REVIEW

The boreal–temperate forest ecotone response to climate change

Piers Evans and Carissa D. Brown

Abstract: A warming global climate will elicit changes in the distribution of plant species around the planet, and this will become most apparent where biomes converge. Climate exerts the strongest control over the geographic location of ecotones at the continental scale and many, including the boreal forest – temperate forest ecotone (BTE), are expected to shift to higher latitudes under climate change. Fine-scale drivers that define biome boundaries at the sub-continental scale are less well understood for many ecotones. We assembled studies addressing whether a modern distributional shift is occurring at the BTE and what biotic and abiotic factors are driving such a shift. Current research suggests a northward shift is occurring; yet, scant data are available to identify the processes involved. Abiotic and biotic factors are repeatedly identified as key drivers of change, though not all claims are evidence-supported and the interacting effects of these non-climatic factors are poorly understood.

Key words: ecotone, boreal forest, temperate forest, climate change, range shift.

Résumé : Le changement climatique planétaire suscitera des changements dans la répartition des espèces de plantes autour de la planète et ceci deviendra le plus manifeste là où les biomes convergent. Le climat contrôle largement l'emplacement géographique des écotones à l'échelle continentale et plusieurs, dont l'écotone de forêts boréales et de forêts tempérées (ÉBT), sont censés se déplacer à de plus hautes latitudes sous l'effet du changement climatique. Les moteurs à petite échelle, qui définissent les limites de biome sur le plan sous continental, sont moins bien compris dans le cas de bien des écotones. Nous avons analysé des études portant sur la question de changement de répartition moderne s'opérant au niveau de l'ÉBT et quels facteurs biotiques et abiotiques influent sur un tel changement. La recherche actuelle suggère qu'un changement se produit vers le nord; cependant, peu de données sont disponibles pour pouvoir identifier les processus en question. Des facteurs abiotiques et biotiques sont identifiés à plusieurs reprises comme les principaux moteurs de changement, quoique pas toutes les affirmations soient généralement prouvées et que les effets combinés de ces facteurs non climatiques soient mal compris. [Traduit par la Rédaction]

Mots-clés : écotone, forêt boréale, forêt tempérée, changement climatique, changement de gamme.

Introduction

The global climate is warming at a faster rate at high latitudes than it is farther south (Stocker et al. 2013), and the effects of this change on forests are expected to be complex and varied. The implications of climate warming on plant distribution patterns seem, on the surface, to be obvious: as the climate at higher latitudes and elevations changes, plant distributions should shift in concert. Strong correlations between recent climate warming trends and latitudinal and elevational shifts in species' distributions have been found in many systems (Walther et al. 2005; Chen et al. 2011; Boisvert-Marsh et al. 2014), yet the complexity of species' responses are becoming increasingly apparent (Lafleur et al. 2010; HilleRisLambers et al. 2013) and the simplified view of a directional shift fails to appreciate the unevenness with which changes in regional climate are occurring (Walther et al. 2002). A commonality across biomes is the occurrence of time lags in climate-induced range shifts; these time lags appear to vary by species and geographic and topographic situation (Parmesan and Yohe 2003; Bertrand et al. 2011; Savage and Vellend 2014). Global-scale predictions of plant distribution patterns are therefore spatially general at best, and even regionalized inferences of future plant distributions based on climate predictions should be considered with caution (Walther et al. 2002).

The boreal forest biome has one of the largest geographic footprints of any terrestrial biome on the planet, encircling the globe in the northern latitudes (Olson et al. 2001). To date, range shift research in this biome has predominately focussed on the advance of boreal tree species into tundra or alpine habitats (i.e., treeline advance; see Harsch et al. 2009), or the species-specific responses of temperate tree species (e.g., Zhu et al. 2012). An ecotone that has received less attention, yet which is a critical transition between two economically, culturally, and ecologically important biomes, is the southern boreal forest – northern temperate forest ecotone (herein referred to as BTE; Goldblum and Rigg 2010). The temperate forest biome is not nearly as expansive as the boreal forest, and so the BTE exists only in eastern North America, northern Europe and European Russia, and eastern Asia (Pastor and Mladenoff 1992). The BTE is still largely intact in North America, contrary to Europe and eastern Asia where human activities such as agricultural expansion and logging have eliminated or modified large tracts of ecotone forest (Pastor and Mladenoff 1992; Goldblum and Rigg 2010), creating substantial hurdles to our understanding of this ecotone.

