Piecing together the fragments: elucidating edge effects on forest carbon dynamics

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Forest fragmentation is pervasive throughout the world's forests, impacting growing conditions and carbon (C) dynamics through edge effects that produce gradients in microclimate, biogeochemistry, and stand structure. Despite the majority of global forests being <1 km from an edge, our understanding of forest C dynamics is largely derived from intact forest systems. Edge effects on the C cycle vary by biome in their direction and magnitude, but current forest C accounting methods and ecosystem models generally fail to include edge effects. In the mesic northeastern US, large increases in C stocks and productivity are found near the temperate forest edge, with over 23% of the forest area within 30 m of an edge. Changes in the wind, fire, and moisture regimes near tropical forest edges result in decreases in C stocks and productivity. This review explores differences in C dynamics observed across biomes through a trade-offs framework that considers edge microenvironmental changes and limiting factors to productivity.

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Forests worldwide are increasingly being fragmented into smaller patches; at present, as much as 20% of global forests are within 100 m of a non-forest edge and 70% are within 1 km of a non-forest edge (Haddad *et al.* 2015). Across the northeastern US, 23% of the current forest area is within 30 m of a developed or agricultural edge, with strong regional gradients in the dominant land-cover type adjacent to forests (Figure 1). The consequences of forest fragmentation on biodiversity have been well described (Ries *et al.* 2004), but the impacts of fragmentation and edge effects on the carbon (C) cycle are just beginning to receive attention. Research has demonstrated that forests near edges have distinct growing conditions, but the magnitude of these differences – and even whether productivity is enhanced or diminished as a function of proximity to an edge – appears to vary across biomes. There is therefore an urgent need to understand how pervasive forest fragmentation is affecting the terrestrial C cycle.

The forest edge is a "zone [that] experiences the climate buffering effects of a tree canopy immediately above, but has lost the lateral protection afforded by trees to one side" (Matlack 1993). From the forest edge to the interior, there are gradients in microclimate (Young and Mitchell 1994; Davies-Colley *et al.* 2000; Gehlhausen *et al.* 2000); biogeochemistry and resource availability (Weathers *et al.* 2001; Pohlman *et al.* 2009; Remy *et al.* 2016); and forest productivity and structure (Chen *et al.* 1992; Laurance *et al.* 2011; Reinmann and Hutyra 2017). However, the aggregate response of forest C dynamics may differ between biomes that vary in structural characteristics and limiting factors on productivity, such as climate. In tropical forests, Chaplin-Kramer *et al.* (2015) analyzed remote-sensing data and determined that biomass within 500 m of an edge was 25% lower than in the forest interior. Similarly, using field observations in an Amazon rainforest, Laurence *et al.* (1997) found 36% less biomass within 100 m of an edge, and in a boreal forest in Sweden, Jönsson *et al.* (2007) showed that tree mortality was considerably higher in fragmented as compared to intact stands. In contrast, biomass densities in a temperate broadleaf forest were 64% higher near the forest edge than the forest interior, scaling to a 10% increase in regional estimates of biomass through southern New England in the US (Reinmann and Hutyra 2017), and biomass density in a temperate coniferous forest was 31% higher near the edge relative to the interior (Bowering *et al.* 2006).

Edge effects create distinct growing conditions that vary across biomes; nonetheless, current forest C accounting methods and ecosystem models largely neglect their influence. This represents an important gap in our understanding and modeling of the terrestrial C cycle and its response to disturbance, climate, land-use or land-cover changes, and land management policies. Here, we synthesize the literature related to edge effects on the C cycle and posit how fragmentation affects the C dynamics of the world's remaining forests.

In a nutshell:

- Forest fragmentation is ubiquitous, altering forest growing conditions
- Edge effects can both degrade and enhance forest carbon (C) pools and productivity, depending on biome type
- Ecosystem models and C accounting frameworks do not include edge effects
- Systematically assessing edge effects across the globe will improve C accounting and yield new insights into the impacts of land-use and land-cover change

