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Quantifying flooding regime in floodplain forests to guide river restoration

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Abstract

Determining the flooding regime needed to support distinctive floodplain forests is essential for effective river conservation under the ubiquitous human alteration of river flows characteristic of the Anthropocene Era. At over 100 sites throughout the Connecticut River basin, the largest river system in New England, we characterized species composition, valley and channel morphology, and hydrologic regime to define conditions promoting distinct floodplain forest assemblages. Species assemblages were dominated by floodplain-associated trees on surfaces experiencing flood durations between 4.5 and 91 days/year, which were generally well below the stage of the two-year recurrence interval flood, a widely-used benchmark for floodplain restoration. These tree species rarely occurred on surfaces that flooded less than 1 day/year. By contrast abundance of most woody invasive species decreased with flooding. Such flood-prone surfaces were jointly determined by characteristics of the hydrograph (high discharges of long duration) and topography (low gradient and reduced valley constraint), resulting in increased availability of floodplain habitat with increasing watershed area and/or decreasing stream gradient. Downstream mainstem reaches provided the most floodplain habitat, largely associated with low-energy features such as back swamps and point bars, and were dominated by silver maple (*Acer saccharinum*). However, we were able to identify a number of suitable sites in the upper part of the basin and in large tributaries, often associated with in-channel islands and bars and frequently dominated by sycamore (*Platanus occidentalis*) and flood disturbance-dependent species. Our results imply that restoring flows by modifying dam operations to benefit floodplain forests on existing surfaces need not conflict with flood protection in some regional settings. These results underscore the need to understand how flow, geomorphology, and species traits interact to produce characteristic patterns of floodplain vegetation, and that these interactions should form the basis of effective river restoration and conservation.

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Introduction

Critical thresholds in river flows have long been considered of fundamental importance to fluvial geomorphology in general (Schumm, 1979; Leopold, 1994), and more particularly in the analysis of channel change and the emerging field of river restoration channel design (Rosgen, 1996; Brierley and Fryirs, 2005; Wohl et al., 2005). Understanding the role of these flow thresholds is particularly critical given the increasing extent and magnitude of river regulation via dams and water diversions that is a hallmark of the Anthropocene Era (Skalak et al., 2013). River ecologists interested in diminishing the negative downstream ecological impacts of dams have recognized flow as a potential master variable affecting species abundance and distribution as well as underlying the integrity of river ecosystems (Instream Flow Council, 2004; Doyle et al., 2005; Poff et al., 2010). High flows affect floodplain habitats and ecosystem processes directly through flooding and indirectly by controlling floodplain topography via depositional and erosional processes (Gurnell et al., 2012). The operation of flood control and other large dams has dramatically reduced peak flows, ultimately causing a decline in flood-dependent species (Dister et al., 1990; Auble et al., 2005; Frazier and Page, 2006; Burke et al., 2009; Stallins et al., 2010; Johnson et al., 2012). To help mitigate the loss of floodplain communities due

to flow regulation, many scientists, NGOs, and government agencies have proposed a full suite of potential solutions, including controlled flow releases to approximate natural flow regimes to help restore downstream in-channel and riparian ecological processes (Richter, 2010; Arthington, 2012; Olden et al., 2014; Warner et al., 2014).

Research on ecological river flows is by necessity interdisciplinary combining fluvial geomorphology and hydrology with ecology (Vaughan et al., 2009; Meitzen et al., 2013), and suggests that floodplain habitats may best be defined from a combined perspective, especially in delimiting the optimal flow characteristics for habitat development and maintenance. One of the key hydrologic parameters driving channel processes and initiating overbank flooding is the bankfull discharge. By definition it is the discharge where stream water begins to flow out of the channel margins onto the "active floodplain" – the flat area immediately adjacent to the channel. The active floodplain is a morphologic feature constructed by either lateral channel migration or overbank flooding that generally has a recurrence interval of about 2 years or less (Wolman and Leopold, 1957). This bankfull discharge is often also referred to as the "effective discharge" or "channel forming flow" because it generates sufficiently high bed and bank shear stress for channel mobility, but frequent enough to contribute maximally to maintaining channel shape and construction of the active floodplain (Wolman and Miller, 1960). As such, the 2-year recurrence interval flood discharge represents an attractive target for ecological flow prescriptions and channel restoration. The assumption that this bankfull discharge will also establish flood-dependent vegetation communities such as floodplain forests is common among fluvial geomorphologists that design constructed river channels (Rosgen, 1996). At the same time research by floodplain forest ecologists has emphasized the importance of flood duration and species relative flood tolerance across a wide range of frequency and magnitude in governing the composition of floodplain forests both in the temperate region (Dister, 1983; Sharitz and Mitsch, 1993; Benke et al., 2000; Townsend, 2001) and the tropics (Junk et al., 1989; Wittmann et al., 2004). Many flood-dependent tree and shrub species are able to survive many weeks or even several months of flooding (Hall and Smith, 1955; Hosner, 1960; Bell and Johnson, 1974; Whitlow and Harris, 1979) implying that these species occur where flooding is of much greater duration than the 2-year discharge. Therefore for our purposes, we define the term floodplain more broadly to also include the lower surfaces sometimes referred to as the "floodplain under construction" (Wolman and Leopold, 1957). These lower surfaces include channel bars, point bars, channel shelves, backswamps, sloughs, swales and oxbows (Hupp, 2000). Further, upland species may in some cases readily tolerate infrequent flooding of short duration, allowing these species to co-occur with or exclude flood-dependent species, preventing the development of a distinct floodplain vegetation (Shankman, 1993; Kotowski et al., 2010). Finally, relationships between flooding and vegetation composition may be profoundly affected by the relative flood tolerances of invasive species (Tickner et al., 2001; Cooper et al., 2003; Stromberg et al., 2007), many of which are favored by the high level of disturbance associated with floodplain habitats (Zedler and Kercher, 2004; Richardson et al., 2007).