Pastor (2016) warns of the disassembly of the BTE as plant species' shifts with climate will be asynchronous both spatially and phenologically with dependent fauna, causing the dismantling of ecological communities. To accurately predict the shift of the boundary between temperate and boreal forests, which has considerable implications for ecosystem function and processes, a continental and global understanding of the actual response of the BTE to recent warming is needed. To that end, we see three

P. Evans and C.D. Brown. Department of Geography, Memorial University, 230 Elizabeth Avenue, St. John's, NL A1B 3X9, Canada.

Corresponding author: Carissa D. Brown (email: carissa.brown@mun.ca).

Table 1. Typical tree species occurring in the boreal forest – temperate forest ecotone (BTE) mixed-wood forest in North America and Eurasia (modified from Pastor and Mladenoff 1992).

North America	Europe	Asia
Boreal species		
Abies balsamea	*Betula pubescens*	*Abies nephrolepis*
Betula papyrifera	*Picea abies*	*Betula ermanii*
Picea glauca	*Pinus sylvestris*	*Betula platyphylla*
Picea mariana	*Populus tremula*	*Picea jezoensis*
Pinus banksiana	*Sorbus aucuparia*	*Populus davidiana*
Populus tremuloides		
Northern temperate deciduous species		
Acer saccharum	*Carpinus betulus*	*Acer mono*
Betula alleghaniensis	*Fagus sylvatica*	*Fraxinus mandshurica*
Fagus grandifolia	*Quercus robur*	*Pinus koraiensis*
Pinus strobus	*Tilia cordata*	*Quercus mongolica*
Tilia americana		*Tilia amurensis*
Tsuga canadensis		*Ulmus propinqua*

Note: Since we are attempting to make global observations about this particular ecotone, a broad range of species belonging to each biome must be considered; however, even at the global scale, many of the genera are common among geographically disparate instances of the BTE.

critical questions for which a synthesis is needed: (*i*) What determines the current position of the BTE? (*ii*) How has this ecotone changed in the past? (*iii*) How will the BTE change in the future? We approached these questions by synthesizing current knowledge on temperate tree species response to climate change at the BTE using a standardized, focussed literature search. Specifically, we investigated whether a modern distributional shift has occurred in the BTE across the globe, identified the most common biotic and abiotic factors involved in limiting or facilitating this shift, and assessed whether knowledge gaps exist for specific regions, species, and processes.

We had a number of expectations prior to our literature synthesis. Loehle (2000) showed that ecotone response to climate warming along a latitudinal transect would be slow, exhibiting a lag effect owing to resistance of the retreating forest biome. At the BTE, we anticipated that lag would be due to a combination of abiotic and biotic factors: (*i*) the porous structure of moss- and lichen-dominated boreal substrates would limit the germination and establishment of temperate tree species; and (*ii*) the palatability of large-seeded temperate tree species (e.g., *Acer* spp.) would result in their preferential predation by small mammals in boreal forest sites. We also expected that range expansion of species with distributions that predominately occur in the BTE (rather than centred in the temperate forest biome; see Table 1) could be an early indicator of temperate forest shifts into historically boreal forest stands, as they are already established in marginal environments for temperate species. To our knowledge, this is the first global synthesis to date of the response of the BTE to recent climate change (but see Goldblum and Rigg 2010 for an excellent review on the North American portion of this ecotone). Such a synthesis is critical, given recent rapid climate change and subsequent ecosystem shifts and community re-organization occurring globally (Beckage et al. 2008; Hobbs et al. 2009; Jump et al. 2012; Trant and Hermanutz 2014).

The BTE

Before we begin dissecting how this ecotone is changing, a clear picture of the general principles governing its location and spatial extent are needed. An over-arching theme of all ecotones is the inter-specific competition that takes place under considerable environmental stress, as these areas are typically where distributional range edges converge (see Table 1 for species list; Burns and Honkala 1990 and references therein). The North American BTE (Fig. 1a) offers some exception to this, as the BTE is wide enough here to host the majority of some tree species' distributional range (Pastor and Mladenoff 1992). The European BTE (Fig. 1b) is comparatively narrower, and much more fragmented owing to anthropogenic activities. The latter can also be said about the Asian BTE, which compounds the difficult definition of the ecotone with its predominant occurrence along spatially distributed elevational gradients rather than a continuous latitudinal gradient (Fig. 1c; BTE not defined; Ohsawa 1990).