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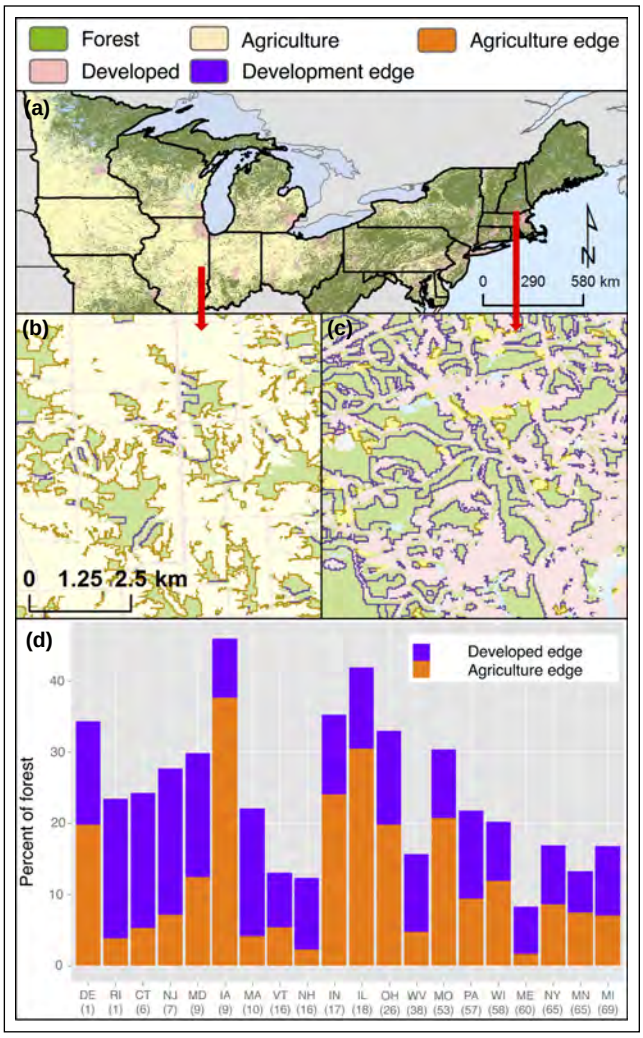

Figure 1. *(a) Of the 54 million ha of forest cover in the northeastern US, (b) 12% is within 30 m of an agricultural field and (c) an additional 11% is within 30 m of a road or development. (d) States are sorted based on total area of forest cover, which is given below the state abbreviation (in km² × 1000). Estimates are based on the 2011 National Land Cover Database (NLCD; Homer* et al. *2015) and the US Census TIGER Roads layer. Forest cover = NLCD codes 41, 42, 43, 52, and 90; agriculture = NLCD codes 81 and 82; development = NLCD codes 41, 42, 43, 52, and 90; and roads = TIGER codes S1100, S1200, S1400, S1630, and S1640.*

Trade-offs at the forest edge

Microclimatic changes at the forest edge can create both favorable and adverse conditions for plant growth, depending on the local limiting factors to growth and vulnerabilities to stress (Figure 2). Fragmentation creates a mosaic of forested and non-forested land with altered material and energy fluxes across ecological boundaries. The biotic and abiotic transitions between adjacent land covers can have variable spatial scales (Schmidt *et al.* 2017) and may induce increases, decreases, or no change in the factors controlling forest structure and productivity with proximity to the edge (Ries *et al.* 2004). Light, air temperature, soil temperature, vapor pressure deficit (VPD; the difference between actual versus potential moisture content of the air, measured as atmospheric pressure), and wind increase between the forest interior and edge, whereas soil moisture declines toward the edge (Figure 3; Raynor 1971; Kapos 1989; Ritter *et al.* 2005). Edges can affect vulnerability to fire by enhancing flammability through desiccation of fuels and greater exposure to potential human ignition sources (Cochrane and Laurance 2002; Laurance and Curran 2008), but fragmentation also creates fuel discontinuities that can inhibit wildfire spread (Agee *et al.* 2000). In addition, forest edges can be predisposed to biotic disturbances, such as pest infestations, through heightened invasion probability (Kautz *et al.* 2013). Nitrogen deposition and availability can be elevated at the forest edge due to a combination of inputs from nearby vehicle emissions, fertilizer applications, and altered canopy roughness characteristics (Weathers *et al.* 2001; Remy *et al.* 2016). Overall, increased incident solar radiation is perhaps the key factor differentiating the edge's microenvironment from that of the interior forest (Matlack 1993).

The magnitude of the edge response varies not only with proximity to the edge but also as a function of the edge aspect (the compass direction that the edge faces), adjacent land-cover type, and the size of the forest opening. For example, in the Northern Hemisphere, the response of variables driven by radiation can be dampened near edges with a northern exposure relative to those with a southern exposure (Burton 2002; Heithecker and Halpern 2007). Aspect also influences the duration and temporal patterns of abiotic changes related to radiation levels (Chen *et al.* 1995). The penetration depth and intensity of edge effects are influenced by the forest patch size and management characteristics of adjacent land covers. Gálhidy *et al.* (2006) found that increasing the diameter of temperate broadleaf forest gaps from 12–14 m to 36–40 m resulted in a relative increase of 10% to 20–25%, respectively, in above-canopy light availability at the edge of the gap. In the case of linear openings in the forest, Pohlman *et al.* (2009) found that air temperature and VPD gradients were stronger along the edges of forests adjacent to anthropogenic infrastructure, such as power lines and highways, than natural edges adjacent to streams.

