthrow than plantation, thinning could be used to modify plantation height and density
Duperat *et al.* (2021)	Boreal (Quebec, Canada)	*A. balsamea*	Precommercial (1) + commercial—below and above		0/–		Thinning from above decreased critical wind speed
Bigelow *et al.* (2021)	Temperate (USA)	mixed longleaf pine-hardwood	Commercial		+		Only marginal effects

Positive and negative effects are indicated by + and –, respectively; 0 indicates no effect; empty cells represent non available data. Authors of meta-analyses and reviews are marked with * and **, respectively.

Table 5 Overview of published evidence on the opportunities and limitations of thinning to increase tree and forest resilience and resistance to stressors.

Stressor	Opportunities	Limitations	Evidence	References
Drought (*n* = 33)	Heavy thinning improves the physiological and growth performance of trees and reduces mortality during and after drought conditions.	The effect of a single thinning treatment may reverse as stands mature, resulting in higher vulnerability.	Strong	(D'Amato *et al.*, 2013, Elkin *et al.*, 2015, Calev *et al.*, 2016, Sohn *et al.*, 2016, Aldea *et al.*, 2017, Ameztegui *et al.*, 2017, Diaconu *et al.*, 2017, Lechuga *et al.*, 2017, Ruzicka Jr. *et al.*, 2017, Seidl *et al.*, 2017, Trouvé *et al.*, 2017, Bottero *et al.*, 2017a, Cabon *et al.*, 2018, Cardil *et al.*, 2018, Dănescu *et al.*, 2018, Mausolf *et al.*, 2018, Shenkin *et al.*, 2018, Vernon *et al.*, 2018, Bello *et al.*, 2019, Jones *et al.*, 2019, Navarro-Cerrillo *et al.*, 2019, Ogaya *et al.*, 2019, Restaino *et al.*, 2019, Sinacore *et al.*, 2019, Wang *et al.*, 2019, Steckel *et al.*, 2020, van Mantgem *et al.*, 2020, Bosela *et al.*, 2021, Bottero *et al.*, 2021, Comeau, 2021, Knapp *et al.*, 2021, Low *et al.*, 2021, Zamora-Pereira *et al.*, 2021)
Fire (*n* = 19)	Heavy thinning is an effective approach to reduce fire hazard and the adverse effects of severe fires.	The accumulation of aboveground biomass following thinning may lead to increasing fire hazard and severity. To be highly efficient, thinning treatment often needs to be complemented by understory clearing and slash burning.	Strong	(Safford *et al.*, 2012, Martinson and Omi, 2013, Collins *et al.*, 2014, Prichard and Kennedy, 2014, Thomas and Waring, 2015, Barnett *et al.*, 2016, Kalies and Yocom Kent, 2016, Madrigal *et al.*, 2017, Palmero-Iniesta *et al.*, 2017, Hevia *et al.*, 2018, Piqué and Domènech, 2018, Russell *et al.*, 2018, Tardós *et al.*, 2019, Volkova and Weston, 2019, Arellano-Pérez *et al.*, 2020, Banerjee, 2020, Jain *et al.*, 2020, Taylor *et al.*, 2021, Stoddard *et al.*, 2021)
Insect and pathogen outbreaks (*n* = 22)	Thinning offers potential at mitigating the spread and severity of eruptive organisms and improving overall stand growth and vigor of infected stands.	Thinning may increase root rots infection severity. Complementary stump chemical or biological treatments or direct stump removal may be used to reduce root rots incidence.	Weak	(Fajvan *et al.*, 2008, Hood and Kimberley, 2009, Ellis *et al.*, 2010, Oliva *et al.*, 2010, Fajvan and Gottschalk, 2012, Bulman *et al.*, 2013, Ferchaw *et al.*, 2013, Stadelmann *et al.*, 2013, Dodds *et al.*, 2014, Régolini *et al.*, 2014, Roach *et al.*, 2015, Bulman *et al.*, 2016, Ganley and Bulman, 2016, Hood and Sala, 2016, Menkis *et al.*, 2016, Brantley *et al.*, 2017, Muzika, 2017, Negrón *et al.*, 2017, Scheller *et al.*, 2018, Roberts *et al.*, 2020, Steel *et al.*, 2021, Morris *et al.*, 2022)
Wind (*n* = 18)	Pre-commercial and commercial thinning performed at an early stand stage reduce wind damage vulnerability by promoting the development of structural roots and reducing height/diameter ratio.	If not performed at an early stage, thinning destabilizes stands by increasing wind exposure of residual trees. This higher vulnerability lasts from 2 to 10 years after thinning. The negative effect of thinning on short-term wind damage vulnerability increases with stand age and tree height.	Moderate	(Achim *et al.*, 2005, Kamimura *et al.*, 2008, Albrecht *et al.*, 2012, Lavoie *et al.*, 2012, Byrne and Mitchell, 2013, Gardiner *et al.*, 2013, Hanewinkel *et al.*, 2014, Albrecht *et al.*, 2015, Pukkala *et al.*, 2016, Subramanian *et al.*, 2016, Kamimura *et al.*, 2017, Novák *et al.*, 2017, Díaz-Yáñez *et al.*, 2019, Morimoto *et al.*, 2019, Torita and Masaka, 2020, Bigelow *et al.*, 2021, Duperat *et al.*, 2021, Gardiner, 2021)

n = number of relevant papers.

