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PERSPECTIVE

Inferring the effects of partial defoliation on the carbon cycle from forest structure: challenges and opportunities

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Disturbances are increasing in forests worldwide (McDowell *et al* 2015) and, in some regions, disturbance regimes are shifting to include a greater number of partial defoliation events that differ in timing, duration, distribution, and extent of leaf loss (Cohen *et al* 2016, figure 1). The global area already affected by defoliation is immense. For example, biotic disturbances impact 44 million hectares or 3% of the total forestland worldwide on an annual basis (Kautz *et al* 2017). Rather than causing complete and immediate tree mortality across entire landscapes, biotic disturbances from insects and pathogens and disturbances from drought and extreme heat are often spatially diffuse and slow-acting, making their effects on the carbon (C) cycle uncertain, variable, and difficult to predict (Amiro *et al* 2010). This uncertainty is important: the impacts of partial defoliation scale nonlinearly with C cycling processes (Medvigy *et al* 2012) and, in some regions, exert a fundamental control on landscape-level C balance (Clark *et al* 2010). As a result, partial defoliation-C cycling interactions represent a key knowledge gap relevant to ecological forecasting, remote sensing, and disturbance ecologists (Hicke *et al* 2012).

In this *perspective*, we highlight current challenges and emerging opportunities for improving the characterization of partial defoliation and inferring its effects on ecosystem-to-landscape C cycling processes from observations of forest structure. As members of FLUXNET, a global network of eddy-covariance C flux towers, we emphasize the tower footprint scale, which typically encompasses tens of hectares. We focus on ground and remote sensing tools used to characterize disturbance, because field inventories and satellite data are commonly used to infer

functional, including C cycling, responses to disturbance. Highlighting examples from our site, the University of Michigan Biological Station, we underscore three challenges and areas of joint opportunity for C flux researchers, remote sensing scientists, and field ecologists: (a) sustaining long-term complementary ground-and space-based measurements of moderate severity disturbances and their C cycling consequences; (b) developing meaningful ecological indicators of partial defoliation that can be remotely sensed; and (c) resolving, representing, and interpreting spatial and temporal heterogeneity associated with partial defoliation.

1. Challenge: sustaining coordinated ground- and space-based measurements of partially defoliated forests

Long-term, detailed, and systematic records documenting partial defoliation events are often lacking or incomplete for FLUXNET sites, limiting generalized understanding of how this form of disturbance affects C fluxes. While the network has extensively characterized the effects of severe, stand-replacing disturbances on the C cycle, few forested sites report defoliation source, extent, and severity (Balodochi 2008). For example, a query of the FLUXNET2015 dataset (Pastorello *et al* 2020), an open dataset of C fluxes for ecosystems worldwide, returned only ten North American forests reporting at least ten consecutive years of open C flux data (totaling 121 site years) and none of those documented partial defoliation in their metadata (supplement A available online at stacks.iop.org/ERL/17/011002/mmedia); this lack of reporting is true for our Ameriflux US-UMB

