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**Impacts of a regional multi-year insect defoliation event on seasonal runoff ratios
and instantaneous streamflow characteristics**

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Abstract

Repeated moderate severity forest disturbances can cause short- and long-term shifts in ecosystem processes. Prior work has found that stand-replacing disturbances (e.g., clear-cutting) increases streamflow in temperate forests, but streamflow responses to repeated moderate severity disturbances are more equivocal. This study examined a moderate disturbance caused by an unexpected population irruption of the invasive insect *Lymantria dispar* (common name: gypsy moth) in 2015-2017. This irruption resulted in major but spatially heterogeneous defoliation due to leaf consumption by larvae during the summer growing season, which reduced leaf index area and associated evapotranspiration. Our regional approach in southern New England, USA used data from 88 U.S. Geological Survey (USGS) stream gages to assess whether changes in watershed runoff ratios and instantaneous streamflow characteristics were associated with satellite-derived metrics of forest condition (i.e., defoliation). Using stream gages with at least 15 years of baseline flow data, we calculated subwatershed runoff ratio values for a baseline period and quantified anomalous departures from baseline runoff ratios for the 2015-2017 period of *L. dispar* defoliation. We found a small linear increase in seasonal runoff ratio anomalies that was associated with defoliation intensity. We also found larger volumes of high and medium instantaneous streamflows compared to baseline flow conditions in watersheds with more intense defoliation. This study provided important insights into the impacts of moderate

disturbance on ecohydrology in mesic temperate forests with a methodological approach that assessed the impacts of spatially heterogeneous and repeated moderate disturbance at a regional scale.

1. Introduction

Forest insects and pathogens (FIPs) are globally widespread agents of disturbance that may exhibit complex and potentially synergistic feedbacks with climate change processes and impacts (Anderegg et al., 2015; Hicke et al., 2012; Seidl et al., 2017). Large or repeated FIP outbreaks cause tree stress and mortality, which can increase water runoff at the ecosystem scale through the reduction in the evapotranspiration flux through trees (Kim et al., 2017). The stress and mortality impacts of FIPs can change ecosystem carbon and nutrient cycling, ultimately altering associated ecosystem services (Kim et al., 2017; Metcalfe et al., 2014). Forests in the Northeastern U.S. have become host to a broad diversity of introduced or nonnative FIPs (Liebhold et al., 2013). At a regional scale FIP disturbances to Northeastern U.S. ecosystem processes have major economic and ecologic costs (Lovett et al., 2016). This study focused on the ecohydrological impacts of *Lymantria dispar* (common name: gypsy moth) during an unexpected population irruption in 2015-2017 across Southern New England within the Northeastern U.S.

Lymantria dispar is a moth species native to the temperate forests of Western Europe that causes tree stress by consuming leaves (*i.e.*, defoliation) in its larval stage. At high population densities *L. dispar* are generalists, but *Quercus spp.*, which represent 62% of forested area in Southern New England, are the preferred hosts (Liebhold et al., 1997). *Lymantria dispar* was introduced to the Eastern U.S. in 1869, and severe outbreaks

occurred periodically until the late 1980s, when an introduced fungal pathogen, *Entomophaga maimaiga*, decimated *L. dispar* populations and has since played a key role in maintaining low population densities (Andreadis and Weseloh, 1990; Hajek and Roberts, 1991). The 2015-2017 *L. dispar* population irruption, or outbreak, was the most widespread and intense series of repeated *L. dispar* defoliation events in Eastern U.S. forests since the introduction of *E. maimaiga* in the late 1980s. Range expansion and the increasing likelihood of drought (since drought conditions diminish *E. maimaiga*'s control of *L. dispar*) mean that future *L. dispar* irruptions might occur again in the Northeastern U.S. region (Huntington et al., 2009; Liebhold et al., 1994). *Lymantria dispar* irruptions are particularly hard to predict and are generally heterogeneous across a landscape (Liebhold et al., 2013).

During the summer growing season, forest water storage and transport in the Northeastern U.S. is primarily restricted to upper permeable soils (Easton et al., 2007), and tree evapotranspiration (ET) is the dominant water flux out of the ecosystem (Dingman, 2015). Since defoliation by *L. dispar* larvae disrupts the ET flux through trees, we expected defoliation to increase streamflow through an increase in water runoff that otherwise would have been released to the atmosphere as ET. Previous studies have found that watersheds affected by stand-replacing disturbances like harvest or fire experience quasi-linear increases in seasonal water yield with declines in vegetative cover, but that changes are negligible with a decline less than 20% in vegetation

abundance (Bosch and Hewlett, 1982; Brown et al., 2005). Additional recent work has confirmed that in forests with severe tree mortality, water yield increases with declines in evapotranspiration (Poon and Kinoshita, 2018), and this relationship has been observed through increased streamflow across different ecoregions (Wine et al., 2018).

Research thus far suggests that the hydrological responses to biotic disturbance from FIPs are more complex than fire or logging. Most studies on FIPs and ecohydrology are within water-limited Western U.S. forests (Mirus et al., 2017) where researchers found that tree mortality from bark beetles can increase streamflow (Bearup et al., 2014) and soil moisture (Reed et al., 2018) due to the reduction in tree evapotranspiration. However another study found that tree mortality from bark beetles enhanced soil evaporation due to reduced tree cover, leading to no net change in streamflow (Biederman et al., 2014). A meta-analysis of mesic temperate forests, which are similar to those found in the Northeastern U.S., found that most defoliating FIPs caused no change in runoff within forested ecosystems, with a few exceptions that created a slight increase in runoff (Oda et al., 2018). In Massachusetts specifically, a study on the ecohydrological impacts of the invasive insect hemlock woolly adelgid (*Adelges tsugae*) found a 15.6% annual increase in stream discharge with a 24-37% decrease in evapotranspiration during infestations (Kim et al., 2017).

The life cycle and temporal dynamics of FIPs can also influence the extent and severity of ecosystem impacts. For example, the temporal dynamics of *A. tsugae* stress

are quite different from those of *L. dispar*, where *A. tsugae* causes a persistent, long-term stress and *L. dispar* disturbance is a short-term pulse disturbance that occurs over a few months. Despite the shorter temporal window of *L. dispar* impacts, deciduous trees defoliated by *L. dispar* could influence ecosystem water budgets since these species have significantly higher ET rates during the growing season than hemlock (Munger et al., 2012). A previous study investigated changes in carbon and water cycling associated with defoliation by *L. dispar* in the New Jersey pine barrens and found that defoliation was associated with an ET decline of about 7% for a single year of defoliation in oak-pine forests (Clark et al., 2012). Another study during the 2015-2017 *L. dispar* irruption noted changes in stream nutrient cycling and a nearly five-fold increase in stream discharge in a single small watershed in Rhode Island (Addy et al., 2018). This prior work indicates a strong potential for streamflow to change with moderate and repeated defoliation from *L. dispar*, and in this study we conducted a regional analysis of streamflow changes across multiple watersheds in response to the 2015-2017 *L. dispar* defoliation event.

To assess the regional impacts of *L. dispar* defoliation during the 2015-2017 irruption on streamflow, we combined a published satellite-based forest disturbance data product (Pasquarella et al., 2017) with data from the U.S. Geological Survey (USGS) stream monitoring network. Due to spatial heterogeneity in regional defoliation patterns, subwatersheds across the region experienced large variation in defoliation

severity during the multi-year irruption event, which ranged from no defoliation to three consecutive years of severe defoliation. In this analysis we investigated two primary hypotheses:

1. Watersheds with more severe defoliation will have larger departures from the baseline runoff ratio.
2. Defoliation intensity will change instantaneous streamflow characteristics, specifically increasing the volume of instantaneous 15-minute streamflow.