The BTE is located in the mid to high latitudes, which means it will be exposed to large increases in both mean annual temperature and annual precipitation over the next century (Stocker et al. 2013). These are important factors affecting the location of the BTE, although the exact combination of agents that act to define its location (e.g., climatic, topographical, edaphic, or otherwise) are not yet wholly understood (Goldblum and Rigg 2010; Graignic et al. 2014). Arris and Eagleson (1989) found a strong association between the mean annual −40 °C minimum isotherm and the BTE in North America, yet the same relationship was not as strong in Europe or Asia. Even so, there is ample evidence that at the continent scale, climate is the most significant factor determining the location of the BTE (Woodward and Williams 1987). To date, work on the current and future impact of the most recent warming on the BTE has been primarily regionally focused.
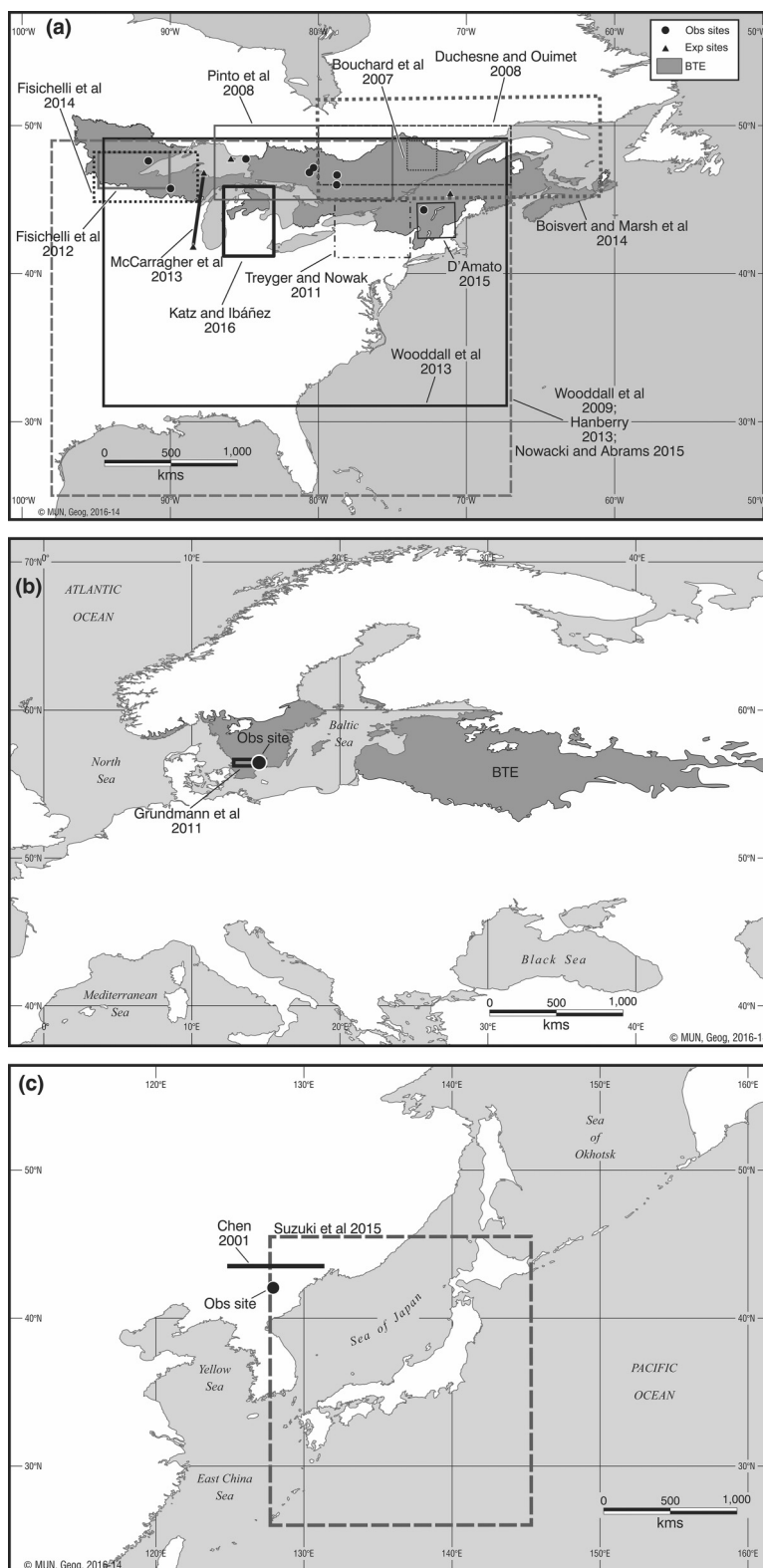
Contemporary BTE change

We reviewed the literature pertaining to the response of the BTE (methods summarized below) and revealed three key findings: (*i*) approximately one-third of the studied BTE species and communities had evidence of a distributional shift in the direction predicted by climate change (Table S1[1]); (*ii*) while climate is a dominant driver of species' distributions in the BTE, non-climatic factors play a critical role in determining a species' ability to respond to changing climatic conditions; and (*iii*) scant data are available on the response of the BTE to climate change or the mechanisms driving that response. Here, we discuss those findings further.

