Edge cases: fragmentation and ecosystem processes in temperate forest landscapes

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Temperate forests are the most fragmented forest biome, yet current understanding of fragmentation effects on ecosystem processes, such as carbon (C) cycling, is rooted in tropical forest research. We review the effects of persistent fragmentation on temperate forest ecosystem processes and quantify the extent to which the US national forest inventory and land-cover maps represent forest edge area. We found systematic underrepresentation of forest edges across all methods. As compared with very high resolution (1 m) maps, conventional 30-m resolution forest cover maps underestimated forest edge area by 16.4%, on average. Accounting for all forest edge area and edge effects on forest structure and growth resulted in a 14.8% median increase in aboveground forest C estimates, with 23.8% and 74.2% increases in agriculturally and urban dominated counties, respectively. We conclude by proposing improvements to forest inventories, maps, and models to better represent the fragmented temperate forest landscape.

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Global land-use change is driving deforestation and forest fragmentation, or the division of continuous forest into separate areas or fragments, exacerbating biodiversity loss and climate change (Foley *et al.* 2005). It is well-established that landscape pattern influences ecological processes (Turner 1989), but how patterns of forest fragmentation primarily caused by anthropogenic land-cover change alter critical ecosystem processes (eg forest structural development and carbon [C] cycling) remains understudied (Franklin *et al.* 2021). Moreover, widespread efforts to map forest area and quantify forest C storage often focus on total forest area and neglect forest pattern and configuration (Olofsson *et al.* 2014).

While fragmentation affects all forest biomes, temperate forests are the most fragmented, with approximately 17.5% (217 million hectares) of forested area located within 30 m of a non-forest edge (Morreale *et al.* 2021). Understanding of the impacts of anthropogenic fragmentation on forest structural development, biogeochemical cycling, and forest succession is rooted in modern tropical deforestation (Laurance *et al.* 2011), often evoking images of large swaths of intact forest being logged, burned, and converted to agriculture or development. In tropical forests such as those in the Brazilian Amazon, deforestation cleared more than 11 million hectares of forest in 2021 alone (WRI 2022). Many temperate forests, however, have a long history of intense land use and a landscape ecology that is distinct from their tropical counterparts (Haddad *et al.* 2015). In the eastern US, Europe, and Southeast Asia, the modern mosaic of temperate fragmented forests results from a mix of ongoing deforestation and legacy of clearing for agriculture and development followed by partial reforestation, termed a "forest transition" (Mather 1992; Kauppi *et al.* 2006). Ecological and climatic characteristics (eg species abundance and traits, temperature, light availability) further differentiate temperate from tropical forest ecosystems. Given the differences in land-use history, climate, and ecology of temperate and tropical forests, patterns of fragmentation and its consequences should not be assumed to be analogous across biomes.

Accounting for fragmentation requires a mechanistic understanding of ecosystem processes within fragmented forests, as well as accurate characterizations of fragmentation patterns themselves. Recent syntheses have advanced ecological understanding of some dimensions of forest fragments (Franklin *et al.* 2021), but the capacity to scale empirical measurements remains limited by the ability to quantify affected areas. Here, we review the state of knowledge on fragmentation effects on temperate forest structural development, demography, and C cycling. We then analyze how alternate delineations of fragmentation via forest maps and inventories influence understanding of its scope. To demonstrate the need to

In a nutshell:

- Human land use fragments forests, changing forest ecosystems by creating edges with distinct environmental conditions
- Forest inventories and maps systematically exclude forest edges, ignoring large amounts of forest in fragmented regions
- Precise quantification of fragmentation and forest edges will improve understanding of both forest patterns and ecosystem processes
- Forest observations and models need specific adjustments to include forest edges

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accurately account for fragmentation, we quantify aboveground C storage across an example region of fragmented temperate forest. Finally, we offer recommendations for better characterizing pattern and process in the modern temperate forest landscape.

Processes at the edge

Forests once covered vast geographic regions largely interrupted only by geologic features (eg water bodies), environmental ecotones (eg wetlands), or natural disturbances (eg wildfires). Through human land use over time, forests were cleared and often converted to a persistent non-forest land cover. In addition to a reduction in total forest area, once-contiguous forests are divided by agriculture, roads, and settlements, with remaining fragments maintained by continued anthropogenic perturbations. Landscape alteration into a configuration of many smaller fragments results in a proliferation in the areal extent of forest edges. Forest edges refer to the transitions or boundaries between forest and non-forest land covers (Fletcher *et al.* 2007). Here we focus on forest edge area (that is, the portion of forest directly altered by adjacent non-forest land cover), rather than on fragments as a whole.