To test these hypotheses, we used a regional approach that assessed changes in streamflows associated with defoliation by connecting a Landsat-derived assessment of forest condition, stream discharge data from regional USGS stream gages, and Daymet precipitation data. We compared runoff ratios and instantaneous streamflow characteristics during the 2015-2017 *L. dispar* irruption years to a 1995-2014 baseline time period to test whether departures from the baseline runoff ratio and streamflow were associated with *L. dispar* defoliation intensity.

2. Data and Methods

2.1 USGS stream gage data

We used data from 88 USGS stream gages in Connecticut, Massachusetts, and Rhode Island to quantify potential changes in streamflow across Southern New England during the 2015-2017 *L. dispar* irruption. Using the USGS stream gage metadata

(Falcone, 2011), we only included stream gages that met three criteria: 1) the gage had at least 10 years of baseline data from 1995-2014 for comparison to the 2015-2017 defoliation time period, 2) the gage remained in continuous operation from 2015-2017, and 3) the gage had high quality instantaneous stream discharge data at 15-minute temporal resolution, with fewer than 5% missing values for each 1 June to 30 September growing season period.

Subwatersheds (12-digit level; henceforth 'watershed') were delimited by the USGS watershed boundary dataset for the Northeastern United States (U.S. Geological Survey, National Geospatial Technical Operations Center, 2018). In watersheds with multiple stream gages we used the metadata to select stream gages that captured the largest upstream area. Stream gages were located in standard watershed types and included 11 reference stream gages, which are characterized as being much less likely to be impacted by anthropogenic development (Falcone, 2011). We downloaded instantaneous stream discharge data for each of the 88 stream gages that met our inclusion criteria at 15-minute temporal resolution using the dataRetrieval R package (De Cicco et al., 2018) for all available data between 1995-2017 (Figure 1). We subset the analyses to focus on the growing season, which we defined as 1 June through 30 September. Of the 88 USGS stream gages included in this study with high-quality 15-minute baseline data (1995-2014), 94% of gages ($n = 83$) had between 18-20 years of

baseline data, 2% of gages (n = 2) had between 15-17 years of data, and 3% of gages (n = 3) had between 11-14 years of baseline data.

2.2 Watershed defoliation intensity

We used a forest condition assessment product derived from Landsat satellite imagery (Pasquarella et al., 2017) to quantify annual defoliation intensity in the Southern New England region at the watershed scale (Pasquarella, 2018). Specifically, we used annual forest condition data products for 2015, 2016, and 2017, which average changes in vegetation in greenness relative to a fitted baseline modeled for each pixel over the summer growing season. Interpretation of this data product values is analogous to a z-score, where larger values indicate a larger departure from baseline conditions (Pasquarella, 2018; Pasquarella et al., 2017), and thus we interpret the magnitude of the forest condition assessment product values as “defoliation intensity”.

We used this forest condition assessment product to quantify the mean defoliation intensity within each watershed that contained a United States Geological Survey (USGS) stream gage in Connecticut, Massachusetts, and Rhode Island (described above in Methods 2.1). For each of the 2015-2017 growing seasons we calculated mean defoliation within each watershed by overlaying the watershed boundary vector data onto the forest condition assessment product and using QGIS zonal statistics (QGIS Development Team, 2018) for the subset of watersheds that included USGS stream gages. Before spatial averaging within watersheds, we removed

any erroneous 30 m data product pixels with defoliation values that exceeded six times the baseline model RMSE and excluded pixels that were masked as non-forested.

2.2 Seasonal precipitation data

We calculated the total seasonal precipitation at each USGS stream gage within each watershed with the Daymet data product, a data-driven model that downscales daily meteorological variables to a 1 km spatial grid (Thornton et al., 2018). We used the spatial coordinates for each USGS stream gage to download the associated pixel of Daymet daily total precipitation (mm) from 1995-2017 for 1 June through 30 September using the `daymetr` R package (Hufkens et al., 2018). We calculated the total seasonal precipitation as the sum of total daily precipitation at each stream location for the 1 June to 30 September time period in each year from 1995-2017. We compared the sum of growing season precipitation values measured at each stream gage location to assess variation in total precipitation varied by year among the southern New England stream gages. The *L. dispar* irruption occurred in tandem with a regional drought that began in 2014 and lasted until 2017 and the year with the lowest total growing season precipitation was 2016. Total growing season precipitation in the years 2015-2017 was all below the 20-year baseline (1995-2014) mean for the region (Supplementary Figure S1).

2.3 Seasonal water yield analysis

Before calculating the total growing season (1 June to 30 September) stream discharge for each stream gage in each year, we examined the time series of discharge data for substantial changes in discharge characteristics from the 1995-2014 baseline period by assessing trends in maximum daily discharge, mean daily discharge, 7-day minimum discharge, and the standard deviation of discharge using the EGRET water analysis package (Hirsch and De Cicco, 2015). We calculated total seasonal stream discharge at each gage as the sum of the 15-minute seasonal discharge time series, where we assumed that the 15-minute instantaneous values were constant across each 15-minute interval. For each stream gage, we divided the total seasonal stream discharge by the upstream watershed area to represent the total discharge as water yield in units of mm.

We used the total growing season water yield and total growing season precipitation data to calculate the seasonal runoff ratio at each stream gage as yield divided by precipitation, which represented the fraction of total growing season precipitation recovered as streamflow. This approach assumed that there were consistent streamflow contributions from groundwater over the study period and that there were no directional trends in water storage within each watershed. Assessing changes in the seasonal runoff ratio theoretically captured the combined effects of potential changes in evapotranspiration and interception that were associated with

defoliation severity and potentially altered the seasonal water yield during the growing season, given the total seasonal precipitation at each stream gage.

With the runoff ratios for each regional stream gage, we calculated the gage-specific mean runoff ratio for a 1995-2014 baseline period. We then calculated runoff ratio anomalies as the difference between the 2015-2017 gage-specific runoff ratios and the baseline runoff ratio. Since the goal of our analysis was to assess the impact of defoliation across a broad, regional suite of watersheds, we used the runoff ratio anomalies for subsequent statistical analyses that compared associations with defoliation intensity across regional watersheds. We also calculated water yield anomalies and precipitation anomalies at each stream gage to assess how these two fluxes were driving any patterns between runoff ratio anomalies and defoliation intensity. At each stream gage, we calculated the water yield anomaly for defoliation years as the difference between each of the 2015-2017 growing season water yields and the mean growing season baseline water yield (the 1995-2014 mean). We quantified the same anomaly between each defoliation year (2015-2017) and baseline period for the total growing season watershed precipitation at each stream gage.

2.4 Flow duration curve analysis

To assess the impacts of defoliation intensity on high-resolution instantaneous 15-minute instantaneous streamflow volumes, we produced flow duration curves at each stream gage for the growing season period (1 June to 30 September). Flow duration

curves characterize the occurrence of stream discharge values of different magnitudes by parameterizing the statistical frequency of different stream discharge values over a season or year (Hirsch and De Cicco, 2015). Streamflows from flow duration curves that are exceeded less than 25% of the time are considered high-flow events, values that are exceeded between 25% and 75% of the time are representative of normal stream flow, and values that are exceeded 75% of the time are considered low-flow events (McMahon et al., 2003).

We used the instantaneous 15-minute streamflow values measured at each stream gage during the growing season (1 June to 30 September) to calculate a baseline flow duration curve for the 1995-2014 period. We compared each of the flow duration curves in the 2015-2017 *L. dispar* defoliation years to this baseline flow duration curve for each stream gage. Due to differences in the flow magnitudes among the 88 subwatersheds in this study, at each stream gage we calculated the percent difference between each of the 2015-2017 defoliation year flow duration curves and the baseline growing-season flow duration curve at the 75th, 50th, and 25th percentile values (high-, medium-, and low-flow events). We used these statistics to investigate the potential impact of defoliation intensity on changes in growing-season streamflow at high-, medium-, and low-flow events.