Literature synthesis of BTE response to recent climate change

We used the Scopus online database to search the literature published prior to February 2015 using the search terms focussed on "temperate", "boreal", measures of range expansion, migration, or shifts (see Supplementary Materials for full literature search methods and parameters[1]). This search produced 1095 titles, which were then scanned to identify articles relevant to the subject of this study, producing a list of 123 candidate papers. To ensure that as many relevant articles were included as possible, subsequent searches were performed on the Scopus database using search terms that included resurvey and elevational gradient studies, which we found were not captured by our initial search. We also searched specifically for climate-response studies on species whose ranges centre in the BTE, rather than belonging to one biome or another, identified by Pastor and Mladenoff (1992; see Table 1 for species list). These secondary searches produced a further 18 relevant publications. Finally, we scanned the reference lists of relevant publications for titles that the primary or secondary searches may have missed. This produced an additional 56 articles, raising the total of relevant articles in our study to 178.

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/er-2017-0009.

Fig. 1. The spatial extent of the boreal forest – temperate forest ecotone (BTE) and distribution of studies in (*a*) North America, (*b*) Europe, and (*c*) Asia. The North American BTE was assembled here using Nearctic mixed forest terrestrial ecoregions from Olson et al. (2001) and closely resembles the outline of Goldblum & Rigg's (2010) boreal–deciduous ecotone (BDE). The European BTE is represented here using the Sarmatic Mixed Forest Ecoregion from Olson et al. (2001), which matches earlier descriptions of the Hemiboreal zone outlined by Ahti et al. (1968). Studies show small- and large-scale observational and experimental studies, with linked study sites indicated.

Papers were individually evaluated to determine suitability for the current study. The response variable of interest was the detection, or lack thereof, of temperate tree establishment in boreal forest stands using experimental or observational methods. Studies needed to experimentally test or observe whether a range shift of ecotone-forming species was possible at or beyond the current BTE. We did not require the confirmation of range shift at the ecotone, as this would effectively omit many experimental studies that tested the possibility of range shift (e.g., Kellman 2004; Brown and Vellend 2014). Additionally, information was collected for each study as follows: study design, geographic location(s) of study site(s), habitat type(s), tree species studied, life stage studied, a/biotic variables studied, measurement method(s), important (a/biotic) drivers, temporal duration of study, and qualitative tree responses to climate (Supplementary Materials[1]). Elimination of studies from our database were designated as being a result of subject, exposure, or response (Koricheva et al. 2013). After the article scan, 62 candidate papers remained from the initial search. After a final reading of individual papers and the inclusion of the latest relevant publications as of December 2016, the final list of titles was cut to 27 papers (Fig. 1; Table S1[1]).

Have temperate tree species' ranges shifted northward?

Our synthesis indicated that 9 of the 27 published studies detected through our methods provided evidence of a distributional shift of the BTE in the direction predicted by climate change (~33%). That ratio is lower than that found by Harsch et al. (2009) for the forest–tundra ecotone, where ~52% of treelines had shifted upward or northward with warming. When we compare our results to Harsch et al. (2009), some interesting contradictions are revealed between species at the southern and northern end of the boreal forest. Black and white spruce (*Picea mariana* and *Picea glauca*, respectively) are two common species in North American northern treeline research, both of which have been found to be shifting northwards with climate change (Lescop-Sinclair and Payette 1995; Payette 2007). This northward shift is often associated with a southern range contraction to form an overall distributional shift (Davis and Shaw 2001); however, Boisvert-Marsh et al. (2014) found that while many southern species had expanded beyond their northern ranges, neither black nor white spruce had experienced southern range contraction. They note that climate change and human-altered disturbance regimes in the BTE may be opening up niche space for boreal and temperate species alike.

At both the northern and southern edge of the boreal forest, it is interesting to look at the examples of ecotones that did not respond as predicted. The number of examples of a BTE shift in the opposite direction than expected in our search results was limited to one (Foster and D'Amato 2015), whereas the remaining studies reported that no shift had occurred as species' distributions were simply static, or only shifts in abundance or species dominance were observed (Table S1[1]). In the boreal–tundra ecotone (treeline), the remaining 48% of treelines were predominantly static, showing no discernible response, and the authors hypothesized a combination of complex climatic constraints on treeline advance (e.g., ice damage, winter desiccation; Harsch et al. 2009) in concert with ecological time lags. We propose that the lack of BTE response to climate warming at the southern margin of the boreal forest is the outcome of ecological time lags driven by complex biotic and abiotic interactions.