Edge environments change over time as vegetation responds to the altered conditions, with successive trade-offs. When a forest edge is created by deforestation, it produces sharp spatial transitions in energy fluxes. However, over time, increases in leaf area index (the amount of leaf area per unit ground area, m^2 m^{-2}) and understory vegetation density near the edge can dampen gradients in energy fluxes (Didham and Lawton 1999; Laurance *et al.* 2011). The density of edge understory growth is related to time since edge creation, species assemblage, edge adjacency, aspect, and potentially man-

agement. In the tropics, the depth of penetration of most microenvironmental variables at newly created edges can be two to five times higher than at older, more densely vegetated edges (Didham and Lawton 1999). Following edge creation in tropical forests, the abundance of clonally reproducing lianas (woody vines) increased by 46% within 100 m of an edge (Laurance *et al.* 1997). Tree seedling recruitment and growth also increased within 10 m of a newly created edge (Sizer and Tanner 1999). This edge stimulation can seal the forest edge and dampen microclimatic changes over time (Harper *et al.* 2005). Although forest edge creation tends to change the microenvironment in a predictable direction, the magnitude of the change is highly variable.

Biogeographical variations in the relative trade-offs influencing forest C fluxes due to fragmentation (Figure 2) may account for the qualitatively different impacts of edges on C cycling across forest biomes. For example, in the tropics, elevated air temperature near an edge might reduce forest productivity as the trees at the edge become more susceptible to heat stress and drought, whereas in the boreal region, where forest growth is often limited by temperature (Nemani *et al.* 2003), higher air temperatures at the edge can stimulate forest productivity by bringing trees closer to photosynthetically optimal temperatures for a larger proportion of the growing season.

The terrestrial C cycle

Forests are a major C sink, offsetting nearly one-third of anthropogenic C emissions (IPCC 2014), but the size of the terrestrial C sink and the impacts of deforestation and land-cover change on the C cycle remain poorly defined (Pan *et al.* 2011). Moreover, gross primary production has been increasing in recent decades (by 31% ± 5% during the 20th century; Campbell *et al.* 2017), complicating efforts to quantify the role of forests. Although C emissions from land-use change have been relatively stable since 1850, variations in estimates of the magnitude of emissions have increased in recent decades (Houghton 2010).

Carbon stocks

Current methods for forest C accounting do not consider spatial variation in the strength of the forest C sink due to edge effects. Edge effects on aboveground C pools vary considerably across forest types, with aboveground biomass reported to increase (Bowering *et al.* 2006; Bell *et al.* 2017; Reinmann and Hutyra 2017), decrease (Laurance *et al.* 1997; Chaplin-Kramer *et al.* 2015; Bell *et al.* 2017), or remain essentially unchanged (Ziter *et al.* 2014) with proximity to forest edges.

In the tropics, aboveground forest C generally declines with proximity to edges. Using 30-m-resolution, satellite-derived maps of forest cover, Brinck *et al.* (2017) reported that increased tree mortality near tropical forest edges caused an additional 0.34 Gt of C emissions annually, representing 31% of the current estimated C releases attributed to tropical deforestation. The key mechanisms responsible for the reductions in C stocks in tropical