River conservation and management practitioners are increasingly being asked to make decisions in the context of whole landscapes or watersheds (Nislow et al., 2010). To support these large-scale efforts, practitioners need a way to predict the location and distribution of sites within large river basins where floodplain-dependent vegetation is most likely to be favored. While many studies have addressed site-specific factors favoring distinct floodplain vegetation (Connecticut River examples: Metzler and Damman, 1985; Nislow et al., 2002), few have attempted to translate this information into basin-scale predictions and decision-support (e.g. Friedman et al., 2006). For example, in many river systems, floodplain forests are more likely to develop in downstream locations, as a function of increasing basin size and decreasing stream gradient, which all serve to increase peak flow duration and extent, but these landscape determinants will manifest differently across ecoregional settings (Shankman and Hart, 2007). Further, they will interact with reach-scale variation in topography and hydrology, as well as with the hydrologic tolerances and habitat requirements of the local species pool (Meitzen et al., 2013). These mechanisms have been well-studied for floodplain forests in some ecoregions (Mahoney and Rood, 1998; Lytle and Merritt, 2004), but in others, such as northeastern North America, this basic information is lacking. The combination of essential data gaps and challenges in applying species-flow relationships across large basins has generally prevented necessary integration at the whole-basin scale. In this study we used data on species composition and site-specific flood regime and topography at 103 sites in the Connecticut River basin, the largest river system in New England, to develop species-flooding relationships for floodplain vegetation communities. We then used these relationships to predict the distribution of potential floodplain conservation and restoration sites at the whole-basin scale, and to uncover the basic factors underlying these distributions and their relationship to critical flow thresholds. Our goal is to develop a framework for integrating these sources of information to inform conservation and management, and at the same time fill critical gaps in our understanding of factors determining the distribution and abundance of floodplain forests.

Materials and methods

Sites

The study included 103 field research sites distributed across a range of river types throughout the Connecticut River watershed (Figure 1). Although the distribution of sites was broad and across river types, it targeted major floodplain areas that were identified previously by state natural heritage programs (Bechtel and Sperduto, 1998; Sorenson et al., 1998; Kearsley, 1999; Metzler and Barrett, 2006) and a basin wide study combining a topography-based GIS model with remote sensing (Anderson et al., 2010). For more details on the individual sites please refer to Table S1 in the appendix.

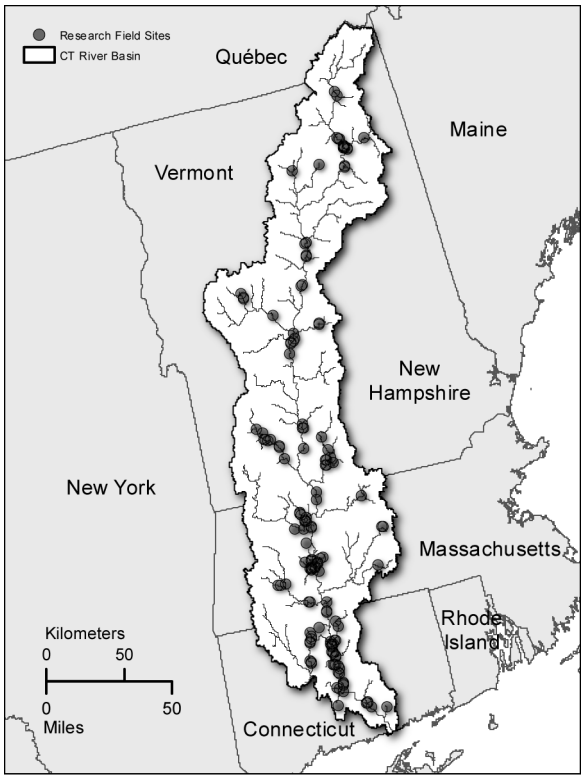

Figure 1

Connecticut River watershed with the locations of the 103 research sites.

Note that some dots are overlapping because of proximity of sites at this large scale.

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Climate and vegetation

The Connecticut River watershed experiences a temperate climate with ample precipitation during most years. Average precipitation for most of the watershed is between 1000 and 1250 mm/year, but exceeds 1500 mm/year in parts of the White Mountains. At higher elevations and especially in the northern part of the watershed (Green Mountains of Vermont and White Mountains of New Hampshire) a considerable part of the annual precipitation accumulates as snow over the winter. In most years, this accumulated snow pack results in a spring freshet (March or April). The associated flooding can last for several weeks on the mainstem Connecticut River, especially in Connecticut where the waters initially rise from snowmelt in Connecticut and Massachusetts but are subsequently sustained by later snowmelt in Vermont and New Hampshire. When combined with rain or ice jams the snowmelt related flooding can become protracted as in the rain-on-snow flood of March 1936, which, prior to the recent Tropical Storm Irene flooding, was the flood of record for most of New England and still is the flood of record on the mainstem Connecticut River (Jahns, 1947). Other catastrophic flood events are associated with late summer or early fall hurricanes as in the 1938 and 1955 floods (Wolman and Eiler, 1958), and most recently during this study with Tropical Storm Irene (August 28, 2011), but more moderate flooding can occur at any time of year.

Botanical studies of the floodplain forests in New England have recognized four basic floodplain forest community types; the large river floodplain forest dominated by *Acer saccharinum* L., the small river floodplain forest dominated by *Acer rubrum* L. or *Quercus palustris* Münchh., the rich high terrace floodplain forest dominated by *Acer saccharum* Marsh., and the high gradient river floodplain forest dominated by *Acer negundo* L. or *Platanus occidentalis* L. (Nichols, 1916; Bechtel and Sperduto, 1998; Sorenson et al., 1998; Kearsley, 1999; Nichols et al., 2000; Metzler and Barrett, 2006). These floodplain forest types also exist in

the adjacent parts of Canada and at least as far West as the Upper Mississippi River (Eyre, 1980). These northern floodplain forests can have high species richness but are less diverse than the floodplain forests further south, significantly lacking the most flood tolerant tree species (e.g. *Taxodium distichum* (L.) Rich., *Nyssa aquatica* L.). These floodplain forest communities are ranked as imperiled (S2) by most of the New England state natural heritage programs.

Quantifying flood regime

Wherever feasible (see Table S1), we quantified the flood regime using a hydraulic model, HEC-RAS (US Army Corps of Engineers, 2013). HEC-RAS is a 1-D gradually varied flow model that iterates to a best fit solution to balance energy distribution between cross-sections. Besides our interest in stage-discharge relationships, HEC-RAS determines hydraulic variables at each site including mean flow velocity, bed shear velocity, shear stress, unit stream power, and total stream power (Magilligan, 1992). We measured two or more valley and channel elevation cross sections perpendicular to the river at each HEC-RAS site. These geometry data were used to calculate a stage-discharge rating curve for each transect. With these rating curves and flow data from USGS stream gages (US Geological Survey, 2012), we calculated a stage history for each transect over the period of record. The flow data were taken from the nearest appropriate USGS stream gage (see Table S1 for gages used) and scaled linearly to account for small differences in watershed area between the study site location and the gage location. The rating curve was validated by repeated field measurements as well as from aerial photographs showing the extent of flooding during particular events. Where sites occurred at a USGS stream gage, we used gage stage data for validation. For large field sites with more than two transects, we validated the models by several methods to insure a high accuracy for these important sites (see Table S1 for a summary of the hydrology methods used at each site).