Biotic and abiotic determinants of the current BTE location

While we stress that we are simply identifying observable trends in the limited research available on this topic, there are undeniably common themes that have emerged in our results— the strongest of which appears to be how changing climate regimes are affecting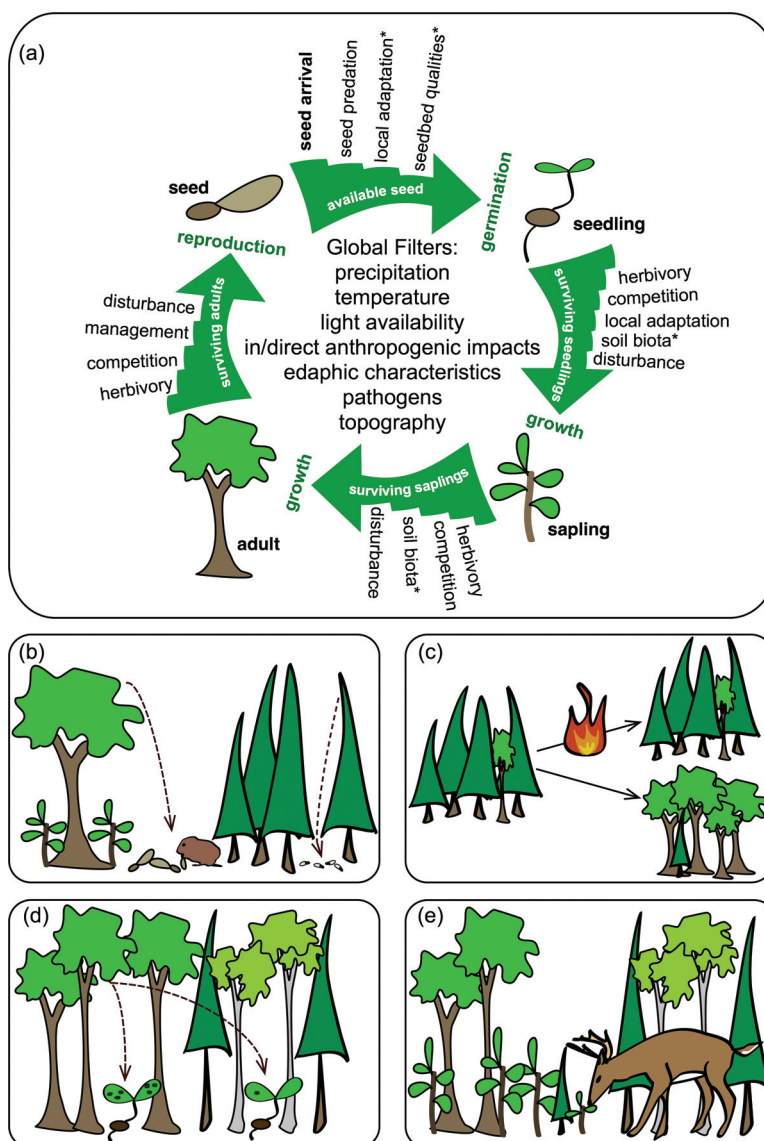 the BTE. The effect of climatic factors, particularly changes in temperature and precipitation regimes, on other biomes and ecotones around the world are better studied (Parmesan and Yohe 2003; Olivares et al. 2015). From these changes, some species stand to benefit from climate change in the form of expanding fundamental niches (Williams et al. 2014), while others are expected to have increasingly reduced available niche space (e.g., alpine meadows; Brandt et al. 2013). Sixteen of the 27 studies in our database demonstrated (11/27) or suggested (5/27) temperature as a factor in determining the position of the BTE (Table S1[1] for this and all following enumerations). Half the studies (14/27) also suggested some other form of climatic control over the position of the BTE, which can be broken down into three groups: (*i*) precipitation or moisture availability, (*ii*) storm severity or wind throw events, and (*iii*) growing season length or timing of frost events.

Climate change could provide a common thread throughout the majority of the research our study uncovered; however, changes occurring in the global BTE are by no means solely climate-dependent, and the degree to which non-climatic a/biotic factors contribute to the observed changes is still poorly understood. Many studies tested, hypothesised, or made inferences to biotic interactions that could act as a negative feedback to northward shifts in the BTE (e.g., temperate sapling herbivory, Fisichelli et al. 2012; seed predation and soil biota, Brown and Vellend 2014). In some cases these interactions were quantified and were found to have the effect of slowing the northward advancement of southern temperate tree species. When the biotic interaction was herbivory, that slowing was often due to the higher nutritional value and better palatability of the seeds or foliage of deciduous tree species compared to predominantly coniferous boreal species (Kellman 2004; Fisichelli et al. 2012; Frelich et al. 2012). In contrast, biotic interactions can also result in a net positive feedback with regards to temperate tree species' northward advancement. Pest infestations in southern boreal stands have been found to increase likelihood of a northward shift in the BTE at the regional scale by creating gaps that facilitate the establishment and often lead to dominance of southern species at the local scale (Grundmann et al. 2011; Boisvert-Marsh et al. 2014).