Across biomes, anthropogenic forest edges are distinct from those that occur naturally (eg forested lakeshores, mountain balds) because they do not arise from preexisting environmental conditions (Schmidt *et al.* 2017; Smith *et al.* 2018; Franklin *et al.* 2021). Persistent anthropogenic edges also differ from those created through disturbances such as wildfires, treefall gaps, or silvicultural treatments because vegetation is unable to regenerate due to ongoing interference beyond the initial disturbance event (Harper *et al.* 2005; Hanson and Stuart 2005; Schmidt *et al.* 2017). These edges tend to exist as hard boundaries (ie abrupt ecological transitions to crops, pavement, or other abutting human land covers; Esseen *et al.* 2016). As compared to a closed-canopy forest interior, anthropogenic forest edges experience increases in light through lateral exposure to solar radiation. Consequently, edges are hotter and drier than the interior (Schmidt *et al.* 2017), while also experiencing greater wind exposure and altered atmospheric deposition (Weathers *et al.* 2001). Management of the adjacent non-forest area can further alter water and nutrient gradients (eg fertilizer use can increase nitrogen and phosphorus inputs, and run-off from impervious surfaces and/or irrigation can increase hydrological inputs while also depositing salts and other chemical compounds into the forest; Pocewicz *et al.* 2007). Microclimatic (Zellweger *et al.* 2019) and nutrient gradients vary from the forest edge to the interior, and meta-analyses suggest that the influence of temperate forest edges can extend from 10 m to 40 m into the interior (Schmidt *et al.* 2017; Franklin *et al.* 2021). For our analyses, we defined forest edge area as forest within 30 m of a non-forest land cover (Reinmann and Hutyra 2017; Meeussen *et al.* 2021; Morreale *et al.* 2021; Garvey *et al.* 2023).

While microclimatic and other physical gradients along abrupt forest edges have been thoroughly documented and are generalizable across biomes, their resultant effects on ecosystem processes are more variable and less well understood. In many tropical forests, forest edges exhibit elevated tree mortality and suppressed growth relative to the interior as a result of increased drought stress, elevated wind exposure, and liana invasions (Laurance *et al.* 2011). Conversely, temperate forest edges are often more productive than their interior counterparts (Remy *et al.* 2016; Reinmann and Hutyra 2017; Meeussen *et al.* 2020; Morreale *et al.* 2021). Increases in leaf area and stem density at the forest edge suggest increased light availability as the mechanism driving increases in biomass and productivity (Reinmann *et al.* 2020; Morreale *et al.* 2021). Studies in European temperate forests suggest that elevated growth is associated with increased nitrogen deposition at the forest edge (Remy *et al.* 2016; Meeussen *et al.* 2020). With limited exceptions, studies of temperate forests have found no increase in tree mortality at persistent edges, although lower overall biomass has been reported at the forest edge in old-growth conifer forests of the US Pacific Northwest and the montane region of southern Europe (Chen *et al.* 1992; Morreale *et al.* 2021; Pöpperl and Seidl 2021). In addition, a growing body of research suggests that C cycling is altered along temperate forest edges, especially when combined with recent findings on belowground C dynamics (Meeussen *et al.* 2020; Reinmann *et al.* 2020; Garvey *et al.* 2022). Observed differences in forest structural development, demography, and microclimate dynamics at the edge suggest that projected trajectories for forest composition may differ from traditional expectations of forest succession based on interior ecosystems (Bormann and Likens 1979; Weathers *et al.* 2001; Schmidt *et al.* 2017; Franklin *et al.* 2021).

Linking pattern and process

Early attempts to establish a unified theoretical framework of ecological edges focused on defining the boundaries between ecosystems (Cadenasso *et al.* 2003). This framing, rooted in both landscape ecology and empirical observations, emphasized that ecological boundaries affect the adjacent systems (Laurance and Yensen 1991; Weathers *et al.* 2001). Further research quantified the depth of edge influence on the abutting forest ecosystem (Harper *et al.* 2005). Due to high variability in edge influence and varying definitions of forest edges, conceptual frameworks have shifted away from an emphasis on a single linear boundary and toward the idea of a transition zone between ecosystems (Erdôs *et al.* 2011). For instance, Schmidt *et al.* (2017) synthesized and adapted the transition zone concept into a framework for understanding biogeochemical cycling across fragmented ecosystems, positing that a defining characteristic of forest edges is the existence of predictable gradients in microclimate and nutrient cycling. The flexibility of the transition zone framework not only allows for variable depths of edge influence and for multiple definitions of both the adjacent forest and non-forest matrices but also includes both vertical and temporal heterogeneity in biogeochemical cycling. While the conceptualization of edges as transition zones is useful for understanding forest boundaries as a landscape feature, it fundamentally does not align with how the distribution of forest ecosystems or forest processes are mapped at larger scales. For example, many countries rely on national forest inventories (NFIs) to provide an empirical foundation for national and global forest assessments and greenhouse-gas emissions reporting (UNFCCC 2014). Complementing ground-based inventories, remote sensing is used to create continuous maps of forests and other land covers. With the opening of the Landsat Archive, a proliferation of forest-focused satellite and airborne measurements, along with increases in computing power, have resulted in the release of multiple land-use and forest-cover products over the past decade (Wulder *et al*. 2012). Ideally, approaches that combine empirical ground measurements with remotely sensed coverage of a region can improve C accounting, mapping of forest structure and function, and parameterization of Earth system models. However, to succeed in representing ecosystem processes, the synthesis of these approaches must consider the role of the transitions and forest edge.