2.6 Statistical analyses

We used linear mixed models to test for a significant relationship between seasonal defoliation intensity and departures from baseline (*i.e.*, anomalies) in both growing season runoff ratio and flow duration curve statistics, with year (2015-2017) as a random intercept effect. We used the lmerTest R package (Kuznetsova et al., 2017) to conduct t-tests with the Satterthwaite's degrees of freedom method for linear relationships between defoliation intensity and runoff ratio anomalies and streamflow response variables. We tested for relationships between defoliation intensity and growing season precipitation anomalies and yield anomalies with the same method to determine how potential responses in the runoff ratio anomalies were related to changes in these fluxes among watersheds.

For each of these statistical models, we estimated model parameters for two different datasets that characterized the relationship with the subwatershed defoliation severity using: 1) data from all 88 stream gages and, 2) data that only included the 11 reference stream gages. This comparison between models fit with all stream gages versus those fit with reference stream gages provided insight into the extent to which patterns between biotic disturbance and impacts to streamflow were different in watersheds known to be less influenced by anthropogenic activities. All code needed to reproduce this project is available at

https://github.com/jhmatthes/Defoliation_StreamFlow.

3. Results and Discussion

3.1 Regional Defoliation Intensity and Precipitation

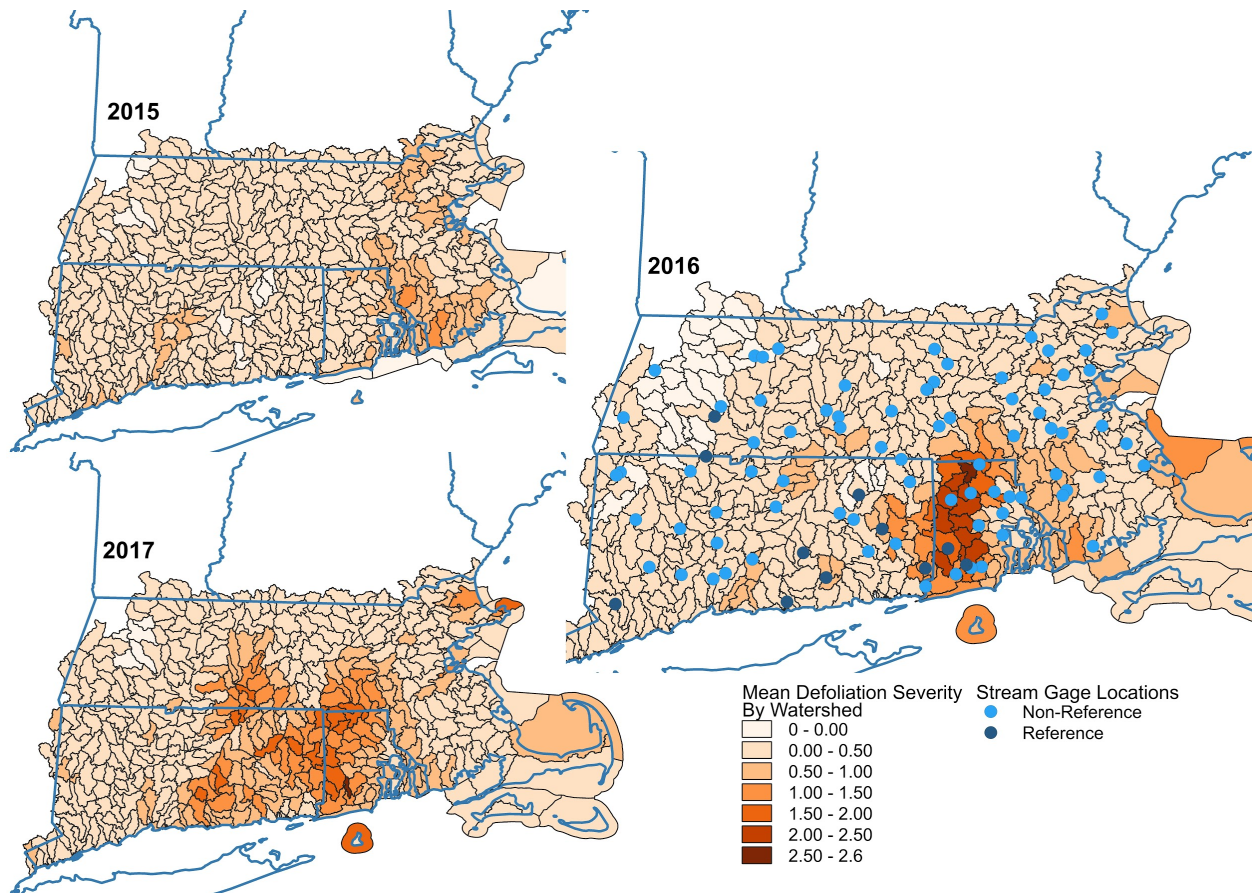


Figure 1. Mean defoliation intensity in 2015, 2016, and 2017 within watersheds.

Watersheds are outlined in black, and states are outlined in blue. Stream gage locations used in this analysis are shown in the 2016 map, which was the most intense defoliation year. Coastal watersheds are excluded from this analysis due to differences in flow regimes.

Changes in defoliation intensity measured by the forest condition defoliation data product varied in extent and severity across Southern New England during the 2015-2017 *L. dispar* irruption, as demonstrated by the broad spread of the mean seasonal defoliation among watersheds (Figure 1). The decline in forest condition, indicating more intense defoliation, was most severe in 2016 where 11 watersheds in southern Rhode Island had average defoliation intensities that were 1-2 times below normal greenness for the growing season (Figure 2). Defoliation of moderate to high intensity was most widespread across the region in 2017, where 18 watersheds had mean defoliation values of 0.5-2 compared to 11 watersheds with the same values in 2016 (Figure 1; Figure 2). In all three years the most intense defoliation occurred in eastern Connecticut and western Rhode Island. Here, five watersheds were repeatedly and intensely defoliated (more than 100% below the normal greenness estimate for the root mean square error of the growing season). Throughout the study region defoliation intensity was highly variable within and among subwatersheds and many watersheds had areas of complete defoliation adjacent to areas with little or no defoliation. There was no significant difference between the defoliation severity of watersheds with reference stream gages that are less impacted by anthropogenic activities compared to watersheds with non-reference stream gages (Figure 2).