Due to the high cost of surveying large sites, we did not generate HEC-RAS models at all sites. We generated HEC-RAS models for 74 of the 103 field research sites (see Table S1). At the 29 other sites, we used data loggers with pressure transducers to record water depth for periods ranging from several months to several years (Hobo U20 Water Level Data Logger, Onset Corporation). We related these stage data to flow data from a nearby USGS stream gage by fitting a piecewise cubic spline. Data from the pressure transducers included at least one 2-year discharge event at all sites except on the Farmington River. In several cases, the record also included a 10-year flood event such as Tropical Storm Irene (August 28, 2011). Thus the model relating stage at the field site to the USGS gage flow data is accurate for flows at least up to the 2-year discharge. The models were also precise with generally high R^2 values (see Table S1 for R^2 values) depending on distance between the USGS stream gage and field site. Precision is not as important as accuracy because errors are normally distributed and should not bias the calculations of flooding statistics based on the stage history. We used this modeled relationship to extend the stage record for the site back in time to the beginning of the period of record of the USGS stream gage.

There were four reservoir sites included in the study. At the reservoir sites we used a record of impoundment water elevations to reconstruct inundation history. At both these reservoir sites as well as sites downstream of dams, we used post-dam construction data of flood regime because the floodplain forests of the Connecticut River basin are generally young and therefore reflect the post dam conditions.

Some sites had data-logger stage data and HEC-RAS modeling. In those cases, we used the data-logger observations to further validate the HEC-RAS model. For analyses we preferred using the data from the HEC-RAS model because it includes output of the stream power as well as stage for a particular discharge. We were interested in using total stream power at the 2-year discharge as a consistent measure to compare stream power across sites. The 2-year discharge was calculated using the instantaneous annual peak discharge data from the USGS gages assuming Log Pearson Type III distribution (Renshaw, 2013).

To quantify ecologically important thresholds in flood regime accurately with a non-parametric measure, we used exceedence probabilities, also referred to as the flow-duration percentile. Exceedence probability (Q) was calculated with the following equation:

$$Q = 100 \times \frac{m}{(n+1)}$$

where m is the ranking of the flow and n is the total number of mean daily flows (Risley et al., 2008). Since ranking of flows and the stages associated with those flows is the same for a site, flow and stage are interchangeable when they are expressed as exceedence probabilities. Thus we could also refer to this measure as a flood-duration percentile. For example, the *Q3* is the high flow that is exceeded 3% of the time. The stage reached by the *Q3* represents the elevations that get flooded 3% of the time.

We state the corresponding number of days flooded in the average year for each Q in the results. In our analyses, we did not differentiate between the whole year and the growing season because much flooding is either in the early spring (snow melt) or in the early fall (hurricane rainfall) which may or may not be part of the growing season depending on how one arbitrarily defines the growing season. Moreover, in trees the

seasonal pattern of root growth and respiration does not follow the same seasonal pattern as in shoots and leaves (Ledig et al., 1976). Roots respire as long as the ground is not frozen and soil anoxia from flooding imposes a physiological stress whenever roots are respiring (Kozlowski, 2002). Similarly some floodplain tree species such as *Ulmus americana* L. start flowering in March, before they leaf out.

Vegetation data

At each field site, we established 6-meter wide belt transects to study vegetation (number of transects at individual sites are listed in Table S1). At all of the sites with HEC-RAS models (74 of 103 sites), transects were oriented perpendicular to the river and coincided with the elevation profiles used in the hydrologic model (HEC-RAS sites are listed in Table S1). At sites where flooding was measured with a pressure transducer only (ie. no HEC-RAS model), there was more freedom in selecting an orientation of transects, but they were generally also perpendicular to the river channel to traverse a range of floodplain elevations and landforms. Since the purpose of the transect is to quantify flooding at transitions in vegetation type associated with topographic variation, we needed to select transect locations that had relatively unaltered floodplain vegetation and went over a range of topographic floodplain features such as bars, swales, oxbows, low and high floodplain terraces, as well as the transition to the lower slopes of the hillside at the edge of the floodplain. Thus the ideal transect crossed over the entire valley profile including the river channel and floodplain in an orientation perpendicular to the river, while avoiding cleared land such as crop fields.

We recorded the species of every living tree over 10 cm circumference on the transects and measured their elevation with a laser level. In total 11,828 trees were surveyed on 234 transects covering 103 floodplain forest field sites distributed across the watershed (Figure 1). At HEC-RAS sites the vegetation belt transects correspond to the elevation profiles used in the hydrologic model. Knowing the elevations of the trees and the stage history for the transect, we calculated the exceedence probability (i.e. flow duration percentile) for inundation of each tree, as described in the previous section. In a 1-meter radius around the base of every tree, we recorded all of the woody species that were present in the understory including tree seedlings, shrubs and woody vines. We also recorded the dominant herb layer species. Botanical names follow the USDA plants database (Natural Resource Conservation Service, 2012).

Statistical analyses

The locations of important transitions in the vegetation were identified manually along each transect to study critical flooding thresholds for different riparian habitats. Transitions in the dominant vegetation were distinct and easy to identify in the data and in the field. We identified transitions between the following habitats: floodplain forest, upland forest, shrub swamp, marsh, floating and submerged aquatic plants, scour shelves, and bare ground in the channel. Floodplain forests included the large river *A. saccharinum* community, the small river *Q. palustris* or *A. rubrum* community, and the high gradient river *P. occidentalis* or *A. negundo* community, as described in the community ecology literature (Nichols, 1916; Bechtel and Sperduto, 1998; Sorenson et al., 1998; Kearsley, 1999; Nichols et al., 2000; Metzler and Barrett, 2006). The rich high terrace *A. saccharum* floodplain community was included with the upland forest communities because it is dominated by upland tree species. Scour shelves occur on high energy riverbanks where scour disturbance from ice and high flows maintain dominance by herbaceous plants and shrubs by preventing establishment of trees. Once the locations of these transitions were identified, we quantified the flood regime (flood exceedence probability and elevation relative to the stage of the 2-year recurrence interval flow) for these locations. Specifically we calculated the mean and standard error of flood exceedence probability and elevation relative to the stage of the 2-year flow for each of these transitions using the R-statistical package (R Core Team, 2013). For the transition for which we had the most data (upland forest to floodplain forest), we also tested if the associated flood exceedence probability depended on ($\log_{10}$-transformed) watershed area using general linear model in R.