To characterize fragmentation patterns, forest inventories and maps must accurately quantify total forest cover and capture forest pattern (ie the complexity of edge configuration). In the US and elsewhere, NFIs are structured to be statistically representative samples of the nations' forests. Despite this, the US NFI (the US Forest Service Forest Inventory and Analysis [FIA] database) excludes forest fragments beneath a minimum area threshold (<0.4 ha; Section 2.5.9 FIA User Manual) and is only now beginning to account for forests in urban areas (Edgar *et al*. 2021). Both NFIs and remote-sensing–based forest maps *implicitly* represent forest edges, but these data products do not account for forest edges *explicitly* in their sampling designs (Haddad *et al*. 2015; Morreale *et al*. 2021). Furthermore, estimation of forest area scales with spatial resolution (Strahler *et al*. 1986), and quantification of forest fragmentation is also affected by resolution (Turner *et al*. 1989). At coarser resolutions, fragment shape and perimeter length (ie edges) are obscured, and small forest fragments can be lost entirely (Figure 1; Moody and Woodcock 1995; Cain *et al*. 1997; Wu 2004). Evaluations of forest maps typically concentrate on their ability to characterize total forest area, rarely interrogating their competency at capturing forest pattern (Olofsson *et al*. 2014). Even when forest fragmentation patterns are evaluated, the focus is frequently on quantifying interior forest at the exclusion of the forest edge (Riitters *et al*. 2016).

Underestimations in forest area and forest edge

To assess the consequences of omitting forest edges on the US NFI and widely used land-cover maps, we compared estimates of forest area and forest edge area, leveraging the increasing availability and computational feasibility of very high resolution (VHR, 1-m pixel size) land-cover products to map forest edge area in selected regions. VHR maps greatly enhance the ability to characterize landscape heterogeneity, including urban canopy excluded from definitions of forest used in traditional land-cover maps (Wickham and Riitters 2019). For our baseline estimation of forest area, we used VHR maps of the 260,000 km^2 Chesapeake Bay Watershed in 2014 and the 27,000 km^2 Commonwealth of Massachusetts (Appendix S1: Figure S1) in 2016, both of which map tree canopy with up to 98% accuracy (Pallai and Wesson 2017). Doing so established a baseline for quantifying bias in forest area and forest edges relative to the other maps. We performed robustness tests on our estimates of forest cover and forest edge area from the VHR data using a 100-m^2 minimum area threshold. Minimal differences were observed at the county level (Appendix S1: Figure S2).

Applying the methods described in Morreale *et al*. (2021) to estimate forest edge prevalence in the US NFI, we present our results for the NFI as the percent of stems categorized as forest edge. We used Google Earth Engine (Gorelick *et al*. 2017) to calculate forest cover and forest edge area across four satellite-imagery–based forest maps. In the US, counties represent a coherent political boundary within which land-use zoning is typically consistent, and they therefore can function as independent samples for the purposes of this analysis. We aggregated forest cover data—from the 2016 National Land Cover Database (NLCD); the 2016 Land Change Monitoring, Assessment, and Projection (LCMAP) annual product; and the 2016 Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover International Geosphere–Biosphere Programme (IGBP) annual product—to the county level (Yang *et al*. 2018; Sulla-Menashe *et al*. 2019; Brown *et al*. 2020). The spatial resolution of these datasets are 30 m, 30 m, and 500 m, respectively, and we condensed the legend of available forest classes for ease of comparability (Appendix S1: Table S1). This approach provided a representative sample of products with differing definitions of and methods for identifying forests that are commonly used in forest area analyses and forest dynamics modeling efforts.