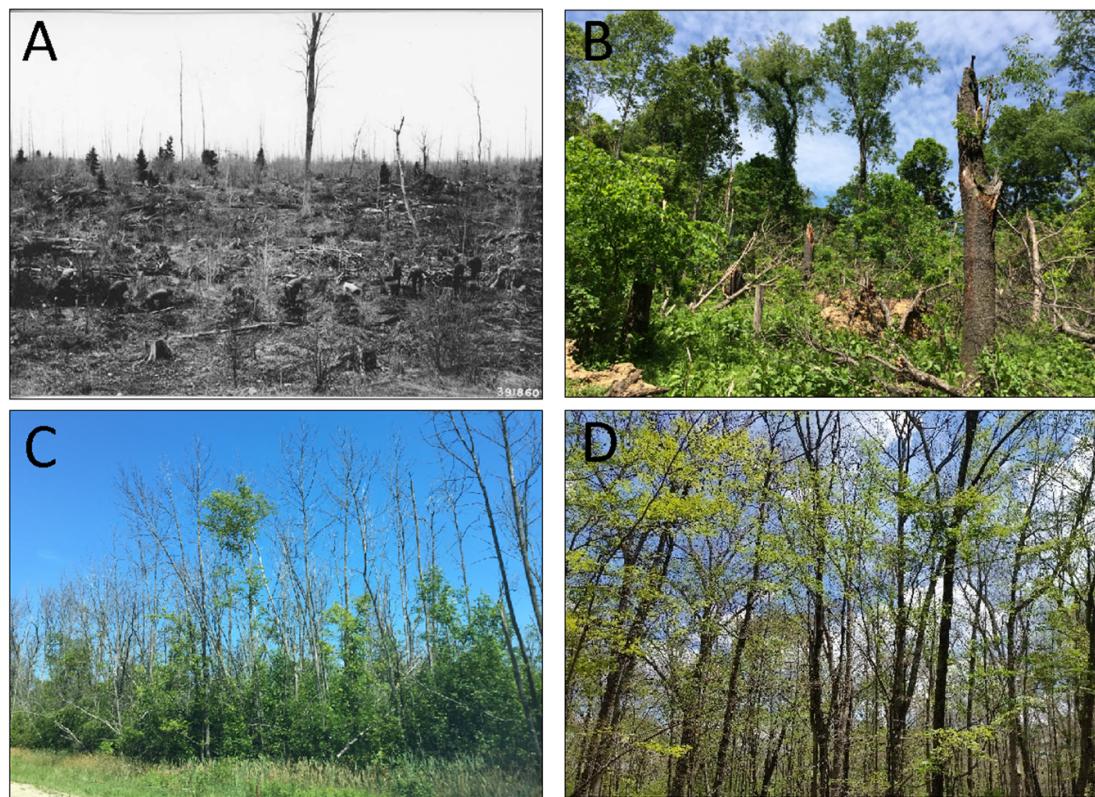


Figure 1. In many forested regions, disturbance sources and severities are diversifying to not only include severe, catastrophic disturbance (A), but also moderate severity disturbance from drought and extreme weather events (B), vascular-disrupting insects (C), and defoliating insects (D). These low-to-moderate severity disturbances partially, rather than fully, defoliate canopies and, in doing so, imprint unique structural signatures that are expected to lead to variable carbon cycling responses. Credit: Forest History Society, Durham, NC. Reproduced with permission.

site, even though forest tent caterpillar defoliation was observed in 2010 and may have temporarily reduced gross primary production (GPP) (Gough *et al* 2013). When defoliation is documented, there is no standardized ground-based characterization of canopy structure across sites, limiting robust network-wide comparisons of disturbance severity, frequency, and source (Amiro *et al* 2010). Consequently, we can align C flux responses to partial defoliation with ground and satellite measures of canopy change at only a few sites with well-documented and ground-verified disturbance histories.

Even when defoliation is extensively characterized, canopy structure and tower footprint-wide C fluxes do not always correspond, limiting the prediction of C cycling responses to disturbance from means of structural information. For example, we did not observe consistent relationships between canopy structural indices and C fluxes within the footprint of the Forest Accelerated Succession Experiment (figure 2, FASET, Ameriflux US-UMd), in which 40% of mature canopy trees within a 39 ha area were killed through stem girdling (Gough *et al* 2013). Mean footprint leaf area index (LAI) correlated moderately well with the mean Landsat normalized difference moisture index (NDMI, $r^2 = 0.59$, $P = 0.04$), an

index used to estimate insect herbivory and partial canopy disturbance (Townsend *et al* 2012). This degree of correspondence is encouraging, indicating that ground- and spaceborne estimates of canopy structure generally tracked one another, even though this moderate level of defoliation can be difficult to detect using existing satellite remote sensing tools (Cohen *et al* 2017). Further, both LAI and NDMI detected peak defoliation in 2010, consistent with on-the-ground observations of tree mortality. However, GPP's relationship with indices of canopy structure varied, underscoring the challenges associated with linking structure and C cycling processes after disturbance. Neither mean LAI nor NDMI correlated with *annual* GPP ($P = 0.73$ and 0.21, respectively), while NDMI, but not LAI, correlated with cumulative *summer and fall* GPP ($P = 0.01$, $r^2 = 0.75$ and $P = 0.14$, respectively). A stronger correlation between NDMI and GPP during the summer and fall is consistent with findings that variable spring leaf phenologies obscure relationships between canopy structural indices and annual production (Richardson *et al* 2010). Correlations that vary by season could also result from our small sample size, a spatiotemporally variable flux footprint, and a GPP signal that is responding to biophysical factors such as climate. Such limitations highlight the utility of