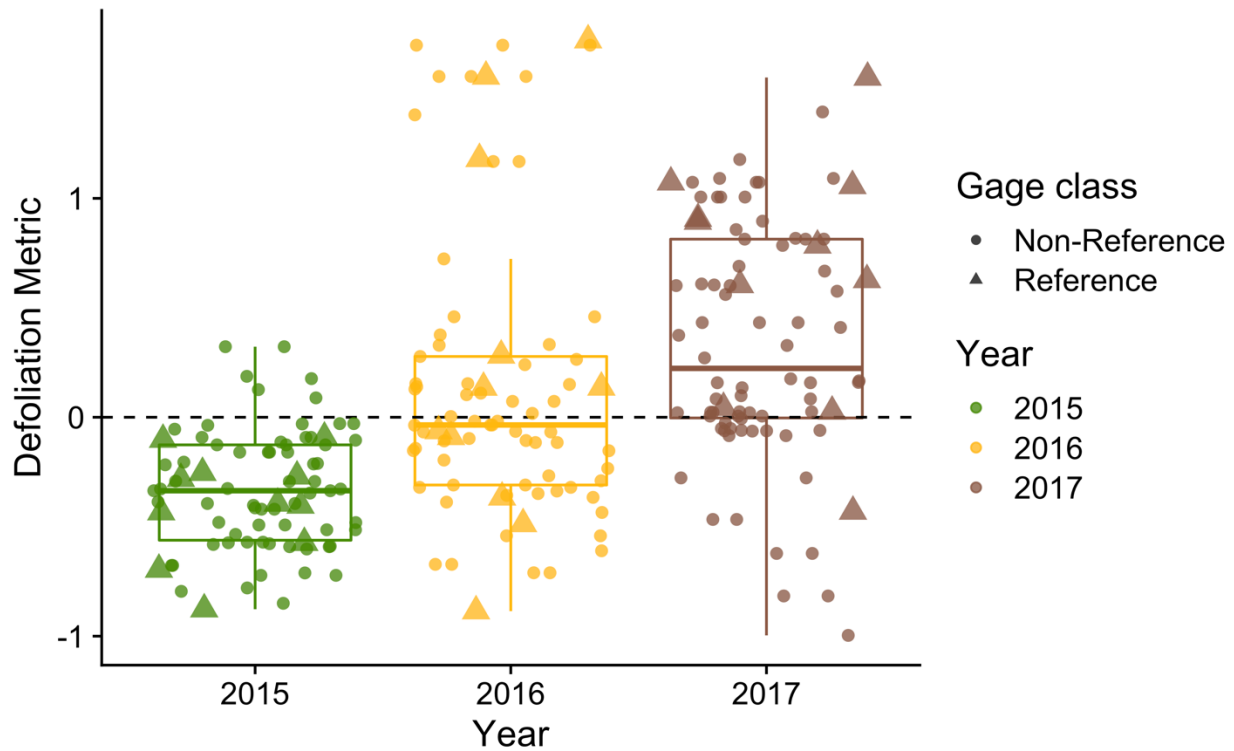


Figure 2. Mean defoliation intensity within each watershed varied across the region. In 2016 there were a few watersheds with severe defoliation intensity and 2017 had the most widespread defoliation at the regional scale. Defoliation is scaled to the change in the root mean squared error (RMSE) of greenness where 0 represents no change from the 10-year baseline greenness condition (Pasquarella et al., 2017).

3.2 Defoliation intensity and runoff ratio anomalies

The gage-specific runoff ratio anomalies in the growing season were positively correlated with defoliation intensity in all years from 2015-2017, with random intercepts that varied by year (Figure 3). The positive correlation between runoff ratio anomalies

and defoliation intensity existed both in the model that was fit to all of the gages and to the model that only included the reference gages that are known to be less impacted by anthropogenic activities (Table 1). During the 2015-2017 time period, defoliation intensity had a significant but small effect of increasing the runoff ratio anomaly relative to the gage-specific baseline values in more intensely defoliated watersheds (+0.017 increase in the growing season runoff ratio anomaly per unit of defoliation severity). The random intercepts representing differences among years for the association between runoff ratio anomalies and defoliation intensity paralleled the patterns of the Northeastern U.S. drought (2014-2017), where runoff ratio anomalies were the farthest below the long-term baseline during the most severe growing season drought in 2016 (Supplementary Figure S1). Importantly, anomalies in the total growing season precipitation at each stream gage were not significantly correlated with defoliation intensity ($p = 0.41$), but water yield anomalies were significantly correlated with defoliation intensity ($p = 0.01$; Supplementary Figure S2). This indicated that regional variation in water yield anomalies, not precipitation anomalies, influenced the relationships between runoff ratio anomalies and defoliation severity among the regional stream gages.

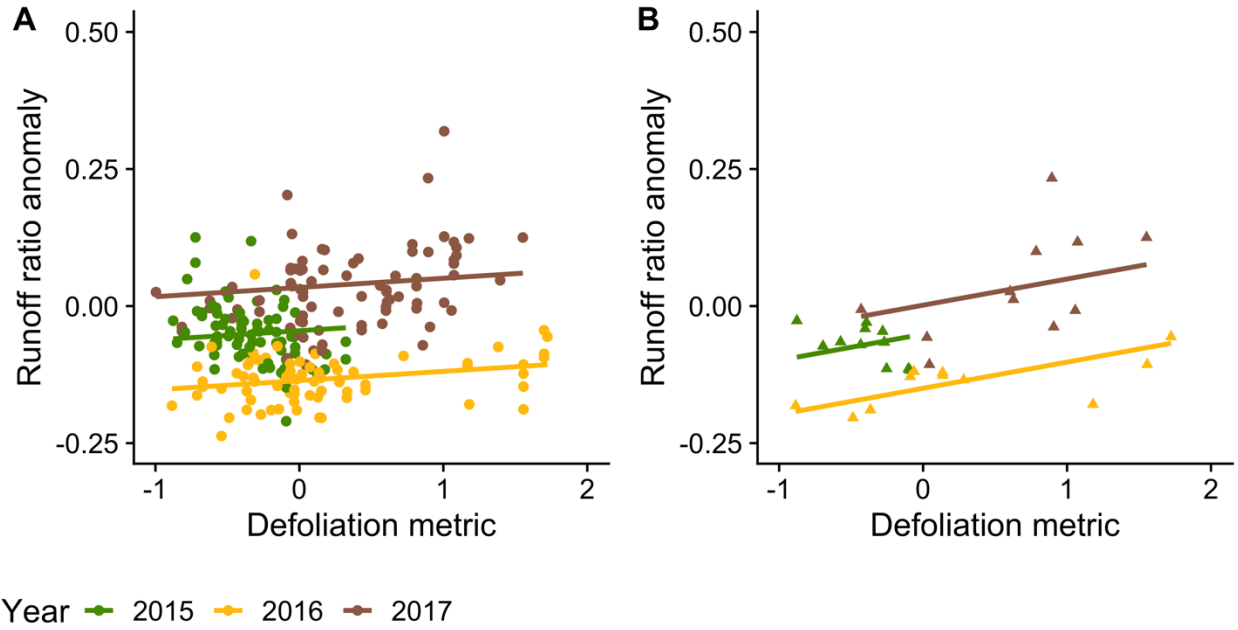


Figure 3. Growing season runoff ratio anomalies are positively correlated with watershed defoliation severity ($p < 0.05$) in estimated mixed effects linear models for two datasets: A) all gages used in this study, and B) reference gages only. Lines show the best-fit linear mixed models with year as a random y-intercept effect.

Gage Dataset	Year	Intercept	Int. Standard Deviation	Slope	Slope Standard Error
All	2015	-0.045	0.050	0.017	0.0088
	2016	-0.14	“	“	“
	2017	0.034	“	“	“
Reference Only	2015	-0.051	0.047	0.048	0.018
	2016	-0.15	“	“	“
	2017	0.0017	“	“	“

Table 1. Estimated model coefficients for the statistically significant relationship ($p < 0.05$) between defoliation severity and the growing season runoff ratio anomalies at regional stream gages, with year as a random intercept (number of all gages = 88, number of reference gages = 11).

While defoliation severity was associated with higher runoff ratio anomalies in all stream gages, the estimated slope for the relationship between defoliation intensity and the runoff ratio anomalies was largest in the model that only included data from reference gages (Table 1). The estimated slope between defoliation intensity and the runoff ratio anomalies using only the reference gages (+0.047 per unit defoliation) was almost triple the magnitude of the model fit with all stream gages (+0.017 per unit defoliation) (Table 1). The stronger effect of defoliation intensity on runoff ratio

anomalies in reference gages existed even though reference gages captured the same range of defoliation intensity as the non-reference gages (Figure 2). Since the reference gages are located within watersheds that are minimally impacted by anthropogenic activities, this could indicate that these less impacted ecosystems are more responsive to biotic disturbances such as defoliation from FIPs.