We also quantified the responses of individual species to the flooding gradient. Specifically, we divded the range of days flooded per year into bins on a logarithmic scale. We calculated the importance values (*IV*) as a measure of relative abundance for the most dominant tree and shrub species in each bin for every site. These site values were then used to calculate a mean and standard error to plot the species response to variation in the amount of flooding. Importance values (*IV*) were calculated as follows:

$$IV = \frac{F + B + D}{3} \times 100\%$$

where F is the relative frequency of the species in the shrub layer presence/absence data, B is the relative dominance of the species in terms of basal area in the tree data, and D is the relative density of tree stems per area in the tree data. This method is a slight variation on the traditional method which uses relative frequency in the tree layer rather than in the shrub layer (McCune et al., 2002). We made this change to the traditional method to be able to more meaningfully include shrub and small tree species in our results. For herb layer

species where we only had dominant species data, we used the percentage of locations in that part of the flood gradient that were dominated by a species to characterize the species' response.

In addition to asking, given a certain amount of flooding which species will likely dominate, we also asked, given a species where along the flood gradient does it mostly occur? Specifically for species with at least 50 occurrences in the data, we summarized their distributions by reporting the amount of flooding that 10th, 50th (i.e. median) and 90th percentile ranked individuals experienced. The resulting values were used to sort the species on a gradient from flood-tolerant to flood-intolerant species.

After quantifying the amount of flooding that occurs in different floodplain forest habitats, we investigated how the availability of this habitat varies across the watershed. We focused on the threshold from floodplain forest to upland forest because floodplain trees in this transition zone are most susceptible to hydrologic alteration. To investigate if a site is likely to have any habitat for floodplain tree species, we calculated the percent of days that the lowest forested floodplain surface on each transect gets inundated. We investigated if the variation among transects in the amount of flooding on the lowest forested surface is systematic with respect to watershed area and stream power using a general linear model regression implemented in the statistical package R (R Core Team, 2013). Specifically we show how the amount of floodplain forest habitat (i.e. floodplain surfaces with sufficient flooding) changes with watershed area and stream power. Stream power data were for the 2-year recurrence interval discharge to have a common basis for comparison. We log transformed (base 10) all of the data prior to analysis to normalize the distributions. Note that this part of the analysis only included the transects from the sites with HEC-RAS hydrologic models (N=183 transects) because we did not have stream power data for the other sites. In a further analysis, we quantified the part of each transect in meters where the amount of flooding fell into the range needed for dominance by floodplain tree species. The range of flooding for floodplain forest habitat was defined based on the results from the earlier analyses. We created a linear regression model of the amount of this habitat available against the watershed area and stream power using log-transformed data (base 10). We also illustrated the measured amount of this habitat as well as stream power and watershed area on a map of the Connecticut River watershed to help guide conservation activities.

Results

Flood regime and vegetation zones

Transitions from floodplain forest community dominance to dominance by other plant communities were readily identified on each study transect. The critical threshold for a shift in dominance from floodplain to upland forest dominance is flooding 1.2% of the year (4.5 d/y) on average (Figure 2). This amount of flooding occurred on floodplain surfaces that were on average 0.3 meters below the 2-year flow stage. The flood exceedence probability at this transition in dominance from upland to floodplain tree species was not affected by location within the watershed. Specifically, we tested if the transition from floodplain forest to upland forest depends on watershed area using a general linear model, and the result was not statistically significant. The threshold for a shift in dominance from floodplain forest to shrub swamp is flooding during 26% of the year (95 d/y) on average. The flooding thresholds for switches to dominance by herbaceous marsh plants and aquatic plants were even greater, 39 % (142 d/y) and 70% (255 d/y) of the year respectively. These wettest floodplain habitats occurred naturally in oxbows and backswamps of low gradient meandering rivers, especially in the tidally influenced lower mainstem, as well as around artificial impoundments. A channel shelf dominated by herbaceous plants and shrubs maintained by scour can occur on high gradient rivers at elevations that flooded between 8 and 34% of the year (29 – 124 d/y). Please refer to Figure 2 for standard errors and replication of these results.

Our tree data allowed examination of these transitions for individual species in the forested part of the flooding gradient (Figure 3). The most common upland tree species like *Acer saccharum* and *Prunus serotina* Ehrh. have low relative abundance (i.e. importance value) where flooding is more than 5% of the year (18 d/y). Similarly, relative abundance of dominant floodplain tree species like *Acer saccharinum* and *Fraxinus pennsylvanica* Marsh. is low where flooding is less than 0.27% of the year (1 d/y). This pattern is confirmed by the distributions of less abundant tree species (Table S2). The threshold for too much flooding to support dominance by trees (26% or 95 d/y) is also confirmed by individual tree species distributions (Table S2). For example, 90% of the individuals of *F. pennsylvanica* and *A. saccharinum* (the most flood tolerant of the dominant canopy tree species) occurred at elevations that flooded less than 25% and 30% of the time respectively. Thus habitat for floodplain tree species occurrence can be defined as the surfaces that flood between 0.27 and 30% of the year, but their dominance is restricted to surfaces that flood between 1.2 and 26% of the year.