Underestimates of total forest area led to inaccurate calculations of edge area. In counties with >75% forest cover, only the 500-m MODIS land-cover dataset had significantly

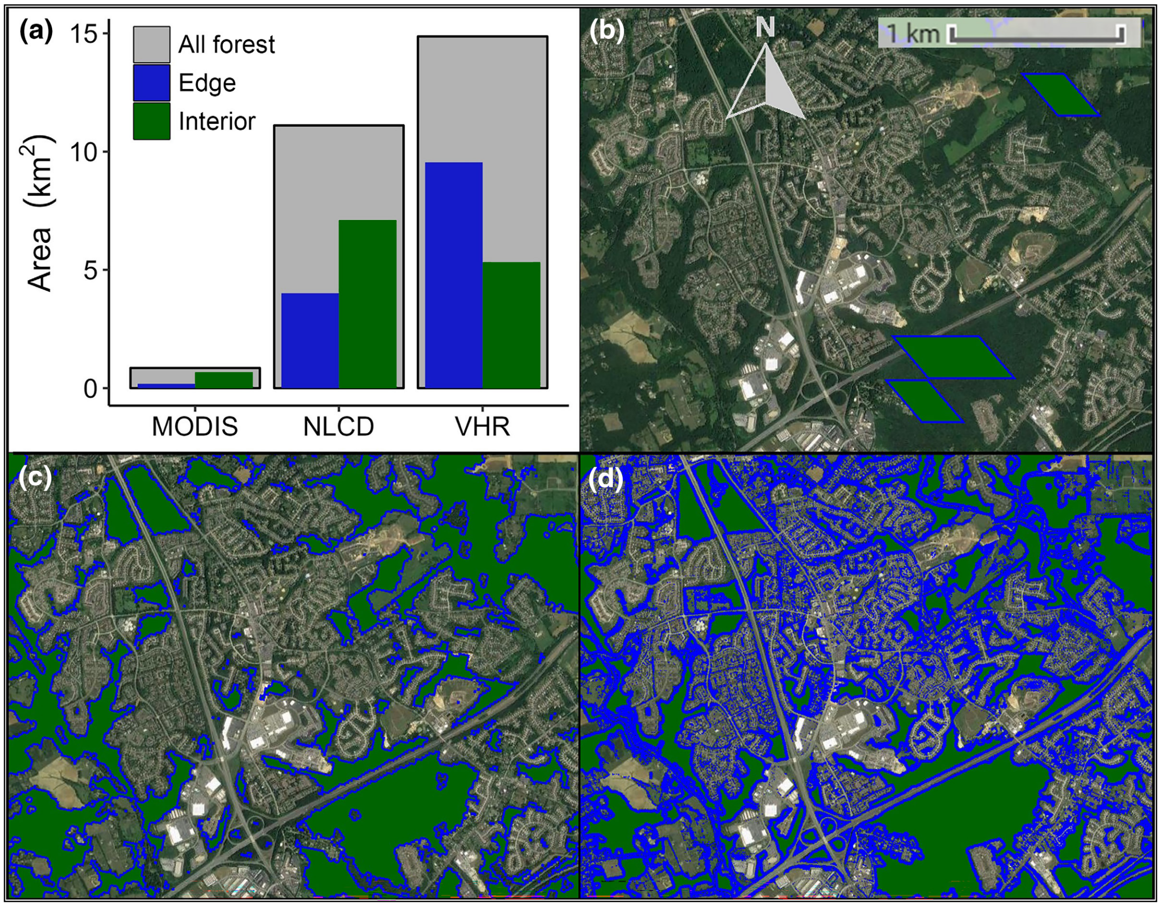

Figure 1. Example of resolution effects on estimates of forest area and forest edge area. Interior forest area (>30 m from a non-forest land cover) is shown in green and forest edge area (≤30 m from a non-forest land cover) is displayed in blue. (a) The area of total forest, edge, and interior from different characterizations of forest fragmentation is shown of a suburban area outside of Baltimore, Maryland. Imagery from Google Earth Engine ©2023 Google (image: NAIP). (b) Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover International Geosphere–Biosphere Programme (IGBP): 500-m pixel size; (c) National Land Cover Database (NLCD): 30-m pixel size; and (d) Chesapeake Bay Watershed Land Cover (very high resolution [VHR]): 1-m pixel size.