3.3 Defoliation intensity and instantaneous streamflow

We found statistically significant positive relationships between defoliation intensity and instantaneous streamflow values in 2015-2017 compared to baseline conditions at the 25% and 50% exceedance probabilities that reflect high and medium flow values (Figure 4). There was not a significant correlation between defoliation intensity and 75% streamflow exceedance probabilities that represent low flows. The positive relationships between defoliation intensity and instantaneous growing season streamflow departures was strongest for high streamflow events (25% exceedance values), where defoliation intensity was associated with instantaneous streamflow anomalies that were up to 50% larger than high flows during baseline years (Figure 4). In particular, intense defoliation had the effect of pushing instantaneous streamflow anomalies within several watersheds from negative to positive values (*i.e.*, above the 1995-2014 baseline) in 2017.

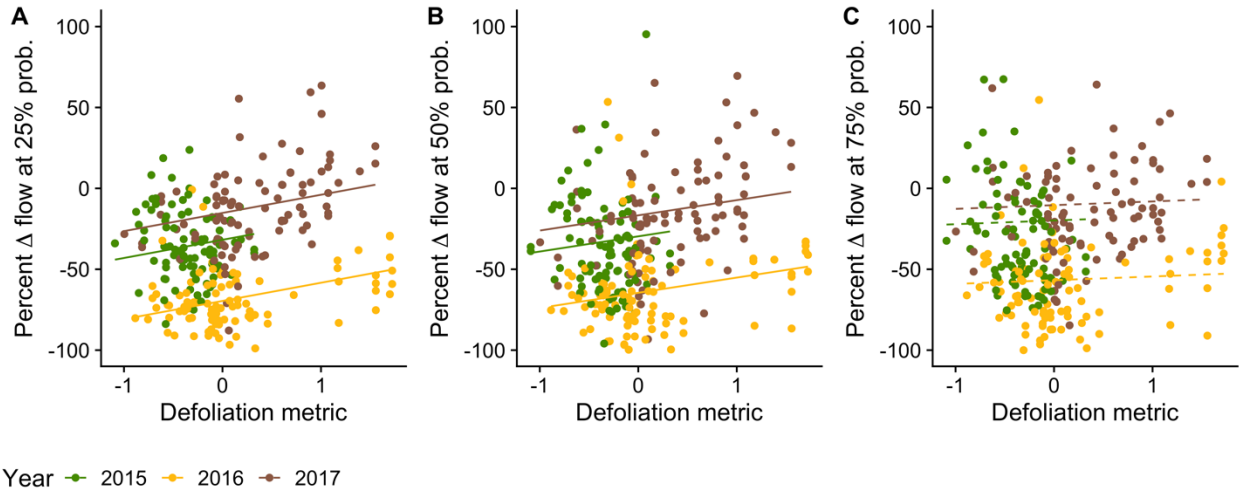


Figure 4. The magnitude of **A)** high streamflow events at 25% exceedance probability and **B)** medium flow events at 50% exceedance probability were significantly positively correlated with defoliation severity ($p < 0.05$). Low streamflow events at **C)** 75% exceedance probability were not significantly correlated with defoliation intensity. The percent change in flow is based on the distance from the 20-year baseline flow duration curve for each stream gage. Lines show linear mixed models with year as a random intercept effect, where the solid lines indicate a statistically significant ($p < 0.05$) effect of the relationship between defoliation intensity and the percent change in flow magnitude.

Gage Dataset	Flow Type	Year	Intercept	Int. Standard Deviation	Slope	Slope Standard Error
All	25th	2015	-32	16	11	2.4
	percentile	2016	-70	"	"	"
		2017	-15	"	"	"
Reference	25th	2015	-39	17	18	6.8
	percentile	2016	-75	"	"	"
		2017	-23	"	"	"
All	50th	2015	-30	15	9.4	3.6
	percentile	2016	-65	"	"	"
		2017	-17	"	"	"
Reference	50th	2015	-44	14	19	7.4
	percentile	2016	-73	"	"	"
		2017	-33	"	"	"

Table 2. Model coefficients for the significant ($p < 0.05$) relationships between watershed defoliation intensity and the percent increase in the magnitude of 2015-2017 instantaneous flow percentiles (compared to the 1995-2014 baseline period) for flows with 25% (high flows) and 50% (medium flows) exceedance probabilities. For flow with 75% exceedance probabilities (low flows) defoliation was not significantly correlated with departures from baseline conditions. Intercepts reflect random effects by year (2015-2017).

The slope of the relationship between defoliation intensity and changes in growing season instantaneous streamflows indicated a larger effect when compared to the changes in the total seasonal growing season anomalies with defoliation intensity. Across all stream gages, there was an 11% increase in the magnitude of high-flow events per unit of defoliation, and a 9.4% increase per unit of defoliation for medium-flow events (Table 2). The slopes estimated for the same model with only data from reference stream gages were even larger, with an 18% increase in the size of high-flow events per unit of defoliation and a 19% increase in the size of medium-flow events per unit of defoliation (Table 2). These stronger associations between defoliation intensity and streamflow effects for models fit with data only from reference gages paralleled the conclusions from the seasonal runoff ratio anomalies, where models estimated only with data from reference gages indicated larger departures from baseline conditions that were associated with defoliation intensity.

5. Discussion

FIPs that cause tree stress and mortality are known to have a wide array of ecosystem-scale impacts. The subsequent impacts on FIPs on ecohydrology are a function of the climate, the type of forest being impacted, and the intensity and pathway of a FIP attack (Dietze and Matthes, 2014; Mirus et al., 2017). Previous studies of FIPs and ecohydrology in mesic temperate forests have typically occurred within

single watersheds or used a paired watershed approach (Addy et al., 2018; Brown et al., 2005; Kim et al., 2017). A recent meta-analysis of these site-specific, paired watershed studies found that defoliating FIPs created significant changes in streamflow in only a few examples (Oda et al., 2018). In this study, we leveraged multiple regional data products across a spatially variable sequence of defoliation years during the regional repeated 2015-2017 *L. dispar* irruptions. Facilitated by regional variation in defoliation intensity, our approach used stream gages located in 88 subwatersheds to test for relationships between defoliation intensity, runoff ratio anomalies, and instantaneous streamflow departures from baseline conditions. The integration of a satellite-based defoliation data product with openly available data from the USGS stream gage network developed in this study could serve as a framework for quantifying future changes in regional streamflow during and after a FIP disturbance.

The 2015-2017 irruption of *L. dispar* was the most intense defoliation event that has occurred in New England since 1981 and is the first major irruption in this region following the successful establishment of *E. maimaiga* in the late 1980s (Elkinton et al., 2019; Pasquarella et al., 2018). We found that over the growing season among watersheds within the Southern New England region, defoliation intensity was associated with a statistically significant increase in the runoff ratio anomalies (Figure 3) and large increases in the magnitude of high-flow and medium-flow events relative to baseline flows (Figure 4). Another recent study found instantaneous streamflow values

up to five times greater than non-defoliation values that were associated with severe *L. dispar* defoliation within a site-level study at a stream gage in Rhode Island (Addy et al., 2018). Increased instantaneous streamflow values of a magnitude as observed in our study (*i.e.*, a ~ 10% increase for high and medium flow events) could potentially create secondary impacts in stream morphology and ecology by changing stream channel size, sediment and nutrient transport, and in-stream and down-stream biota (Burcher et al., 2007). This increase in the magnitude of high and medium streamflows could also increase stream sediment flux, which could potentially shift the aquatic and terrestrial plant communities and impact downstream water quality (Beudert et al., 2015).