In the floodplain forest, the importance of some native wetland shrubs like C*ephalanthus occidentalis* L. was skewed towards even longer duration flooding than for floodplain trees (Figure 3 & Table S3). By contrast, most of the invasive shrub species like *Berberis thunbergii* DC. appear to be relatively intolerant of flooding (Figure 3). With the exceptions of *Celastrus orbiculatus* Thunb., *Frangula alnus* Mill., and *Rosa multiflora*

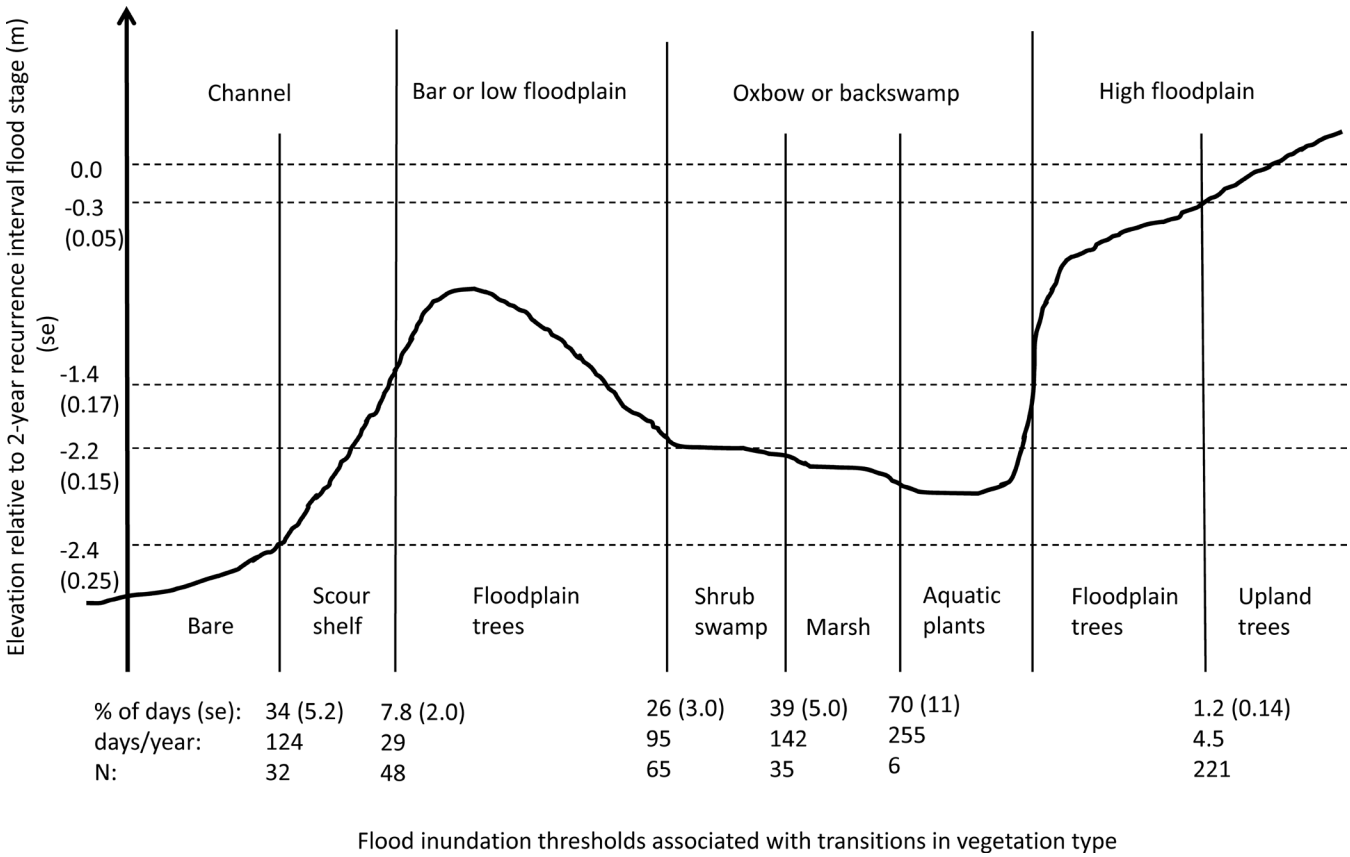

Figure 2

Floodplain vegetation zones showing thresholds in inundation marking the transitions between vegetation types.

The inundation thresholds are the means across all study sites for these vegetation transitions followed by the standard errors in brackets. The line in the Figure represents an idealized floodplain elevation profile for illustration purposes only. The scour shelf dominated by herbaceous vegetation and shrubs occurs only on high gradient rivers where scour is sufficient to eliminate trees. Oxbows with associated shrub swamps and marshes occur only on meandering low gradient rivers. The number of transitions (N) of each type in the data varies because not all types of transitions occurred on all transects.

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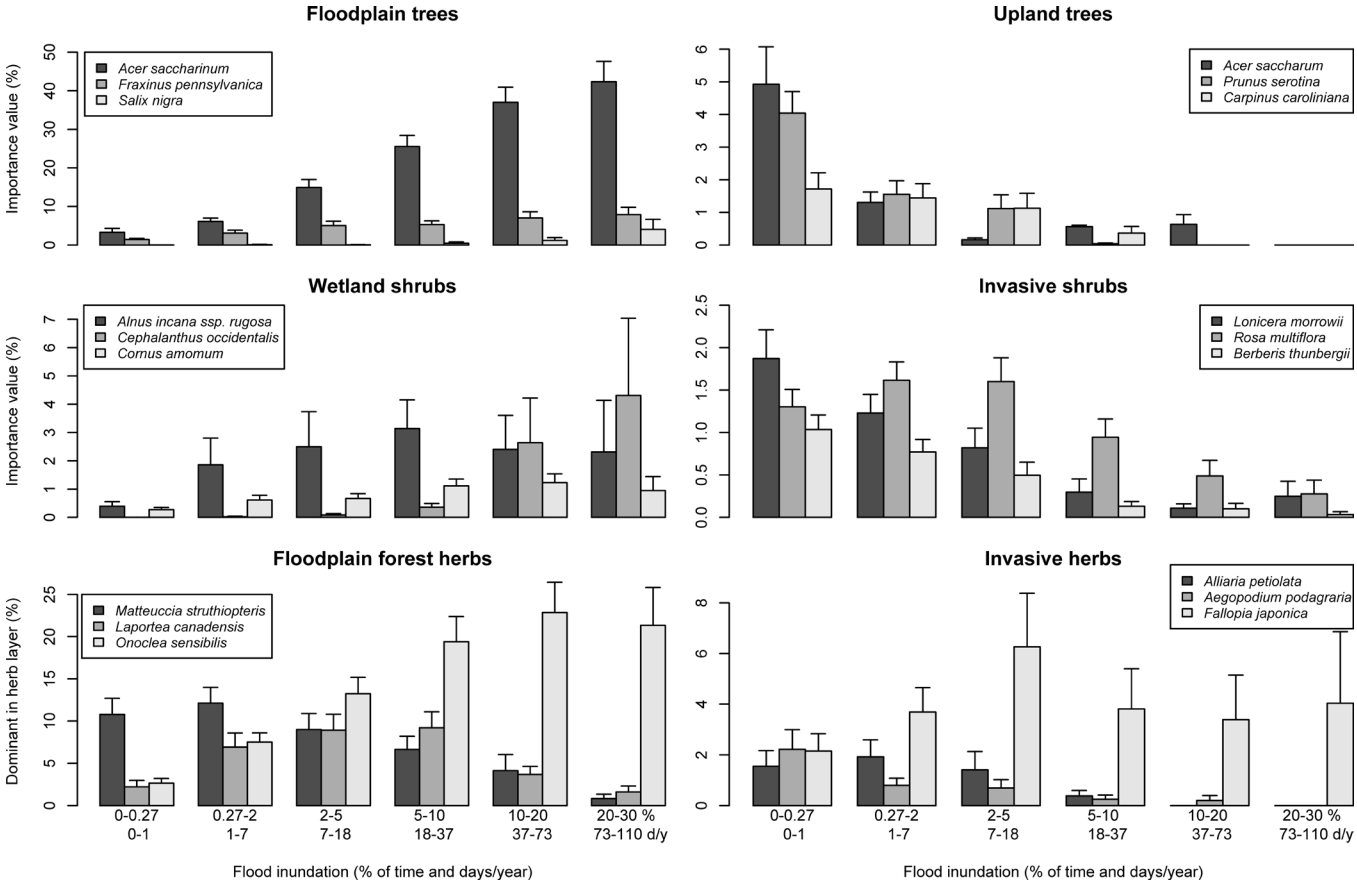
Thunb., all of the non-native invasive woody species had 90% of their occurrences at elevations that flooded less than 2.4% of the year (9 d/y) (Table S2 & S3). The non-native invasive herbaceous species *Alliaria petiolata* (M. Bieb.) Cavara & Grande and *Aegopodium podagraria* L. were also less abundant where flooding was above 2.6% of the year (9.5 d/y), but notably the invasive herb *Fallopia japonica* (Houtt.) Ronse Decr. is tolerant of flooding and occurs across the entire flooding gradient (Figure 3 & Table S4).