different estimates of percent forest coverage of the county land area ($P < 0.001$) when compared to the VHR products (Figure 2a). However, in counties with <75% forest cover, LCMAP, NLCD, and MODIS all underestimated percent forest cover relative to the VHR data products, on average, by 14.5%, 7.9%, and 26.0%, respectively ($P < 0.001$). When we compared estimates of the percent of forest area considered as an edge, the result was more pronounced (Figure 2b). Across all counties in the study areas, average forest edge area was 42.1% of total forest area based on the VHR baseline. The other forest monitoring datasets estimated average edge area across our study region as follows: 25.7% in LCMAP, 24.3% in NLCD, 6.8% in the NFI, and 7.2% in MODIS. When compared with the VHR maps, all products significantly underestimated forest edge area ($P < 0.001$, Tukey's HSD [honestly significant difference] test); in aggregate, underestimates deviated from the average by a range of 16.4% to 35.3%. In addition, we found that in counties with <75% forest cover, coarser-resolution land-cover maps markedly underestimated forest area ($P < 0.001$). Although underestimates of total forest area and edge proportion with increasing resolution are expected, the systematic bias that this introduces in more fragmented areas is rarely, if ever, acknowledged in assessments of forest ecosystem processes. Areas with lower forest cover are frequently more fragmented, with greater numbers of small fragments and larger proportions of edge forest. Moreover, the difference in forest cover estimates from products of the same scale (NLCD and LCMAP) demonstrates that underestimates are driven not only by resolution but also by methodological differences between forest maps. Neither the US NFI nor widely used forest maps accurately account for forest edges as visible in VHR imagery. Systematic undercounting of forest area in counties that are less forested and more fragmented further ensures that forest edges are omitted from evaluations of forest patterns, both implicitly and explicitly.

Forest edge area in each region is also controlled by the drivers and patterns of fragmentation, with alternate land-use regimes resulting in different configurations of forest patches. In our study area, the dominant non-forest land use can