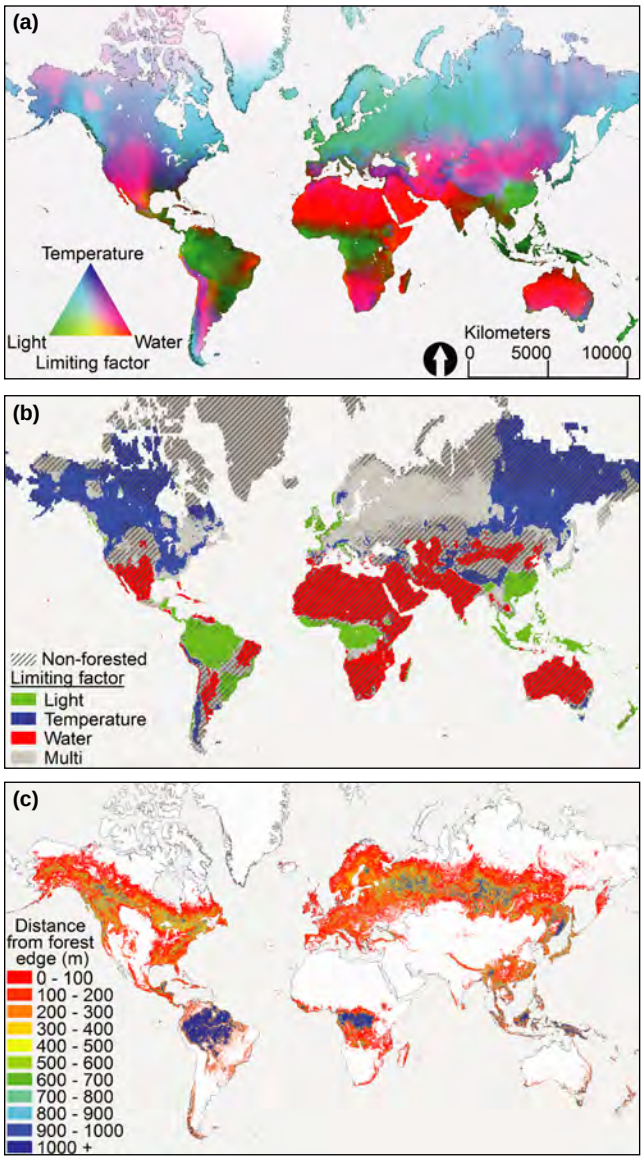

Figure 2. *The world's remaining forests are increasingly fragmented, but the growth response at an edge is highly dependent on existing climatic conditions. (a–b) Integrating factors limiting primary productivity (Nemani* et al. *2003) and (c) the distribution of forest edges worldwide (Haddad* et al. *2015) indicate that no single factor alone limits productivity in the majority of the world's forest edges (WebFigure 1). Limiting factor categorization (b) used a logic model identifying the greatest limiting effect, requiring a minimum difference of 25% between factors; if no single factor dominated, pixels were classified as multi-limited. Panel (c) is displayed at 1-km resolution, as in Haddad* et al. *(2015); calculations of proportional frequencies of limitation by each limiting factor (WebFigure 1) were performed at 90-m resolution, demonstrating strong biome- and continental-level differences in limiting factors across the edge-to-interior gradient.*

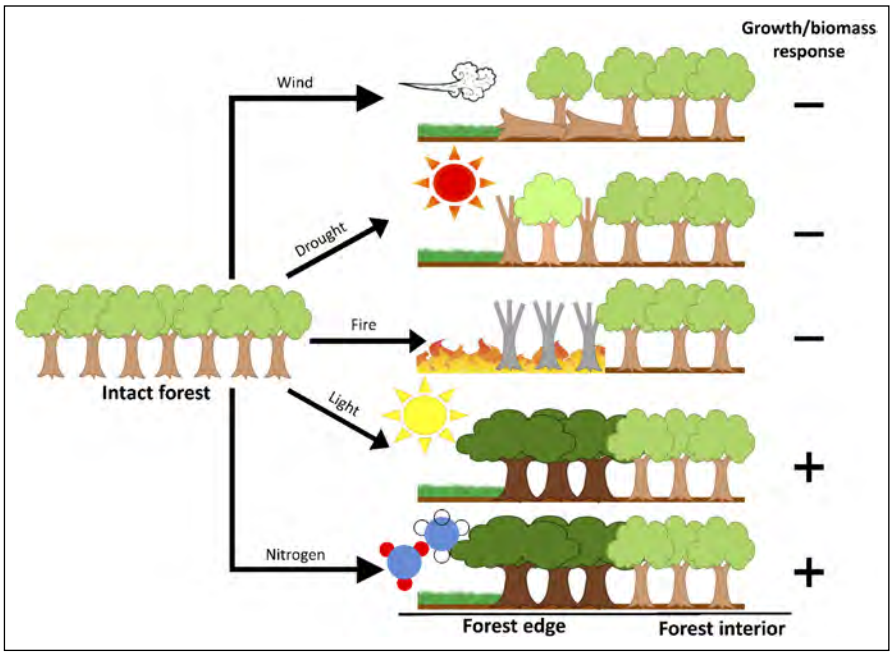

Figure 3. *Changes in the forest edge microenvironment include exposure to more wind, drought, fire, light, and nitrogen. The positive (+) sign and negative (–) sign indicate favorable and adverse conditions, respectively, for growth/biomass.*

edges include increased desiccation stress, fire, parasitic liana proliferation, and blow down of large trees due to greater exposure to wind (Laurance *et al.* 2007, 2011). Although forests in the tropics are largely light limited, most of the forest fragmentation has occurred in the more water-limited regions (Figure 2), for example in the Cerrado forest along Brazil's "arc of deforestation" – the Amazonian frontier for agricultural development. Trees in tropical forests are comparatively tall (up to 60 m in height; Feldpausch *et al.* 2011) and grow in a warm climate, making them particularly vulnerable to increases in wind, drought, and fire. The overall negative response observed in aboveground C stocks near tropical forest edges is probably due to the adverse conditions created by the altered forest edge microenvironment.