While biotic interactions can be difficult to monitor and measure, proving problematic to separate from climatic drivers (see Brown and Vellend 2014), abiotic non-climatic factors such as edaphic qualities and disturbance regimes are better understood. Lafleur et al. (2010) argues that while climate change will likely lead to northward shifts in tree species ranges of boreal and temperate species alike, this progression will be piecemeal and uneven owing to species-specific edaphic constraints. Empirical evidence supporting Lafluer et al.'s (2010) argument is emerging. Edaphic factors are well represented in the research found in the present study; there are a wide range of soil characteristics cited as contributing factors in determining the location of the BTE including moisture and temperature (Goldblum and Rigg 2005), the interplay between moisture and nitrogen content (Pastor and Post 1988), nutrient content (Bai et al. 2011), pH (Fisichelli et al. 2013), and texture and depth to parent material (Lee et al. 2005). Researchers suggest that temperate species' ability to track a warming climate will be constrained by shallow, coarse, poorly drained, and acidic soils.

A critical point that has emerged from our synthesis is that no single variable has stand-alone effects on tree species distributions; instead, the response of BTE tree species to climate change is the result of the interacting effects of multiple drivers. To further complicate the story, those drivers cannot always be categorized as abiotic or biotic, climatic or non-climatic. Soil is an excellent example. A combination of biotic (e.g., soil biota) and abiotic (e.g., moisture capacity) drivers, soil characteristics can have immensely complex influences on tree species' abilities to track changing climate (Brown and Vellend 2014; Lankau et al. 2015; Katz and Ibáñez 2016), including feedbacks between newly

Fig. 2. (*a*) Conceptual framework showing filters acting on potential colonising tree species at the boreal forest – temperate forest ecotone (BTE), each of which reduces the number of individuals available for the next demographic stage. Filters were assembled from the 27 most relevant papers pulled from the literature in the present study, with an adjacent asterisk (*) representing filters that were inferred, hypothesised, or were otherwise not supported with evidence in studies encountered and therefore in particular need of research. Specific filters (or their removal) are depicted to show (*b*) preferential seed predation of temperate species by boreal vertebrates (Brown and Vellend 2014), (*c*) the impact of fire suppression on forest successional pathways and subsequent canopy composition (e.g., Drever et al. 2006), (*d*) the escape from pathogens with increased distance from conspecific individuals (Katz and Ibáñez 2016), and (*e*) increased browse pressure on more palatable temperate species in boreal stands (Fisichelli et al. 2012).

arriving tree species and the soils they encounter (e.g., increasing soil fertility through increased nitrogen input; Pastor and Post 1988). Disturbance regimes are also the result of complex interactions between climatic and non-climatic factors (e.g., temperature and fuel load) or biotic and abiotic variables (e.g., climate-induced range expansion of herbivores). The disruption of these regimes can have far-reaching consequences on species composition that must be considered when contemplating the modern composition of the BTE, and its future (Nowacki and Abrams 2015). The message, then, is that any study of a species distributional response to climate change must not only incorporate climatic and non-climatic factors, but also the interactions between them.

Constraints on life history stages

Many factors that act to constrain the northward expansion of temperate tree species into boreal stands reoccur frequently in

the literature, and act as filters that weed out potential colonising tree species at different life stages. In organising them into a conceptual framework (Fig. 2), one can view the normal life-cycle of a given tree species that has the chance to establish a population in an area it previously did not inhabit. This population will, under normal conditions, begin with the arrival of seeds in a new location and which must then germinate, survive, and propagate. At each life stage, filters can have different levels of impact on or relevance to a new colonising population given its genetics, demographics, physical setting, and proximity to disturbance and vectors of dispersal. Global filters act on a given tree species at all life stages. It is important to note that many of the filters in our conceptual framework are hypothesized in the literature, and not directly supported by evidence. The inclusion of unsupported filters is meant to draw focus to areas that we have found to be

under-represented in the literature to date, and serve as a road-map for future work to address knowledge gaps in our understanding of which and how drivers interact with species occurring in the BTE. Additionally, more work is needed to solidify the relationships between known drivers and those yet to be revealed, as well as to quantify their influence on the location of the BTE under the influence of climate change.