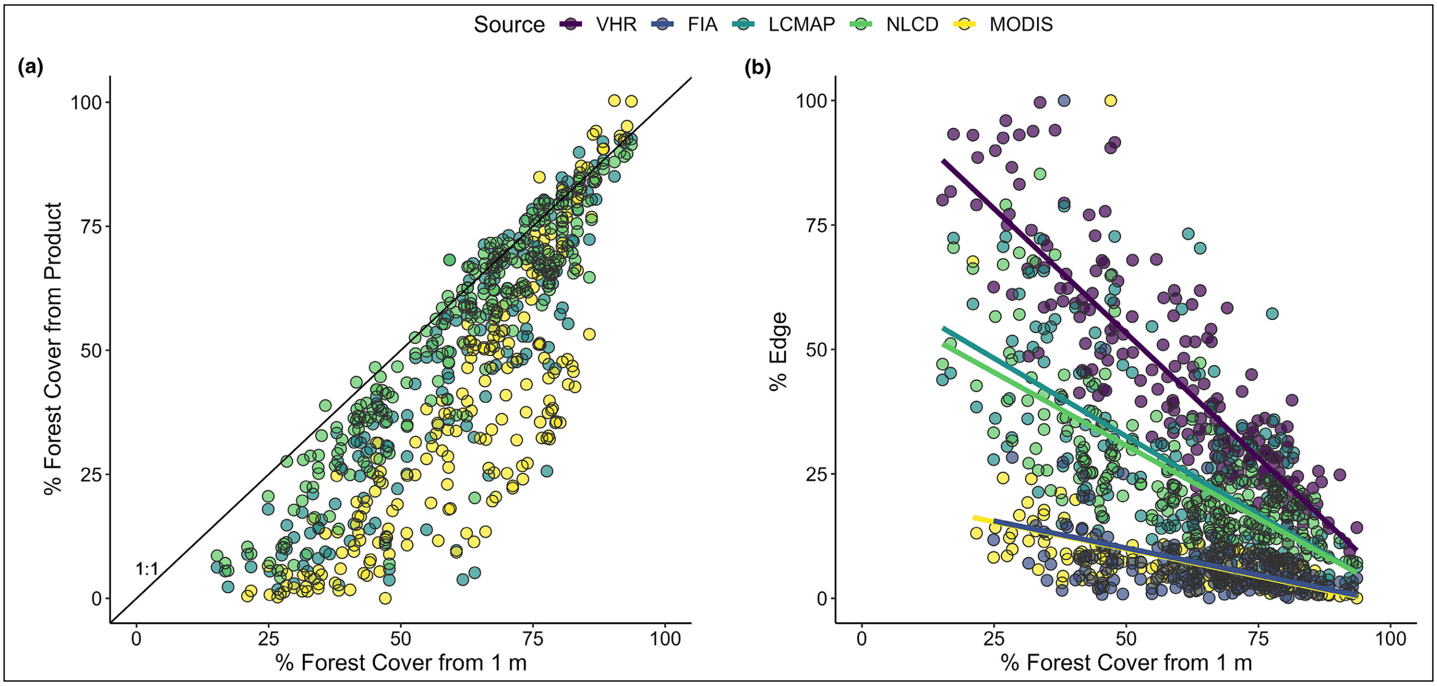

Figure 2. Underestimates of forest edge percent increase with decreasing forest cover. (a) The relationship between county-level percent forest cover from VHR products (*x* axis) and county-level percent forest cover estimates from coarser-resolution remote-sensing products (*y* axis). (b) Relationship between county-level percent forest cover from VHR products (*x* axis) and county-level percent of forest area within 30 m of an edge from all forest monitoring methods (*y* axis). Lines represent best-fit relationship for each product. Pixel resolution for VHR, Land Change Monitoring, Assessment, and Projection (LCMAP), NLCD, and MODIS is 1-m, 30-m, 30-m, and 500-m, respectively.

broadly be subdivided into regions of agriculture and development (Smith *et al.* 2018). In metropolitan regions, the pattern of fragmentation is largely driven by residential development set within the dominant forest matrix (Figure 3b). This results in many small forest fragments divided by roads and buildings, with high proportions of edge forest. In contrast, forests in agricultural areas are often more consolidated or in longer riparian sections or hedgerows within a matrix of farmland (Figure 3a). We found that the relationship between forest edge percent and forest cover differed significantly between forests surrounded by agricultural and urban developed uses (Figure 3, a and b). On average, in areas dominated by development, the percent of all forest categorized as edge was 72.0%, whereas in agricultural counties that percent fell to 37.0%. Two regions with the same total forest area can have large differences in forest edge area depending on the dominant land-use regimes and consequent forest configuration. Approaches that depend solely on total forest area and do not address landscape heterogeneity will ultimately neglect this distinction and the consequences of fragmentation on ecosystem processes.

Edges as a distinct class

One reason that edges are undercounted in forest maps is that they pose a special challenge for categorical land-cover classification. These datasets are produced by relating satellite measurements of spectral reflectance with discrete land-cover or land-use labels (eg forest, development, water). Pixels that intersect a forest edge often include a mixture of both forest and the adjacent non-forest; these so-called "mixed pixels" are not easily classified into a single category (Woodcock and Strahler 1987). Classifier training data, derived from manually labeled high-resolution imagery, often focus on examples that are most representative of the chosen classes (ie full forest pixels), while the designation of unlabeled mixed pixels in the mapped output is left to the algorithmic classifier. As a result, class labels associated with these pixels often have higher uncertainties and can result in frequent misclassification of forest edges as non-forest, especially when compared to the forest interior.

In an accuracy assessment of a land-cover map created for the Massachusetts Audubon's 6th Losing Ground Report (Ricci *et al.* 2020), human interpreters were explicitly directed to identify pixels containing forest edges to evaluate how the classifier performed on literal edge cases. Analysis of interpreted results indicated that pixels labeled as forest edge were only classified as forest 44.8% of the time, as compared with a 94.6% rate for pixels labeled as the forest interior (Appendix S1: Figure S4). The high misclassification rate of mixed pixels contributes to systematic underestimates of forest edges, a bias that increases with pixel size as mixed pixels become more common. To address this problem, we advocate for leveraging the distinct spectral signature of mixed pixels to create a new class for forest edges. The creation of a forest edge class in land-cover maps would allow for explicit mapping of edges, more accurate