Determinants of floodplain forest habitat in the Connecticut River basin

Watershed area and stream power appear to be the primary geomorphic and hydrologic determinants of basin-scale distribution of floodplain habitat. Specifically, we observed many more individuals of floodplain tree species on low-gradient river reaches than on high gradient reaches with greater stream power. Similarly the incidence of floodplain tree species was observed to be higher on larger rivers (greater watershed area). The flow exceedence probability for the elevation of the lowest tree on each transect represents a measure of the habitat available for floodplain tree species. Regression of these exceedence probabilities versus watershed area (A) and the stream power of the 2-year discharge (P) was highly significant ($p<0.001$) and explained over half of the variation (adjusted $r^2= 0.55$, AIC=388) using log-transformed data ($\log_{10}(Q_{lowtree}) = -3.45 -0.58*\log_{10}(P) + 0.46*\log_{10}(A)$, where Q in %, A in m^2 and P in N/m s). The lowest elevation trees on the floodplain were flooded more of the time, the larger the watershed area and the lower the stream power (i.e. the lower the stream gradient and the finer the channel bed material) (Figure 4). Note that models with just watershed area (adjusted $r^2= 0.22$, AIC=599, model not shown) or just stream power (adjusted $r^2= 0.35$, AIC=466, model not shown) explained much less of the variation than the model combining both variables.

Another measure of habitat available for tree species endemic to floodplains like *A. saccharinum* is the amount of the valley width that is flooded between 1 and 30% of the time. Regression of this valley width habitat measure versus watershed area (A) and the stream power of the 2-year discharge (P) was highly significant ($p<0.001$) and explained three quarters of the variation (adjusted $r^2= 0.75$, AIC=194) using log-transformed data ($\log_{10}(W_{floodtree}) = -2.44 -0.43*\log_{10}(P) + 0.51*\log_{10}(A)$, where W in m, A in m^2 and P in N/m s). Thus the habitat available to floodplain tree species increased with greater watershed area and lower stream power (i.e. lower stream gradient and finer channel bed materials) (Figure 5). Note that linear regression models with just watershed area (adjusted $r^2= 0.51$, AIC=366, model not shown) or just stream power (adjusted $r^2= 0.36$, AIC=412, model not shown) explained much less of the variation than the model combining both



variables. Similarly measures correlated with stream power such as energy gradient, velocity, and shear had significant relationships with floodplain habitat but explained less of the variation than stream power (results not shown). We mapped the distribution of floodplain tree species habitat throughout the entire Connecticut River basin as approximated by the part of the valley width that floods between 1 and 30% of the time (Figure 6). We also mapped the variation in stream power and watershed area for comparison. As expected, floodplain tree species habitat is larger in extent in downstream, mainstem locations, but there is also some floodplain tree species habitat in upstream and tributary locations where the stream gradient is low (Figure 6).

Figure 3

Importance of common floodplain forest species in response to different amounts of flooding.

Error bars show standard errors. Note that these data are only for the forested part of the floodplain. The percentage of plots where the species was dominant was used for describing herbaceous species distributions on the flooding gradient. This Figure juxtaposes floodplain trees versus upland trees, native wetland shrubs versus invasive shrubs, and native floodplain herbs versus invasive herbs to illustrate the differences in distributions with respect to flooding. *Acer saccharum* includes hybrids with *A. nigrum*, and *Fallopia japonica* includes *F. x bohemica* hybrids.

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Discussion

In this study we demonstrated that flood duration is a major determinant of floodplain forest occurrence and composition in a large northeastern river, and that these relationships can be used to predict and prioritize floodplain habitats for conservation and restoration at large landscape scales. Further, our analysis indicated that distinct floodplain forest assemblages were consistently associated with long-duration flooding (>4.5 d/y) at elevations that were lower than the 2-year flood stage, which has been widely accepted as a critical threshold for reconnecting rivers to their floodplains. This observation also suggests that flow prescriptions aimed at maintaining existing floodplain forests may not result in major conflicts with flood protection in this basin. Overall, this study provides a framework for integrating multidisciplinary data for conservation planning at the scale of large river basins.