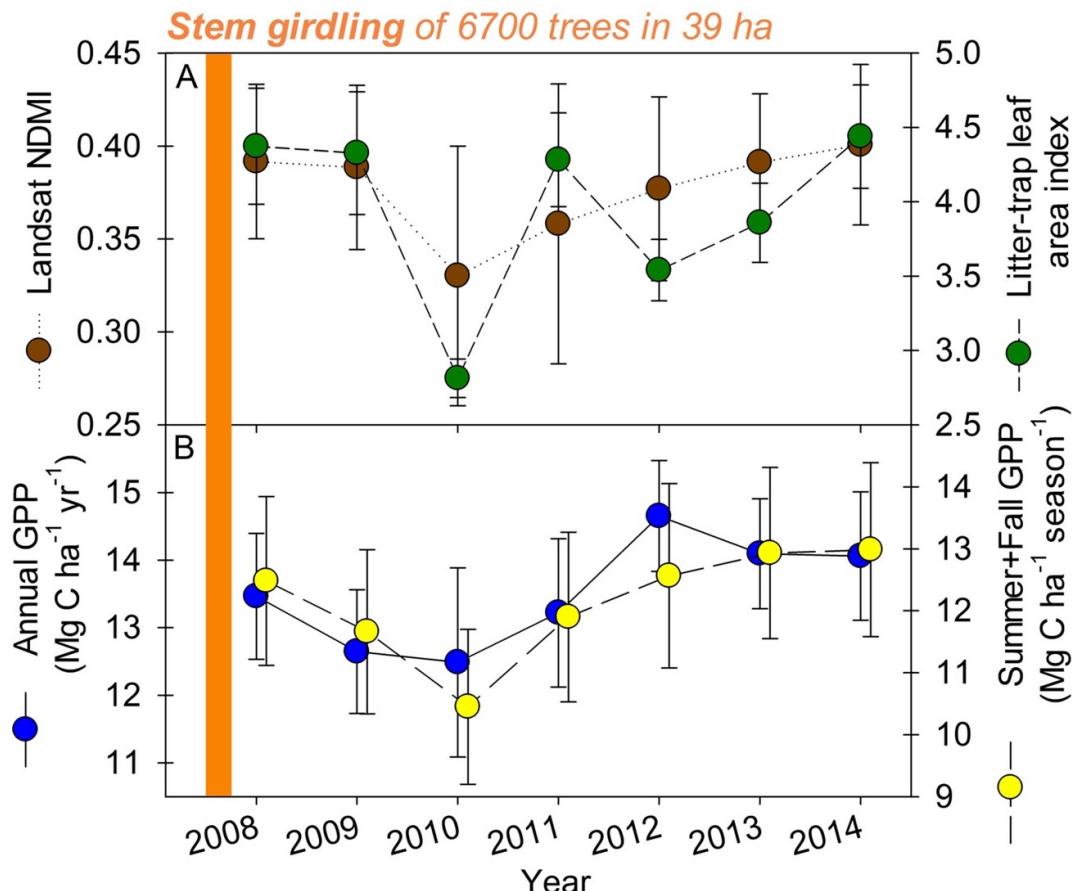


Figure 2. Mean growing-season Landsat NDMI (–1 to 1), litter-trap leaf area index (Gough *et al* 2013, A) and FLUXNET2015 annual and summer + fall gross primary production (GPP, supplement A), (A) for the FASET site, in which >6700 (or ~40% of canopy trees of two species were stem girdled in 2008 within a 39 ha area. Correlation between leaf area and defoliation shown by NDMI (A) shows moderate correspondence of ground- and spaceborne estimates of canopy structure following a well-documented experimental disturbance, and (B) highlights the mixed correspondence between canopy structural indices and GPP. Values are averages for plots in the eddy-covariance flux footprint shown in figure 3.

long-term, coordinated measurements accompanied by well-documented disturbance histories when parsing subtle signals of partial defoliation from variable time-series.

2. Challenge: developing robust ecological indicators of partial defoliation that can be used to infer carbon fluxes

The variable correlation that we observed between canopy structure and C cycling processes after disturbance points to a second challenge: predicting how C fluxes will respond to partial defoliation events requires greater understanding of which canopy structural and spectral properties correspond with changes in C fluxes at ecosystem-to-landscape scales. Defoliation not only modifies the spectral signatures of canopies and reduces leaf area, but disturbance physically restructures vegetation (Atkins *et al* 2020). The physical re-arrangement of vegetation that is precipitated by defoliating disturbances affects plant access to growth-limiting resources and determines leaf physiology, which in turn may alter

whole-canopy C fluxes (Gough *et al* 2013). Consequently, three-dimensional expressions of canopy structural diversity or complexity within tower footprints may be more powerful indicators of C flux responses to partial defoliation than those that are dimensionless and approximate leaf area or quantity. For example, we found that a terrestrial lidar-derived three-dimensional measure of canopy complexity—rugosity—was superior to LAI, species diversity, and biomass quantity as a predictor of first-year net primary production responses to experimental partial defoliation (Gough *et al* 2021). While a number of satellite-derived canopy structural and spectral properties respond to disturbance (Kennedy *et al* 2018), it is unclear which are most useful to inferring C fluxes at the footprint scale, and why.