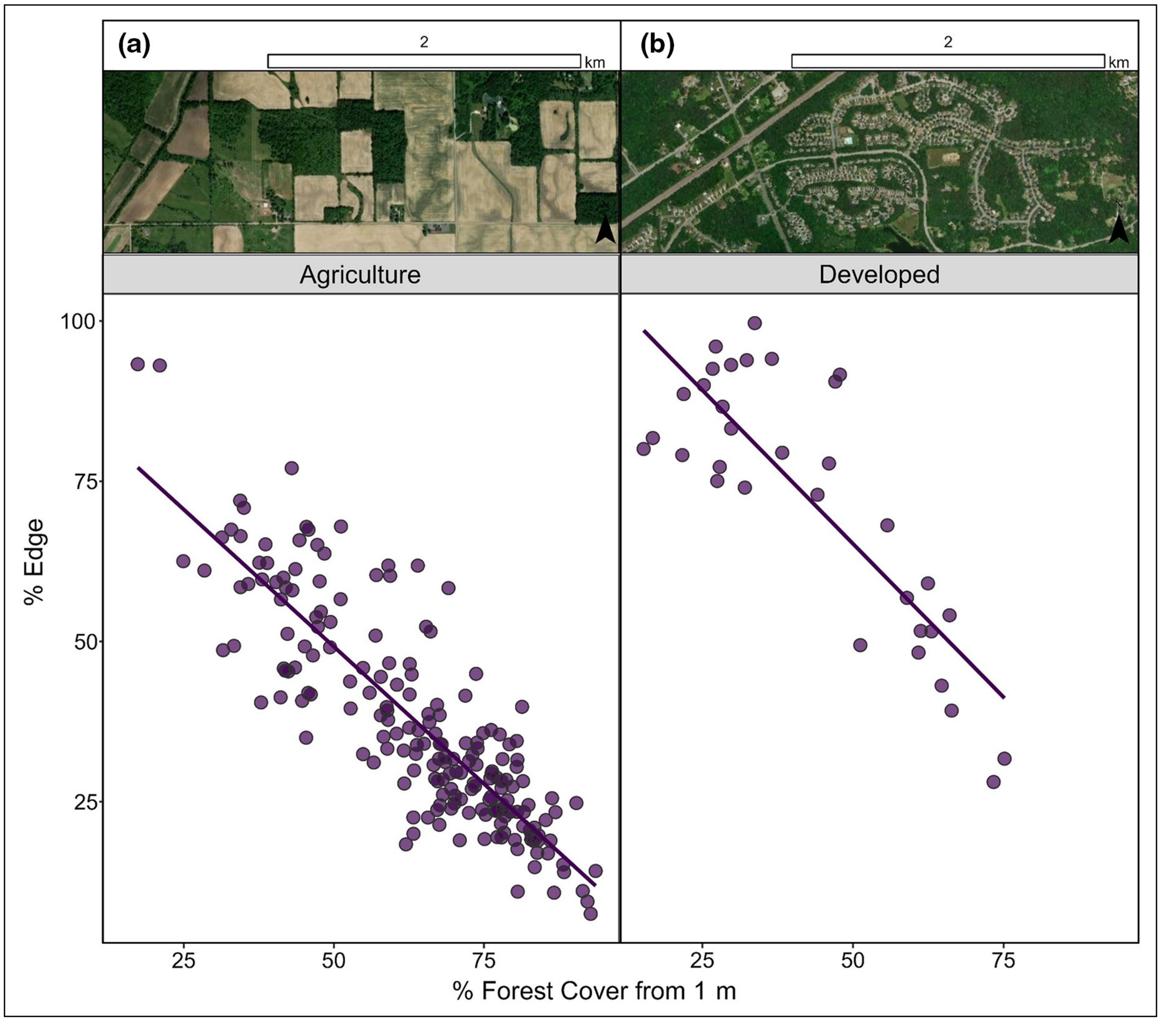

Figure 3. Development leads to higher amounts of forest edge than agriculture. (a) Relationship between percent of forest edge area and percent county forest cover in counties where agriculture is the majority non-forest land cover (an example of fragmentation patterns in an agricultural area). (b) Relationship between percent of forest edge area and percent county forest cover in counties where development is the majority non-forest land cover (an example of fragmentation patterns in a developed region). Individual counties are represented as points and lines represent the best-fit relationship. Imagery from Google Earth Engine ©2023 Google (image: NAIP).

characterizations of fragmentation patterns, and increased overall map accuracy.

Making edges count

Our analyses demonstrate a substantial and systematic underrepresentation of forest area and edge forest area in traditional land-cover maps and the US NFI. Moreover, next-generation forest products created through active remote sensing (eg biomass maps from the Global Ecosystems Dynamics Investigation) rely on the same traditional methods for scaling and interpolation, ensuring that they too will misrepresent fragmentation. Consequently, we conclude that temperate forest edges are misrepresented in large-scale assessments of ecosystem processes, ecosystem models calibrated on NFIs, and forest C budgets (Panel 1 and Figure 4). While our analyses of forest edge area and aboveground C storage focus on temperate forests of the northeastern and mid-Atlantic US, the underlying underestimate of forest edge area is likely applicable throughout the temperate forest biome and beyond. On the basis of our observations, we offer the following recommendations to ensure better representation of the fragmented ecological reality of modern temperate forests.