Research in temperate forests suggests that C stocks can decrease, persist, or even increase near the forest edge. In the temperate rainforests of southern Washington and central Oregon, Chen *et al.* (1992) reported that tree mortality increased and stem density decreased among trees within 120 m of an edge. In old-growth temperate coniferous forests in Oregon, increases and decreases in basal area with proximity to edges were observed in forests at lower elevations (<800 m) and at higher elevations (>800 m), respectively (Bell *et al.* 2017). In the broadleaf forests of Quebec, Canada, no changes in aboveground C stocks were observed within 100 m of an edge, although stem density increased (Ziter *et al.* 2014); in contrast, in broadleaf forests of eastern Massachusetts, Reinmann and Hutyra (2017) found a 64% increase in forest biomass within 20 m of an edge. Similarly, in montane temperate lodgepole pine (*Pinus contorta*) forests in British Columbia, Canada, biomass was 31% higher in edges adjacent to roads than in the forest interior (Bowering *et al.* 2006).

These studies suggest that the forest edge microenvironment in temperate regions can often create conditions that result in enhanced C storage capacity at the forest edge relative to the interior. In temperate broadleaf forests, trees are generally shorter (15–30 m) and have relatively deeper root systems (up to 4 m) than in the tropics (Canadell *et al.* 1996), and most trees lose their leaves seasonally, characteristics that reduce the risk of windthrow relative to other biomes. This allows trees near edges to take advantage of the increased availability of light (Matlack 1993; Chen *et al.* 1995; Pohlman *et al.* 2009), temperature (Matlack 1993; Young and Mitchell 1994; Gehlhausen *et al.* 2000), and/or nutrients (Weathers *et al.* 2001; Remy *et al.* 2016).

In temperate coniferous forests, the response of C storage near the edge seems to be driven by increased wind exposure. In forests at lower elevations and along roadways, where wind gradients are likely weaker, C storage is higher at the edge (Bowering *et al.* 2006; Bell *et al.* 2017), whereas at higher elevations and along clear-cut edges, where winds are likely to be stronger, mortality and basal area declines of large trees increase with proximity to the edge (Chen *et al.* 1992; Bell *et al.* 2017).

Research from boreal forests shows that tree mortality and structural degradation increase with proximity to edges. In an experimentally fragmented Norway spruce (*Picea abies*) forest in Sweden, tree mortality rates in forest fragments were substantially higher (1.2–3.9%) than in intact plots (0.7%; Jönsson *et al.* 2007). In the spruce zone of British Columbia, the density of canopy trees at the edge declined by up to 46% relative to the forest interior (Burton 2002). Trees in boreal forests have shallow roots, with 80% of root biomass occurring in the upper 30 cm of soil (Jackson *et al.* 1996), increasing the risk of uprooting associated with wind exposure near the edge. However, productivity of individual trees at the edge might be enhanced by higher temperatures due to edge effects. Thus, initial decreases in biomass due to windthrow could be offset by increased productivity among the remaining trees and greater resilience of recruited trees to higher winds.

Carbon fluxes

Understanding edge effects requires characterizing both C stocks and fluxes across heterogeneous landscapes. Eddy

covariance measurements of net ecosystem C exchange are an important tool for estimating C flux, but the methodology requires homogeneity within the footprint of the eddy covariance towers. There is a profound selection bias against fragmented landscapes in the distribution of eddy covariance measurements, resulting in a major mismatch between the landscapes we are attempting to characterize and the flux data we are using to characterize them.

In tropical forests, growth rates of individual trees within 10 m of single tree-fall gaps or similar-sized canopy openings increased following gap formation (van der Sleen *et al.* 2014), which the authors attributed to enhanced light availability based on $^{13}CO_2$ (CO_2 with carbon isotope ^{13}C) discrimination in assimilation, representing an opportunity for tree growth near gap edges. These observations of higher productivity near gap edges are contrary to measurements of increased mortality and reduced biomass densities near clear-cut tropical forest edges, but the scale of these disturbances differs substantially. The environmental changes near canopy gaps are not as extensive as those near larger clearings, allowing trees to capitalize on reduced competition and additional light without necessarily experiencing the adverse conditions of increased wind, heat stress, fire, and desiccation that occur near tropical forest edges.