conditions. When complemented by understory clearing and slash burning, heavy thinning is also highly effective at reducing the frequency and severity of fire. We have identified a large number of research studies supporting these effects, which highlight this approach as a good opportunity for using a single management tool for meeting multiple objectives in forests that are threatened by both drought and fire. In cases where stands are also threatened by potential insect and pathogen outbreaks, thinning treatments also offer great potential at limiting the overall risk at the stand level by increasing the growth rates and vigour of potential hosts through density reduction, and by slowing the spread and development of eruptive organisms by direct removal of infected individuals. Regarding root rot infections, complementary stump treatments may be necessary to avoid further infection. Consistent positive effects of thinning at reducing forest vulnerability to invasive organisms are, however, limited to few insects and pathogens. Therefore, our review reveals insufficient evidence from rigorous experiments to draw general conclusions at this point.

Removing part of the canopy through thinning temporarily increases the risk of wind damage to residual trees, which represent the main limitations of the treatment for increasing overall forest resistance to multiple hazards. Because the negative effects of thinning on short-term wind damage vulnerability increase with stand age and tree height, heavy thinning performed at late stand development stages without previous treatments should be avoided in areas where the risk of wind damage is high. However, by promoting the development of structural roots and favouring lower height to diameter ratios, pre-commercial and commercial thinning performed at an early stand age only increase overall windthrow risks slightly over a short period of time, with the subsequent advantage of potentially reducing vulnerability over the longer term. This appears to be the case even for heavy thinning when performed at an early stage, which offers an opportunity to manage stands that are highly susceptible to windthrow events, but that are also threatened by additional stressors. For example, forest stands in windy areas that are threatened by increasing drought and fire risk could be subjected to heavy thinning followed by slash burning at an early age, thus increasing their overall resilience to these multiple stressors. In cases where windstorms are the main stressor, thinning also offers an opportunity to remove the most vulnerable trees of a stand, either by favouring windthrow-prone species or individuals with structural characteristics indicative of poor anchorage. Thinning is thus a tool that could help improve or maintain stands composed of any combination of wind-stable, non-host, fire- and drought-resistant trees in areas where wind, eruptive organisms, fire or drought is predominant stressors.

Whereas thinning shows great potential for reducing the negative impacts of several stressors over a short period, our review revealed that the factors and physiological processes responsible for its positive effects remain poorly understood. Moreover, there is an important lack of understanding of the long-term effects of both single and repeated thinning treatments on forest resilience and resistance, which drastically limits our ability to develop long-term adaptive management strategies. For example, while heavy thinning is beneficial in young stands under drought conditions, the opposite has also been reported for mature stands. A wealth of long-term monitoring experiments is available to help further our collective knowledge on this issue. Targeted re-measurement programs could be implemented to gather new information where necessary, so that key insights are gained on how the long-term responses of forests to changes in environmental conditions can be modulated by thinning regimes (Achim *et al.,* 2021). The current evidence assembled in this review suggests that thinning should not be promoted as a tool that will universally increase the resistance and resilience of forests. However, it could still be an effective tool in the short- to medium-term to reduce forest vulnerability to some stressors, therefore creating a window of opportunity to implement longer term adaptive management strategies such as assisted migration (Bradford and Bell, 2017).

To further our understanding of the effects of thinning on stand adaptation to global change, a first step should be to revisit existing thinning trials and studies with the objective of identifying key stand attributes that can be linked with resistance and resilience to past forest stressors (Seidl *et al.,* 2017). These research effort should focus on linking pre-disturbance stand history and characteristics, such as density, structure and composition to forest vulnerability to multiple stressors and their potential interactions (Achim *et al.,* 2021). Thanks to recent research efforts, results from promising long-term adaptative silvicultural trials are becoming available (e.g. Bigelow *et al.,* 2021; Comeau, 2021; Morris *et al.,* 2022; Muller *et al.,* 2021), although the geographical representation of such trials remains fairly limited. Increased interactions between scientists and managers who have developed focused expertise on specific forest disturbance are paramount so that confounding effects of multiple stressors on long-term forest dynamics can be taken into account. In parallel, there is an imperative for new silvicultural trials that include a variety of thinning treatments, in which a range of adaptive silvicultural strategies are tested and compared with respect to multiple stressors. Such trials would serve as the foundation for comprehensive ecosystem-specific knowledge, which are essential for silviculturists and forest managers worldwide (Achim *et al.,* 2021).

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