Floodplain forests of northeastern North America flood more frequently and for longer durations than commonly perceived by many professionals working in the field of river restoration and management. The almost complete absence of tree species like *Acer saccharinum*, *Fraxinus pennsylvanica, Populus deltoides* Bartram ex Marsh. and *Salix nigra* Marsh. at elevations that flood < 1 day per year shows their flood-dependence. These flood-dependent tree species dominate at elevations that are flooded between 1.2% of the year (4.5 d/y) and 26% of the year (95 d/y). At elevations experiencing shorter duration flooding, upland species like *Acer saccharum* and *Prunus serotina* dominate, while at elevations experiencing longer duration flooding, *Acer saccharinum* and *Salix nigra* which appear to be the most flood tolerant tree species give way to dominance

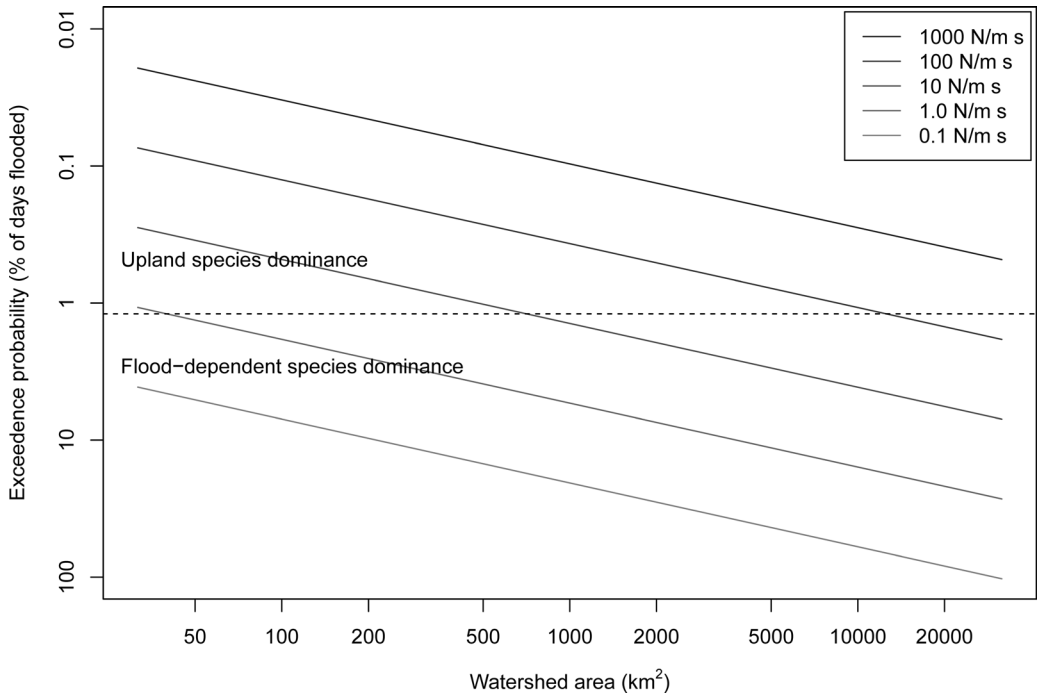

Figure 4

Flood exceedence probability at the elevation of the lowest trees predicted by the model.

The family of curves represents different stream powers at the 2-year discharge flow in N/m s. This plot shows that most habitat for flood-dependent species exists at either large watershed size (i.e. >1000 km^2) or low stream power (i.e. < 10 N/m s), or both. The range of plotted watershed areas and 2-year discharge flow velocities reflects the range of measured values in our field data spanning the Connecticut River watershed. Note that the trees included in this analysis did not include small trees on channel bars because they often do not persist beyond the next flood.

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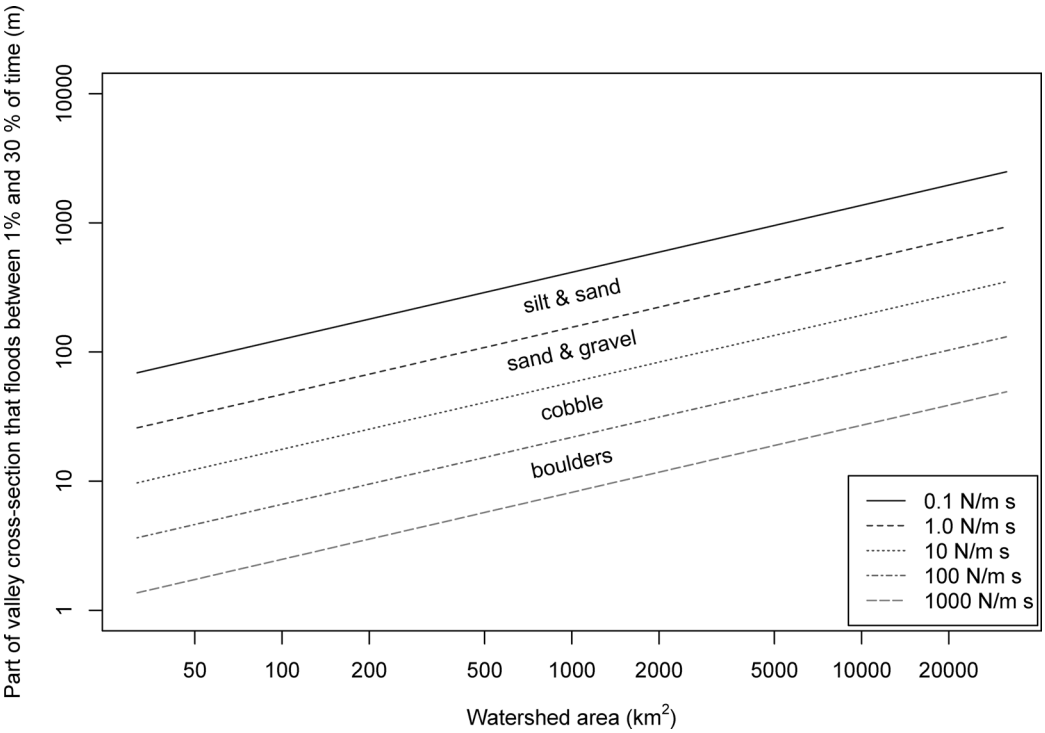

Figure 5

Part of valley width that is suitable habitat for flood-dependent species predicted by the model.