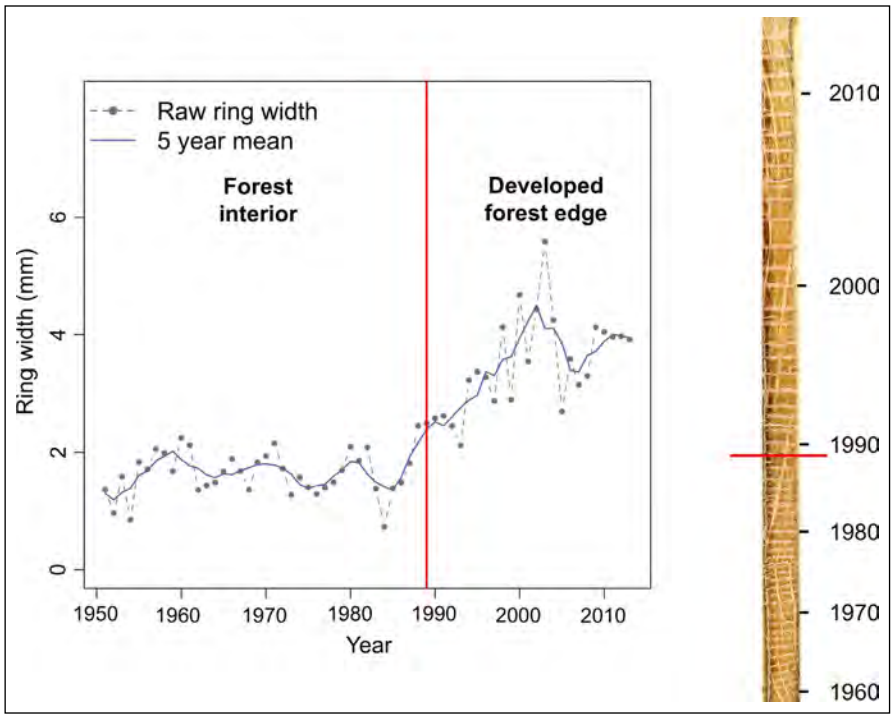

Figure 4. *Example of productivity enhancement, as measured by tree-ring analysis, for an individual tree growing at a developed forest edge (after 1989) relative to when it was growing in the forest interior (before 1989) (data from Briber* et al. *[2015]; n = 75 in the original study). Red lines indicate the year of edge creation.*

More is known about forest edge effects on productivity in temperate forests. In British Columbia, lodgepole pine trees within 5 m of a road grew 32% faster than in the 5 years prior to road establishment (Bowering *et al.* 2006). In eastern Massachusetts, red oak (*Quercus rubra*) growth rates nearly doubled following edge creation due to urbanization (Figure 4; Briber *et al.* 2015). In the Piedmont region of North Carolina, growth rates of loblolly pines (*Pinus taeda*) and tulip trees (*Liriodendron tulipifera*) within 5 m of a forest edge were considerably higher than the growth rates of trees within the forest interior (McDonald and Urban 2004). In the temperate rainforests of southern Washington and central Oregon, western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) growth increased 150% and 33%, respectively, near clear-cut edges (Chen *et al.* 1992). Increased growth rates near the forest edge (Figure 4) are not surprising; foresters routinely thin stands to accelerate tree growth (Meadows and Goelz 2002), and thinning induces changes in the microenvironment, such as increased light and reduced competition, that can be similar to those experienced near forest edges.

Quantifying changes in C sequestration at the forest scale requires an inventory of all trees, given that increases in biomass with proximity to the edge could be attained (1) through faster-growing individual trees at the edge or (2) through a higher density of trees at the edge, with the growth rates of each tree equal to the growth rates of trees within the forest interior. To our knowledge, the only study that has examined forest growth rates in an edge-to-interior context found evidence for both of these mechanistic pathways, leading to an 89% increase in forest growth within 20 m of a forest edge relative to the forest interior (Reinmann and Hutyra 2017). Furthermore, enhancement of temperate forest edge growth was greatest in years with cool summers and lowest in years with warmer than average summers, with absolute rates of forest growth declining nearly three times faster at the edge than in the interior in response to early growing season heat stress (Reinmann and Hutyra 2017).

These findings suggest that shifts in the mean climate and the frequency of climate extremes may trigger subsequent shifts in the response of forest growth to edge effects. Continued warming of air temperatures in combination with more extreme heat waves and droughts (IPCC 2014; Allen *et al.* 2015) will likely increase tree mortality near tropical forest edges, since tropical forests as a whole are vulnerable to increasing moisture stress (Phillips *et al.* 2009). In the warmer, southern portion of the temperate region, where forest growth is limited primarily by maximum temperatures (Martin-Benito and Pederson 2015),

higher maximum temperatures will likely inhibit forest growth near the edge. In the northern latitudes of the temperate region, where forest growth is also limited by precipitation variability (Martin-Benito and Pederson 2015), there is an unclear trade-off between warmer edge temperatures stimulating productivity and stress from more severe droughts. In the boreal forest, warmer temperatures will likely stimulate edge productivity, given that increasing temperatures have been associated with greater C uptake in the northern latitudes (Keeling *et al.* 1996). However, drought may also constrain productivity throughout much of the boreal forest (Barber *et al.* 2000), potentially resulting in overestimated C uptake and storage.