A general constraint that was not captured by our literature review, but is an increasingly important consideration when researching species range shifts, is the potential for phenological mismatch between plant species and their pollinators (Memmott et al. 2007), dispersers (Tylianakis et al. 2008), and pests (Schweiger et al. 2008). This is a complex issue that could affect how the BTE shifts with climate change. Asynchrony between the phenology of specialist insect herbivores and their host tree could lead to some alleviation of herbivory stress (Asch and Visser 2007), whereas asynchrony between insect herbivores and the migration timing of their avian predators could result in un-checked insect outbreaks (Venier and Holmes 2010). These and other examples of how phenological mismatch could simultaneously maintain and disrupt the current species range status-quo offer a glimpse of the intricate, multi-trophic interactions that can confound climate change induced range shifts.

Historical context of range shift in the BTE

The prevailing notion that climate-related factors, primarily temperature, precipitation, and seasonality (Woodward and Williams 1987), are the most important controls on the distribution of vegetation is not new, and can certainly be applied to the modern and historical location of the BTE (Mather and Yoshioka 1968; Allen and Hoekstra 1990; Pastor and Mladenoff 1992). Historical ecotone shifts have been recreated using palynological and macrofossil evidence across North America (Jackson et al. 1997; Hupy and Yansa 2009) and Europe (Amon et al. 2012; Douda et al. 2014) during the warming period since the last ice age. Evidence that as recently as 126 ka the North American temperate biome was located at least 500 km further north than it is today in response to 6–7 °C higher average temperatures (Fréchette and de Vernal 2013) could serve as a regional maxima for the potential of future warming to be reflected by a drastic northward shift of the BTE. The rate of tree species range shift and recolonisation after the last glacial maximum is widely contested with some authors suggesting a maximum rate of 2000 m yr^{-1} (Giesecke et al. 2011) and others a maximum of less than 250 m yr^{-1} (Cheddadi et al. 2013), reflecting the general agreement that the rate of movement varied among species. The disassembly of this ecotone is therefore expected to mirror the process of its assembly as it occurred on a species-by-species basis, owing to the species-specific responses to climate change (Pastor 2016).

Projected changes in the BTE

During our literature review, we opportunistically identified forest modelling or simulation studies dealing specifically with forest dynamics at the BTE. The majority of studies predicted northward shifts of southern temperate species at the expense of boreal species, with a minority of temperate species projected to retain their current range or suffer range contractions (Chen 2002; Koca et al. 2006; Iverson et al. 2008; Hickler et al. 2012). Most of the modelling studies we found dealt with the North American and European BTE, with fewer studies dealing with the eastern Asian portion of the BTE. Because we found little data on field studies of the Russian BTE, we specifically searched for modelling papers addressing the Russian BTE (or hemiboreal/boreo-nemoral zone sensu Ahti et al. 1968), which revealed predictions of northward shifting species ranges, aligning with projections of other regions of the BTE globally (Sykes 2001; Zhang et al. 2009). Additional Russian studies modelled future states of the Russian boreal forest (e.g., Nadezda et al. 2006, Brazhnik and Shugart 2015), or focussed on the future of Russian forests as a whole (e.g., Tchebakova et al. 2009; Kicklighter et al. 2014; Shuman et al. 2014; Schaphoff et al. 2016).

Many regional, community-scale studies have revealed evidence suggesting that recent climate change has affected the BTE location by influencing growth patterns (Goldblum and Rigg 2005), shifting tree species distribution (Weng and Zhou 2005; Beckage et al. 2008; Tang and Beckage 2010), re-positioning temperate species' competitive standing (Bolte et al. 2010), and increasing northern recruitment success of temperate species (Leithead et al. 2010). However, these studies often focus on a narrow subset of species out of necessity, owing to the often monumental task of collecting adequate data upon which to base firm conclusions for large groups of species (see Iverson and Prasad 2002). Likewise, many regional-scale models have been designed to test the implications of future climate change scenarios on the BTE, with northward and upward shifts being common predictions (Weng and Zhou 2005; Koca et al. 2006; Tang and Beckage 2010; Shuman et al. 2014). When combined, regional projections do encompass the global BTE in a piece-wise fashion; however, we are aware of no study that deals directly with the question of how current climate change will affect BTEs globally.