National forest inventories must explicitly account for the prevalence of persistent fragmentation

The ongoing implementation of the Urban FIA as an expansion of the US NFI may serve as a template for how to augment plot sampling without affecting the existing design. In addition, and as with the Urban FIA, the inclusion of more information about abutting non-forest land uses would improve understanding of the edge forest ecosystem and

Panel 1. Consequences of underrepresenting forest area and edges for carbon accounting

Small forest fragments and forest edges are highly prevalent and ecologically distinct from the forest interior. Excluding them from measurements and models has large consequences for calculations of forest ecosystem services, particularly carbon (C) budgets. To illustrate the consequences of underrepresenting forest edges, we made two estimates of aboveground forest C in the Chesapeake Bay Watershed. First, we derived county-level values of aboveground forest C per hectare from the US national forest inventory (NFI), using the *rFIA* package in R (Stanke *et al*. 2020). For a baseline estimate, we followed a traditional approach where we used forest area from the National Land Cover Database (NLCD) to calculate total aboveground C for each county. We then altered our calculation to correctly account for the fragmented forest landscape by using interior and edge forest area totals from very high resolution (VHR) land-cover maps and included observed US Forest Service Forest Inventory and Analysis (FIA) edge enhancements of aboveground C storage (following Morreale *et al*. [2021]). Through the addition of previously excluded forest cover, mostly edge forests, we detected a median 14.8% increase in aboveground C estimates per county in our study area and a total increase of 130.4 teragrams of carbon (Tg C) (Figure 4; Appendix S1: Figure S3). In highly fragmented counties where development or agriculture was the dominant land cover, we found median increases of 74.2% and 23.8%, respectively, in estimated county forest C storage. These increases in aboveground forest C pools are currently unaccounted for in C budgets. As states and municipalities increasingly commit to nature-based climate solutions, complete accounting of forest area and edges is imperative to accurately quantify biogenic sequestration.

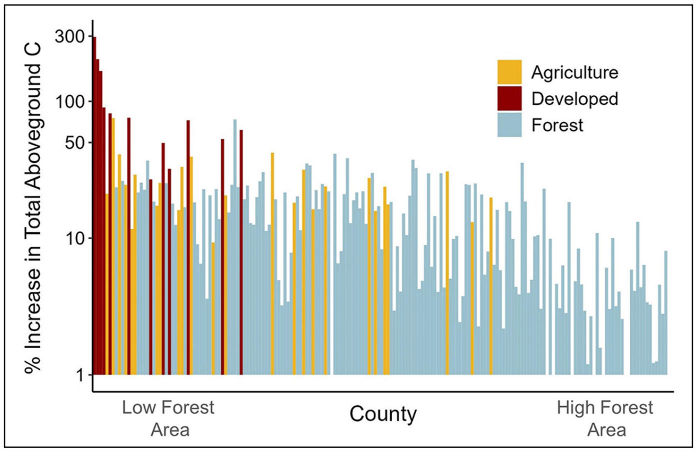

Figure 4. Undercounting forest edges substantially changes estimates of aboveground forest carbon (C). The percent increase per county in total aboveground C across the Chesapeake Bay Watershed portion of our analysis. Counties are colored by the dominant land cover in the county and ordered from lowest forest area to highest forest area. The *y* axis is log-scaled for readability. In four counties, the 1-m maps have smaller total forest area, resulting in slight negative differences in total aboveground C; these counties are not displayed in the figure for visual simplicity.

better align with the forest transition zone framework (Edgar *et al*. 2021).

Increased use of VHR forest maps for detailed characterizations of forest patterns

As we demonstrate, increasingly available VHR forest products reveal large portions of the forest landscape that are invisible to methods with coarser resolution. The need for VHR land-cover data is heightened by distinct patterns of forest fragmentation across land-use contexts. The complexities of fragmentation patterns that result in major changes in edge forest area are also frequently invisible to the traditional methods of forest area assessment. VHR data should be used to develop scaling relationships to enable estimates of forest edge area from coarser-resolution products where VHR data are unavailable.

Forest edges should be included as their own land-cover class or classes in maps derived from coarser-resolution satellite imagery

A key source of inaccuracies in many coarser-resolution remote-sensing products derives from challenges in categorizing edges and mixed pixels as either a forest or a non-forest class. Beyond improved classification of mixed pixels, a discrete forest edge class would enable land-cover maps to directly represent the reality of the modern forest landscape and the distinct forest edge ecosystem.

Explicitly include anthropogenic forest edges in carbon accounting, forest models, and predictions

While limited, the growing literature on forest transition zones can be used to parameterize the altered ecosystem processes of the forest edge, and future investigations should specifically focus on variability in different ecoregions across the temperate forest biome.

Conclusion

Because forest edges are markedly underrepresented in national inventories, land-cover maps, and research, edges are often invisible on the landscape, particularly in areas where they are most prevalent. Nevertheless, edges are a ubiquitous feature of modern forests and are the parts of forests that people interact with the most. To fully understand modern and future forest ecology, we must first acknowledge the forests that we have, not as we imagine them to be.

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Data Availability Statement

Data and code (Morreale *et al*. 2024) are available on the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/1dacd88e847defa27ec978317b4e33a7. These materials are also available in the Harvard Forest Data Archive under accession code HF450.

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