Several subwatersheds in our study had multiple years of moderate to high-intensity defoliation that was comparable to the total percent of vegetation removed in selectively logged paired-catchment studies, which also found significant increases in water yield and runoff ratios (Bosch and Hewlett, 1982; Brown et al., 2005). In these prior studies, a 30-50% reduction in canopy cover from harvesting increased annual water yield by 0.1-0.3 m in many different forest types (Bosch and Hewlett, 1982; Brown et al., 2005; Hornbeck et al., 1997). We found a much smaller impact on runoff ratio anomalies that was associated with defoliation intensity in this study (Figure 3). This difference in runoff ratio impacts when comparing harvesting studies that removed a similar area of tree biomass to the *L. dispar* impacts could be due to differences in the mechanism of tree stress and mortality: whole-tree harvesting causes immediate

mortality of tree biomass, prohibiting the potential for recovery, whereas defoliators cause stress from which trees can potentially recover (Foster, 2017). This highlights the importance of accounting for the mechanism of vegetation disturbance when assessing ecohydrological impacts, even at similar intensities and spatial scales. The small but significant, impact of defoliation on watershed runoff ratio anomalies in this study is corroborated by a meta-analysis of previous research in paired catchment studies, where biotic disturbance from insects and pathogens was correlated to small-scale changes in total watershed runoff (Oda et al., 2018). However over the next several years, it is possible that tree mortality associated with the stress of repeated or novel *L. dispar* outbreaks within the region in this study could further shift the long-term hydrology of impacted areas.

The relationships that we found between defoliation intensity and the watershed runoff ratio anomalies and streamflow characteristics were particularly strong in reference stream gages, which are less impacted by anthropogenic disturbance. The relationships with streamflow and defoliation intensity for models fit only with data from the reference stream gages were particularly strong despite having the same range of variation in defoliation intensity as non-reference stream gages (Figure 2). This could indicate that watersheds with fewer direct anthropogenic impacts are more sensitive to disturbance, or that anthropogenic activity within watersheds can introduce more variability in the relationships between biotic disturbance and runoff or instantaneous

streamflow. To date, many studies of the impact of biotic vegetation disturbance such as FIPs in watersheds have focused on relatively remote areas with a lower anthropogenic impact from fragmentation and development than the mesic temperate forests in this study. The stronger impact of defoliation intensity on ecohydrological processes that we found within reference gages when compared to all stream gages points to a need for future work across a broad range of anthropogenically impacted and less impacted watersheds to better understand the connections between streamflow processes and biotic disturbances such as FIPs.

The range expansion of *L. dispar* and the increased outbreak likelihood of future drought caused by climate change could lead to shifts in forest composition and novel disturbance regimes (Schweitzer et al., 2014). The high probability of increased drought frequency in the Northeastern U.S. with climate change (Hayhoe et al., 2007) could increase the likelihood of *L. dispar* population irruptions and escalate the rate of *L. dispar* spread to new forests (Davidson et al., 1999; Liebhold et al., 1994). *Lymantria dispar* is limited in its geographic range by cold winter temperatures, but warming winters could also facilitate the further range expansion to new regions (Streifel et al., 2019). Our findings support that *L. dispar* irruptions could have regional implications for hydrological flows at the ecosystem scale, possibly impacting long-term forest function.

6. Conclusions

Our regional-scale analysis of a spatially variable and repeated defoliating insect irruption across the Southern New England region found that defoliation intensity across three years was associated with higher growing season runoff ratios and larger volumes of medium and high instantaneous streamflows. Importantly, our findings support that changes in streamflow associated with FIP disturbances can be assessed with a combination of satellite-based data products and the regional USGS stream gage network. Using data from 88 regional stream gages and remotely sensed imagery, this study provides a framework to integrate multiple regional-scale data products to assess how a spatially variable and repeated moderate disturbance can impact seasonal runoff ratios and instantaneous streamflows. The anticipated increase in multiple, sometimes synergistic, disturbance events in temperate mesic forests creates a large imperative for rapidly understanding disturbance impacts within forests (Seidl et al., 2017). The type of framework developed within this paper, which is based on openly available data products, could be used to monitor and assess the ecohydrological impacts of forest disturbance in near-real-time. Future work could build on these initial findings to explore the ways in which compound disturbances, such as extreme weather events, might create interactive impacts within regional ecohydrology. Additionally, this framework could potentially interface with Earth System models that are tasked with

the challenge of simulating the impacts of multiple, simultaneous, moderate disturbances within forests.

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References

- Addy, K., Gold, A.J., Loffredo, J.A., Schroth, A.W., Inamdar, S.P., Bowden, W.B., Kellogg, D.Q., Birgand, F., 2018. Stream response to an extreme drought-induced defoliation event. *Biogeochemistry* 140, 199–215. <https://doi.org/10.1007/s10533-018-0485-3>
- Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208, 674–683. <https://doi.org/10.1111/nph.13477>
- Andreadis, T.G., Weseloh, R.M., 1990. Discovery of *Entomophaga maimaiga* in North American gypsy moth, *Lymantria dispar*. *Proc Natl Acad Sci U S A* 87, 2461–2465.
- Bearup, L.A., Maxwell, R.M., Clow, D.W., McCray, J.E., 2014. Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nat. Clim. Chang.* 4, 481. <https://doi.org/10.1038/nclimate2198>
- Beudert, B., Bäessler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N., Müller, J., 2015. Bark beetles increase biodiversity while maintaining drinking water quality. *Conservation Letters* 8, 272–281.

- Biederman, J.A., Harpold, A.A., Gochis, D.J., Ewers, B.E., Reed, D.E., Papuga, S.A., Brooks, P.D., 2014. Increased evaporation following widespread tree mortality limits streamflow response. *Water Resour. Res.* 50, 5395–5409.
<https://doi.org/10.1002/2013WR014994>
- Bosch, J.M., Hewlett, J.D., 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *J. Hydrol.* 55, 3–23. [https://doi.org/10.1016/0022-1694\(82\)90117-2](https://doi.org/10.1016/0022-1694(82)90117-2)
- Brown, A.E., Zhang, L., McMahon, T.A., Western, A.W., Vertessy, R.A., 2005. A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. *J. Hydrol.* 310, 28–61.
<https://doi.org/10.1016/j.jhydrol.2004.12.010>
- Burcher, C.L., Valett, H.M., Benfield, E.F., 2007. The land-cover cascade: Relationships coupling land and water. *Ecology* 88, 228–242. [https://doi.org/10.1890/0012-9658\(2007\)88\[228:TLCRCL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[228:TLCRCL]2.0.CO;2)
- Clark, K.L., Skowronski, N., Gallagher, M., Renninger, H., Schäfer, K., 2012. Effects of invasive insects and fire on forest energy exchange and evapotranspiration in the New Jersey pinelands. *Agric. For. Meteorol.* 166–167, 50–61.
<https://doi.org/10.1016/j.agrformet.2012.07.007>

- Davidson, C.B., Gottschalk, K.W., Johnson, J.E., 1999. Tree Mortality Following Defoliation by the European Gypsy Moth (*Lymantria dispar* L.) in the United States: A Review. *For. Sci.* 45, 74–84. <https://doi.org/10.1093/forestscience/45.1.74>
- De Cicco, L.A., Lorenz, D., Hirsch, R.M., Watkins, W., 2018. dataRetrieval: R packages for discovering and retrieving water data available from U.S. federal hydrologic web services. <https://doi.org/10.5066/P9X4L3GE>
- Dietze, M.C., Matthes, J.H., 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters* 17, 1418–1426. <https://doi.org/10.1111/ele.12345>
- Dingman, L.S., 2015. *Physical Hydrology: Third Edition*. Waveland Press.
- Easton, Z.M., Gérard-Marchant, P., Walter, M.T., Petrovic, A.M., Steenhuis, T.S., 2007. Hydrologic assessment of an urban variable source watershed in the northeast United States. *Water Resour. Res.* 43.
- Elkinton, J.S., Bittner, T.D., Pasquarella, V.J., Boettner, G.H., Liebhold, A.M., Gould, J.R., Faubert, H., Tewksbury, L., Broadley, H.J., Havill, N.P., Hajek, A.E., 2019. Relating Aerial Deposition of Entomophaga maimaiga Conidia (Zoopagomycota: Entomophthorales) to Mortality of Gypsy Moth (Lepidoptera: Erebidae) Larvae and Nearby Defoliation. *Environ Entomol* 48, 1214–1222. <https://doi.org/10.1093/ee/nvz091>
- Falcone, J., 2011. GAGES-II: Geospatial Attributes of Gages for Evaluating Streamflow.