Echoing the calls of others (McDowell *et al* 2015), we encourage scientists across multiple areas of expertise to partner in advancing more potent, ecologically-informed measures of canopy structure that predict how C fluxes respond to partial defoliation. Thinking beyond LAI and proxies of leaf area and quantity, next-generation canopy structural indices may integrate spectral and three-dimensional

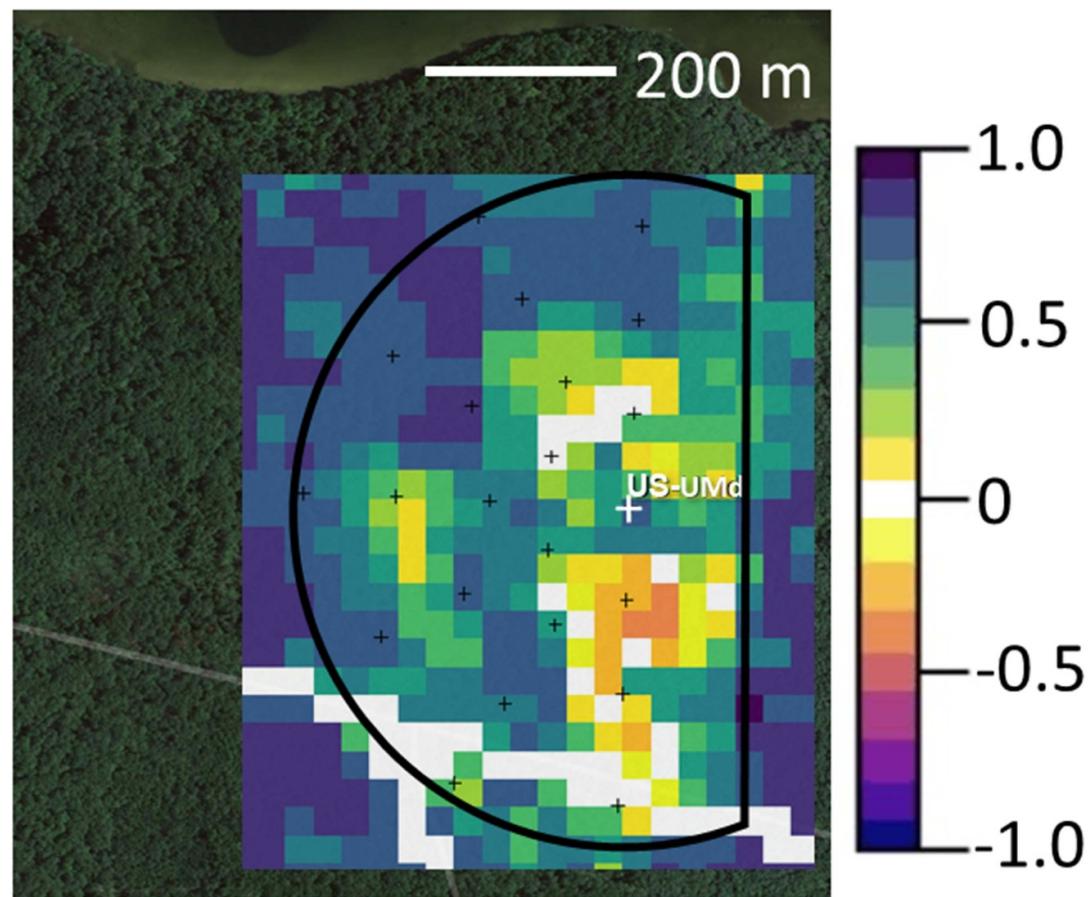


Figure 3. Correlation coefficients (r) for 30 m NDMIs and US-UMd eddy-covariance based gross primary production (June–August) within the (half-circle) FASET treatment area illustrates the high degree of spatial heterogeneity associated with partial defoliation and the correspondingly variable relationships with eddy-covariance carbon fluxes. The white '+' symbol highlights the Landsat pixel centered on the eddy-covariance tower and black '+' symbols illustrate sampling plots for which leaf area index is measured.

structural information and thus require multiple platforms and expertise to develop (Huang *et al* 2019). Advances on these fronts will require the collective knowledge of theorists and modelers, empiricists, and remote sensing scientists and eco-informatics capable of translating and distilling large, complex, and multi-instrumental datasets into next generation integrative ecological indicators of partial defoliation response. Such coordinated, interdisciplinary efforts have led to significant advances in the remote sensing of biodiversity (Asner *et al* 2015), along with the development of widely used standardized metrics for comparing biodiversity and its effects on ecological processes across disturbance sources, studies, and sites.