Autotrophic and heterotrophic respiration responses across forest edge gradients are largely unknown for all forest biomes. Given that soil respiration rates are sensitive to changes in both soil moisture and temperature (Davidson *et al.* 1998), as well as gross primary production (Janssens *et al.* 2001), spatial gradients in soil respiration are likely. Total soil respiration rates have been shown to increase with soil temperature up to approximately 25°C, beyond which rates begin to decline (Carey *et al.* 2016). In the tropical region, where this threshold is liable to be surpassed, relative decreases in soil respiration rates at the edge are expected. In contrast, in the boreal region, where soil temperatures are generally below 20°C (Carey *et al.* 2016), warming is likely to stimulate respiration rates at the edge. In the temperate region, the respiration response is unclear and may vary with latitude. Taken as a whole, it remains uncertain (1) the extent to which warmer soil temperatures will stimulate respiration rates, (2) whether drier soils will offset the impact of warmer temperatures, and (3) how microbial communities will acclimate to warmer temperatures at the edge.

Accurate assessment of the response of the net forest C balance to edge effects requires inclusion of productivity measurements, as well as measurements of mortality and soil respiration, but to our knowledge these variables have yet to be evaluated simultaneously.

Dynamic edge responses

The position and characteristics of forest edges are not necessarily stable over time. If the depth of penetration for microenvironmental gradients decreases over time (Didham and Lawton 1999; Laurance *et al.* 2011), then edge effects on C dynamics may change in magnitude or even sign (positive to negative or vice versa). However, existing studies indicate that the edge influence on C uptake and storage is largely insensitive to long-term recovery processes as long as the edge is present. In old-growth temperate coniferous forests, no effect of harvest age was found on basal area in edges between 13 and 60 years old created by clear-cutting (Bell *et al.* 2017), and edge growth enhancement of Douglas-fir and western hemlock were sustained for at least 10–15 years following edge creation (Chen *et al.* 1992). In the sub-boreal region, lodgepole pine trees within 5 m of an edge experienced growth enhancement for up to 20 years following edge creation, with the largest growth response occurring in the initial 6–10-year period (Bowering *et al.* 2006), and in temperate broadleaf forests, edge growth enhancements were sustained for up to 40 years (Briber *et al.* 2015). Finally, woody plant encroachment – the outward migration of the forest edge – generally results in increased net C uptake (Barger *et al.* 2011).

Although much of the world's forested area is adjacent to an edge, not all edges are man-made. Forest edges can be natural, and may be formed when forests are interrupted by water bodies, reach the tree line, encounter a patch of disturbed forest, and so forth. However, permanent natural forest edges likely have a distinct edge environment and, as with man-made edges, the magnitude of the environmental changes will depend on the adjacent land-cover type (water, rock, peatlands, etc). In natural forest edges that are temporary, edge C dynamics during the recovery of the adjacent disturbed patch are poorly understood. Current knowledge of edge effects is largely derived from permanent, man-made edges, and thus edge dynamics of transient and natural edges should be explored further.

Forest biome C responses

Growth and mortality near the forest edge appear to be more sensitive to environmental stress and extremes than in the forest interior. Whereas growth at the forest edge can be enhanced by higher light and nutrient availability, growth is also affected by increases in fire, heat, drought, and/or wind. Forest edge C dynamics may be predictable if we consider how trade-offs in growing conditions couple with spatially varying limits of ecosystem productivity (Figure 2).

Forest productivity is limited by light, temperature, water, or some combination of the three, depending on geographic location (Nemani *et al.* 2003). Comparing the global extent of fragmentation (Haddad *et al.* 2015) and geographic limitations on productivity (Nemani *et al.* 2003), we determined that much of the world's forested area within 500 m of an edge is not limited by a single factor but rather by a combination of light, temperature, and water (WebFigure 1). Within 500 m of edges, there is a similar amount of light- and temperature-limited forest, although the drivers of fragmentation may vary across biomes. In many temperature-limited systems (eg boreal forests), much of the fragmentation results from natural features on the landscape, such as lakes and wildfires (Figure 5), whereas in light-limited systems (eg tropical forests), much of the fragmentation is due to anthropogenic deforestation and changes in land use. In the temperate region, the prevailing driver of fragmentation is the conversion of forest to development and agriculture. Consequently, differences in the impacts of fragmentation across these biomes depend on differences in both the factors limiting growth and the disturbance agent.