- Foster, J.R., 2017. Xylem traits, leaf longevity and growth phenology predict growth and mortality response to defoliation in northern temperate forests. *Tree Physiol* 37, 1151–1165. <https://doi.org/10.1093/treephys/tpx043>
- Hajek, A.E., Roberts, D.W., 1991. Pathogen reservoirs as a biological control resource: Introduction of *Entomophaga maimaiga* to North American Gypsy Moth, *Lymantria dispar*, populations. *Biological Control* 1, 29–34. [https://doi.org/10.1016/1049-9644\(91\)90098-K](https://doi.org/10.1016/1049-9644(91)90098-K)
- Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T.J., Wolfe, D., 2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Clim. Dyn.* 28, 381–407. <https://doi.org/10.1007/s00382-006-0187-8>
- Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., (Ted) Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., Vogelmann, J., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Glob. Chang. Biol.* 18, 7–34. <https://doi.org/10.1111/j.1365-2486.2011.02543.x>
- Hirsch, R.M., De Cicco, L.A., 2015. User guide to Exploration and Graphics for RivEr Trends (EGRET) and dataRetrieval: R packages for hydrologic data, in: *Techniques and Methods*. U.S. Geological Survey, Reston, VA.

- Hornbeck, J.W., Martin, C.W., Eagar, C., 1997. Summary of water yield experiments at Hubbard Brook Experimental Forest, New Hampshire. *Can. J. For. Res.* 27, 2043–2052. <https://doi.org/10.1139/x97-173>
- Hufkens, K., Basler, D., Milliman, T., Melaas, E.K., Richardson, A.D., 2018. An integrated phenology modelling framework in r. *Methods Ecol. Evol.* 9, 1276–1285. <https://doi.org/10.1111/2041-210X.12970>
- Huntington, T.G., Richardson, A.D., McGuire, K.J., Hayhoe, K., 2009. Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystems. *Can. J. For. Res.* 39, 199–212.
- Kim, J., Hwang, T., Schaaf, C.L., Orwig, D.A., Boose, E., Munger, J.W., 2017. Increased water yield due to the hemlock woolly adelgid infestation in New England. *Geophys. Res. Lett.* 44, 2327–2335. <https://doi.org/10.1002/2016GL072327>
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Liebhold, A.M., Elmes, G.A., Halverson, J.A., Quimby, J., 1994. Landscape Characterization of Forest Susceptibility to Gypsy Moth Defoliation. *For. Sci.* 40, 18–29. <https://doi.org/10.1093/forestscience/40.1.18>
- Liebhold, A.M., Gottschalk, K.W., Mason, D.A., Bush, R.R., 1997. Forest susceptibility to the gypsy moth. *Journal of Forestry.* 95 (5): 20-24. 95, 20–24.

- Liebhold, A.M., McCullough, D.G., Blackburn, L.M., Frankel, S.J., Von Holle, B., Aukema, J.E., 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. *Divers. Distrib.* 19, 1208–1216.
<https://doi.org/10.1111/ddi.12112>
- Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B., Lambert, K.F., Orwig, D.A., Campbell, F.T., Rosenthal, J., McCullough, D.G., Wildova, R., Ayres, M.P., Canham, C.D., Foster, D.R., LaDeau, S.L., Weldy, T., 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecol. Appl.* 26, 1437–1455. <https://doi.org/10.1890/15-1176>
- McMahon, G., Bales, J.D., Coles, J.F., Giddings, E.M.P., Zappia, H., 2003. Use of Stage Data to Characterize Hydrologic Conditions in an Urbanizing Environment1. *JAWRA Journal of the American Water Resources Association* 39, 1529–1546.
<https://doi.org/10.1111/j.1752-1688.2003.tb04437.x>
- Metcalf, D.B., Asner, G.P., Martin, R.E., Silva Espejo, J.E., Huasco, W.H., Farfán Amézquita, F.F., Carranza-Jimenez, L., Galiano Cabrera, D.F., Baca, L.D., Sinca, F., Huaraca Quispe, L.P., Taype, I.A., Mora, L.E., Dávila, A.R., Solórzano, M.M., Puma Vilca, B.L., Laupa Román, J.M., Guerra Bustios, P.C., Revilla, N.S., Tupayachi, R., Girardin, C.A.J., Doughty, C.E., Malhi, Y., 2014. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecol. Lett.* 17, 324–332. <https://doi.org/10.1111/ele.12233>

- Mirus, B.B., Ebel, B.A., Mohr, C.H., Zegre, N., 2017. Disturbance Hydrology: Preparing for an Increasingly Disturbed Future. *Water Resources Research* 53, 10007–10016. <https://doi.org/10.1002/2017WR021084>
- Munger, J.W., Wofsy, S.C., Foster, D.R., 2012. Detection of long-term trends in carbon accumulation by forests in northeastern US and determination of causal factors. Harvard University, Cambridge MA.
- Oda, T., Green, M.B., Urakawa, R., others, 2018. Stream runoff and nitrate recovery times after forest disturbance in the USA and Japan. *Water Resources Research*.
- Pasquarella, V.J., 2018. Landsat-based Gypsy Moth Defoliation Assessment (Southern New England). <https://doi.org/10.5281/zenodo.1493407>
- Pasquarella, V.J., Bradley, B.A., Woodcock, C.E., 2017. Near-Real-Time Monitoring of Insect Defoliation Using Landsat Time Series. *Forests* 8, 275. <https://doi.org/10.3390/f8080275>
- Pasquarella, V.J., Elkinton, J.S., Bradley, B.A., 2018. Extensive gypsy moth defoliation in Southern New England characterized using Landsat satellite observations. *Biol Invasions* 20, 3047–3053. <https://doi.org/10.1007/s10530-018-1778-0>
- Poon, P.K., Kinoshita, A.M., 2018. Spatial and temporal evapotranspiration trends after wildfire in semi-arid landscapes. *Journal of Hydrology* 559, 71–83. <https://doi.org/10.1016/j.jhydrol.2018.02.023>

- Reed, D.E., Ewers, B.E., Pendall, E., Frank, J., Kelly, R., 2018. Bark beetle-induced tree mortality alters stand energy budgets due to water budget changes. *Theor Appl Climatol* 131, 153–165. <https://doi.org/10.1007/s00704-016-1965-9>
- Schweitzer, C., Clark, S.L., Gottschalk, K.W., Stringer, J., Sitzlar, R., 2014. Proactive Restoration: Planning, Implementation, and Early Results of Silvicultural Strategies for Increasing Resilience against Gypsy Moth Infestation in Upland Oak Forests on the Daniel Boone National Forest, Kentucky. *Journal of Forestry* 112, 401–411. <https://doi.org/10.5849/jof.13-085>
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402. <https://doi.org/10.1038/nclimate3303>
- Streifel, M.A., Tobin, P.C., Kees, A.M., Aukema, B.H., 2019. Range expansion of *Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae) along its north-western margin in North America despite low predicted climatic suitability. *J Biogeogr* 46, 58–69. <https://doi.org/10.1111/jbi.13474>
- Thornton, P.E., Thornton, M.M., Mayer, B.W., Wei, Y., Devarakonda, R., Vose, R.S., Cook, R.B., 2018. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 3.