3. Challenge: resolving and interpreting spatial and temporal heterogeneity

Unlike severe, homogenizing disturbances from catastrophic fire or clear-cut harvesting, partial defoliation caused by drought, windthrow, ice storms, insects, and pathogens may increase spatiotemporal heterogeneity in forest structure and biodiversity

(Foster *et al* 2013). Temporally, heterogeneity may arise from differences in the timing, intensity, and duration of defoliation, and, in the case of pathogens, lags between infection and defoliation. Spatially, partially defoliating disturbances may introduce variation to already structurally and biologically variable flux tower footprints, augmenting the patchy spatial distribution of vegetation. Such variability is enhanced because of spatially and temporally uneven tree mortality, variable distributions and specificities of pests and hosts, and pre-disturbance differences in leaf area and plant densities.

At our FASET site (US-UMd), we observe large variation in canopy structure within the C flux tower footprint, illustrating how the Landsat pixels selected for comparison with tower GPP affects interpretation of canopy structure-flux relationships. For example, within the experimentally disturbed area of FASET, we observed variable correspondence (from $\sim -0.21\%$ to 0.86%) between tower-based summer GPP and Landsat pixel-scale (30×30 m) defoliation (figure 3). This large range underscores the spatial dependencies of canopy structure-C flux relationships, demonstrating that where structure is sampled

within the flux footprint—whether from space or on the ground—can significantly influence the sign and strength of correlation, and interpretation of how disturbance reshapes canopy-C flux interactions. Additionally, because C flux tower footprints change in size and location over time, correlations between spatiotemporally dynamic C fluxes and fixed Landsat scenes and ground canopy structural measurements are problematic (Chu *et al* 2021). Consequently, analyses that do not account for changing footprint sizes, shapes, and locations may lead to mismatched canopy structure-C flux comparisons.

4. Opportunities

Despite these challenges, the confluence of new satellite remote sensing platforms, long-term ecological networks collecting ground- and airborne canopy structural data, and a proliferating open science culture and infrastructure suggest that partial canopy defoliation characterization and interpretation is poised to advance (challenge 2). For example, NASA's 2 year old Global Ecosystem Dynamics Investigation satellite-based platform is already supplying global lidar-derived canopy structural information (Potapov *et al* 2021), filling an important three-dimensional data gap that is complementary to decades long-recorded optical earth imagery. Moreover, planned satellite platforms, including ESA's Fluorescence Explorer, Germany's Environmental Mapping and Analysis Program (EnMap), and NASA's Hyperspectral Infrared Imager (HyspIRI), are designed specifically to monitor vegetation health and disturbance. In the future, the combined use of canopy structural and spectral information to detect, differentiate, and make predictions about the effects of partial canopy defoliation on ecosystem C cycling processes should improve ecological forecasting and enable the adaptive management of disturbance in near real-time.

In addition, long-term ecological networks that systematically collect and deliver open data will allow opportunistic multi-platform observations of disturbance responses (challenge 1, Alton 2020). For example, the National Ecological Observatory Network's (NEON) 30 year operating timeframe will inevitably encompass unplanned disturbances ranging in severity and origin, supplying a rich complement of ecosystem C cycling and ground vegetation data paired with co-located airborne and satellite remote sensing datasets for exploration.

Finally, progressive changes in the culture and infrastructure of open science are making an unprecedented quantity of co-collected tower C flux and remote sensing data publicly available through networks such as NEON and FLUXNET (Bond-Lamberty 2018). These open data have the potential to improve equity of access, increase the return on investment to taxpayers, and accelerate

scientific discovery (Lowndes *et al* 2017). Moving forward, we suggest ecologists, remote sensing scientists, and C cycling researchers engage in an iterative cycle, in which the design of remote sensing tools and products is informed by ecological theory, modeling, and prior observation; evaluated against field observations; and the results used to clarify and revise ecological understanding and inform the next generation of remote sensing tools and products (challenges 2, 3). Such an integrative model-remote sensing-experimental framework (Kyker-Snowman *et al* 2022) holds the potential to transform our understanding of how defoliating disturbances reshape the structural and functional attributes of ecosystems in a changing climate.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.17190/AMF/1246107>.

Data and code

Meteorological carbon flux data associated with the Forest Accelerated Succession Experiment are available via FLUXNET2015 (<https://fluxnet.org/data/fluxnet2015-dataset/>); leaf area index data are available via Ameriflux's Biological, Ancillary, Disturbance, and Metadata (BADM, <https://ameriflux.lbl.gov/data/badm/>). Landsat surface reflectance imagery can be downloaded from Google Earth Engine.

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