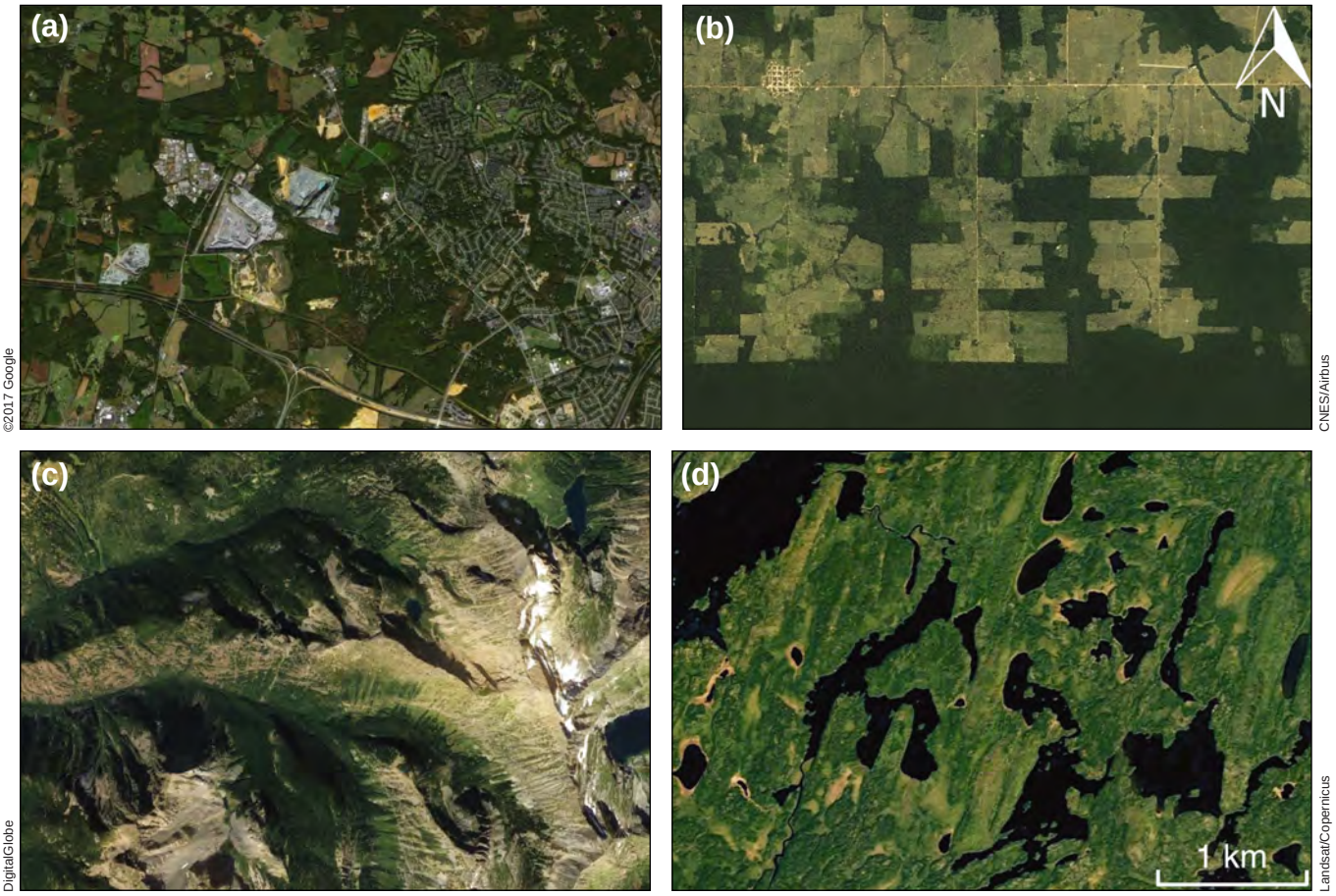

Figure 5. *Examples of the prevailing natural and anthropogenic sources of forest fragmentation across biomes. (a) Anthropogenic conversion of forest to development and agriculture in a temperate forest in Wyndham, Virginia. (b) Anthropogenic conversion of forest to cropland in a tropical forest in Nova Dimensão, Rondônia, Brazil. (c) Natural fragmentation due to elevation at the tree line in a montane temperate forest in Libby, Montana. (d) Natural fragmentation due to lakes in a boreal forest in Ontario, Canada.*

Conclusions

With world populations projected to increase to between 9.6 billion and 12.3 billion people by 2100 (Gerland *et al.* 2014), human settlements and agricultural lands will almost certainly continue to expand into currently forested areas, which will increase the proportion of the world's forests experiencing edge conditions. Projected increases in temperatures and more frequent heat waves and drought (IPCC 2014) could act synergistically with forest fragmentation to put further pressure on forests by intensifying edge-to-interior gradients.

Forest responses to the creation of edges are dynamic, but most of our observations of forest edge C dynamics are based on static edges. Temporal and spatial patterns in biomass, growth, mortality, and recruitment as a function of time since fragmentation, as well as adjacent land-cover types in both permanent and temporary edges, need to be better quantified. Critically, future research must aspire to quantify gradients in net ecosystem exchange in order to capture a more complete picture of edge effects on the C cycle at local, regional, and global scales.

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