Currently, to specifically deal with how the BTE may respond to climate change at the global scale one must refer to studies using global scale models to investigate how climate change will affect vegetation distribution (e.g., Haxeltine and Prentice 1996; Alo and Wang 2008; Warszawski et al. 2013), as inclusion of the BTE is implicit. Predictions can also be informed by historical BTE responses to periods of climate flux, which provide useful insight into how even relatively small changes in a climatic regime have produced ecotonal shifts (Hupy and Yansa 2009) and can serve as a recent historical analogue to modern change at the regional scale. Beyond predicting forest distributional response to climate change, modelling studies in the literature appear to have the purpose of informing policy (Hickler et al. 2012; Steenberg et al. 2013; Bright et al. 2014), addressing combinations of changing climate and non-anthropogenic disturbance regimes (Scheller and Mladenoff 2008; Vanderwel and Purves 2013), or multiple climate scenarios (Iverson and Prasad 2002; Iverson et al. 2008), while others have narrowed in on BTE dynamics at the regional scale (Koca et al. 2006; Anyomi et al. 2012).

Research needs

We identified significant geographic gaps in BTE research globally. Studies in the highly human-influenced portions of the BTE that exist in Europe and eastern Asia may be lacking because of the difficulty in locating the natural BTE. Bolte et al. (2010) conducted research in a reserve in southern Sweden, and took great care in researching the historical land-use patterns that could have left an imprint on their study area. In north-eastern China, where the east Asian portion of the BTE exists, land-use change has occurred more recently and much more rapidly than in Europe. Rapid population growth over the past half century has produced expanding demand for cleared agricultural land and building supplies that has left a characteristic mark on the forested landscape (Yu et al. 2014). Research on BTE response to climate change is growing fastest in North America, yet knowledge gaps remain. Data on the North American portion of the BTE has the best geographical coverage, yet eastern Canada remains under-researched. There, a fragmentary coastline creates geographic barriers between sites with amenable climatic conditions for southern temperate tree species expansion into typically boreal-forested regions, and creates logistical challenges for field research.

A holistic understanding of the processes controlling the location and configuration of the BTE is needed. Our review of the

literature has identified numerous factors that may facilitate or constrain a shift in the BTE. We anticipate these factors will produce a piecemeal ecotone shift, controlled by local and regional non-climatic factors. While we are moving towards gaining a big-picture understanding of the North American BTE, which has relatively abundant empirical data compared to the other regions, we cannot directly apply predictions informed by North American data to other regions with unique combinations of confounding factors and traits. The three broad regions where the BTE exists–North America, Europe, and eastern Asia–also have significant ecological differences; historical colonisation patterns and geography account for much of the tree species richness gradient from high diversity in east Asian forests to lower diversity in Europe (Latham and Ricklefs 1993). At the surface this gradient may seem like yet another complicating factor; however, it also presents a unique opportunity for a direct comparison between how shifts of species-rich ecotones compare with those that are relatively species-poor between the same two biomes.

Moving forward, expanding the focus of research on this topic to include more work in eastern Canada and within the European and Asian ecotones will not only (*i*) allow for a better grasp of spatial differences in rates and morphology of change at the global scale, but (*ii*) through the role of ecotones as bellwethers for climate change (Wasson et al. 2013), the BTE may also offer a glimpse of how biomes around the world may respond to a changing climate. However, the interaction between ecological features and climatic and other (a/biotic) factors is still not clearly understood and clouds our ability to make accurate predictions of future ecological states as a result of the multitude of global and local conditions that must be taken into consideration and the temporal longevity of the systems under study (Woods 2014). It is our opinion that such ecological complexity can only be disentangled through field experimentation (e.g., Kellman 2004; Brown and Vellend 2014) and future research efforts in the BTE should focus on quantifying a/biotic effects on species distributions at their range limits. Scale factors become important considerations here as well, as field experiments are often only able to identify local drivers owing to the inherent limitations of time and resources. Therefore, questions surrounding how local drivers can be scaled to explain regional or continental changes must also be addressed. Despite these challenges, our findings do suggest that the quantity and scope of research on this topic is growing at an accelerating pace and will likely continue to do so in the coming years.

Conclusions

We set out with a number of expectations for our review of current research addressing the response of the BTE to climate change. Those expectations were met in that we uncovered a complex story involving disturbance, biotic interactions, and abiotic characteristics. We did not anticipate that we would only gain an understanding of small pieces of the full story of the historic, current, and future BTE, and only in geographically discrete regions. We lack a holistic understanding of the ecotone globally, which is critical for predictions of species' distributions. What we do know is that, under various circumstances and conditions, the components required for temperate tree expansion into boreal forest stands include a favourable disturbance regime, suitable substrate, predator satiation or absence, presence of symbiotic organisms, and release from pathogens, in addition to the suitable environment created via climate change. The absence of one or more of these conditions will likely result in a time lag between the creation of favourable environmental conditions beyond temperate tree species' current distributions and their response to warming via population advance.

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