Wine, M.L., Cadol, D., Makhnin, O., 2018. In ecoregions across western USA streamflow increases during post-wildfire recovery. *Environ. Res. Lett.* 13, 014010.

<https://doi.org/10.1088/1748-9326/aa9c5a>

SUPPLEMENTARY FIGURES:

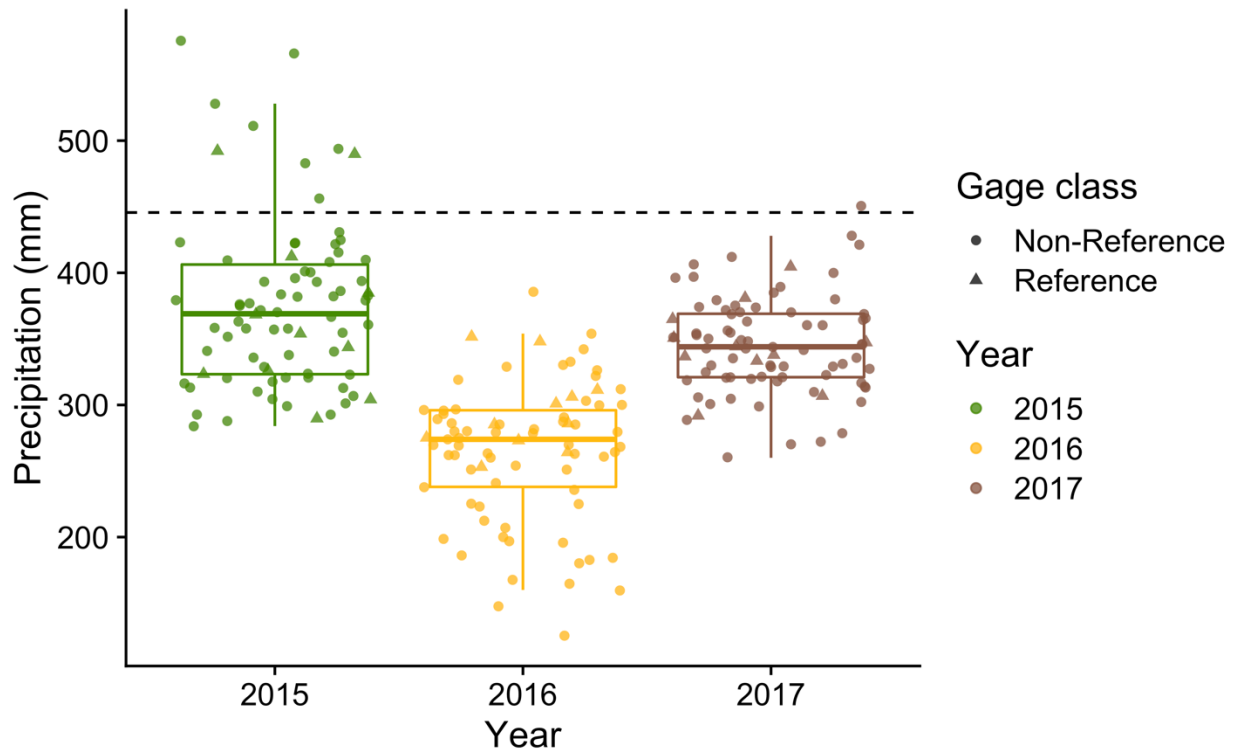


Figure S1. Precipitation boxplot for annual growing season (1 June to 30 September) precipitation at all stream gages, where colors reflect different years (2015-2017), and circles represent non-reference stream gages and triangles represent reference stream gages (*i.e.*, few anthropogenic impacts). The black-dotted line shows the 1995-2014 mean growing season (1 June to 30 September) precipitation value across all watersheds in this study.

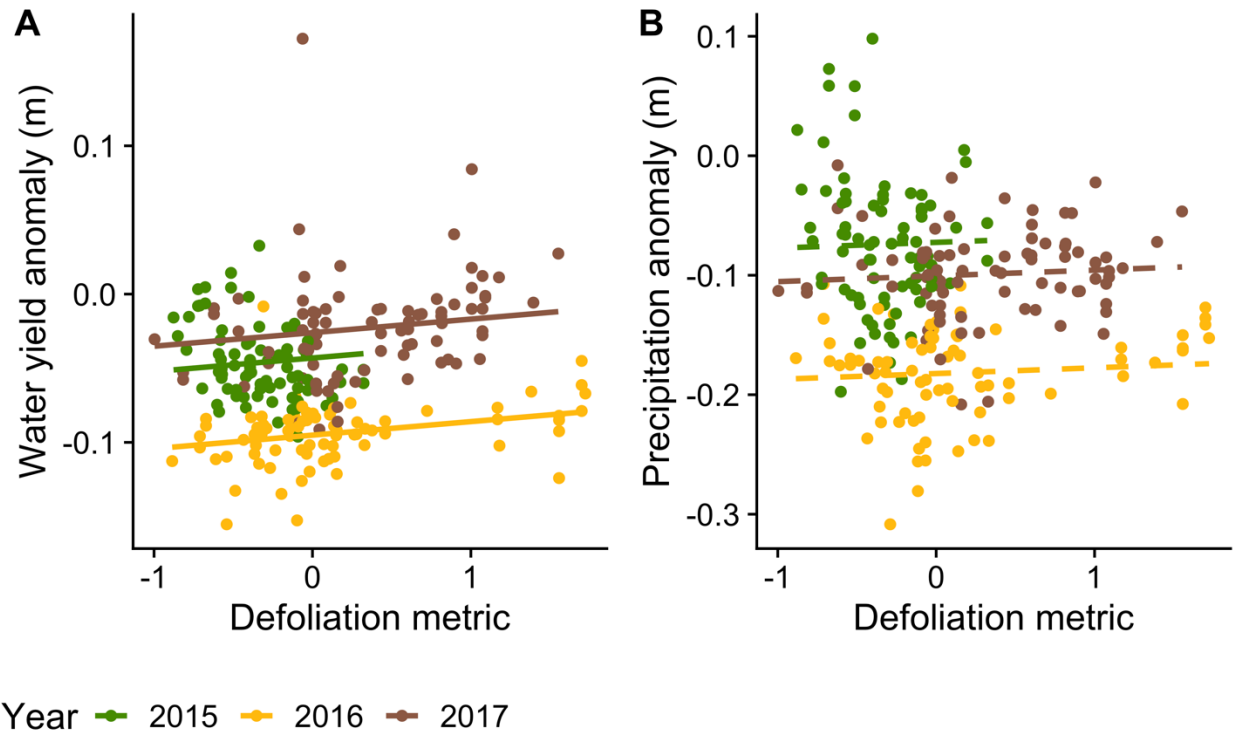


Figure S2. Linear relationships estimated with data from all 88 stream gages for the relationships between defoliation intensity and A) water yield anomalies and B) precipitation anomalies. Lines represent estimated linear mixed effects models, where year (2015-2017) is a random intercept effect. There was a significant relationship between defoliation intensity and water yield anomalies ($p < 0.05$) and the relationship between defoliation intensity and precipitation anomalies was not significant ($p = 0.41$).