Suitable habitat is defined as surfaces with elevations that begin to flood between the Q30 and Q1 flows. The family of curves represents different stream powers at the 2-year discharge flow in N/m s. This plot shows that habitat for flood-dependent species is typically no wider than a single row of trees along the banks when watershed size is below 1000 km^2 and power is over 10 N/m s, as is the case on many high gradient tributaries of the Connecticut River. The range of plotted watershed areas and 2-year discharge flow velocities reflects the range of measured values in our field data spanning the Connecticut River watershed. The Figure also reports the predominant channel bed material associated with ranges of stream power in the Connecticut River basin.

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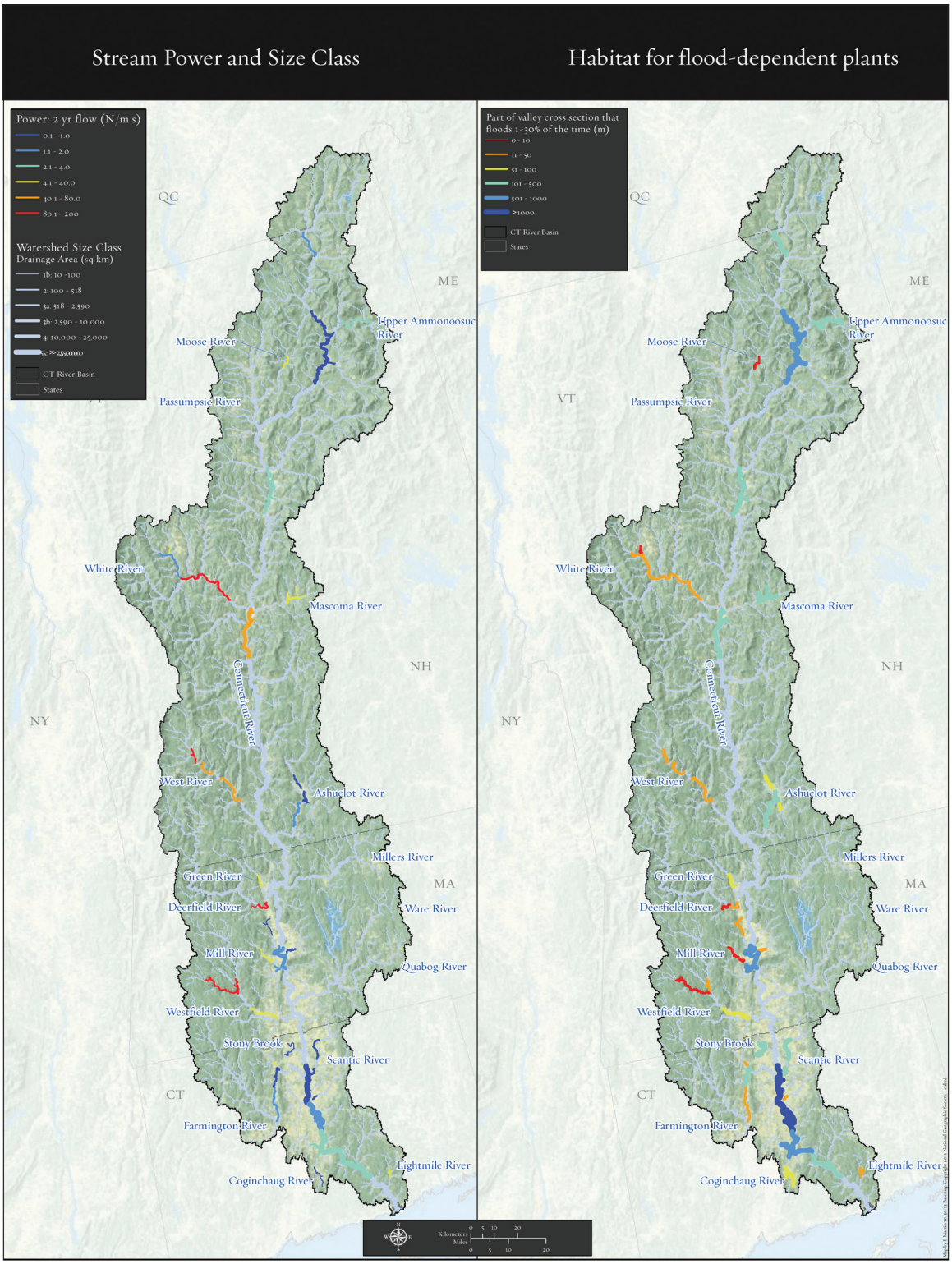

Figure 6

Maps showing stream power, watershed area and habitat available for flood-dependent species across the watershed.

Flood-dependent species habitat is represented by the part of the valley width that is at elevations between the stages of the Q30 and Q1 flows. Only river reaches that had one or more study sites were included in the map. Note that the amount of flood-dependent species habitat tends to increase from headwater streams to the head of the estuary, reflecting increasing watershed area and decreasing stream power.

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by native shrub swamp species such as *Cephalanthus occidentalis* and *Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. These thresholds are generally consistent with the results of two local studies at an individual site (Metzler and Damman, 1985) and two sites (Nislow et al., 2002), as well as in other studies in similar systems in the northeastern and northcentral U.S. (De Jager et al., 2012). For example, on a high gradient stream in Virginia, flood-dependent trees like *P. deltoides* and *S. nigra* were largely absent in the active floodplain that flooded with a recurrence interval of once every 1.5 years, whereas these species did occur on the channel shelf which experienced a flood duration of 13% of the time (47 d/y) (Hupp and Ostercamp, 1985). This generality suggests that the flood duration thresholds we observed in the Connecticut River basin might be widely applicable to similar systems within the northeast, northcentral and mid-Atlantic regions.

The long-duration floods that favored the development of distinct floodplain forests were also associated with lower abundances and less frequent occurrences of most species of invasive shrubs, as also found in a study of invasive *Lonicera* and *Rhamnus* shrubs on the Wisconsin River (Predick and Turner, 2008). These invasive plants can be major threats to native forests, particularly in disturbed habitats. Our results emphasize the importance of both direct (via physiological tolerance) and indirect (via competition with native and non-native species) effects of hydrologic alteration on floodplain forests.

Our findings also underscore the importance of interactions between hydrologic regime, underlying geology, landform, and climate, and local species pool in determining the structure and distribution of floodplain forests. Floods of sufficient duration to exclude upland species but at the same time permit growth of flood-tolerant trees are more likely to be characteristic of large basins and lower stream gradients. Although basin size and gradient effects tend to both increase the availability of floodplain habitat on the mainstem relative to smaller tributaries generally, we identified a number of locations upstream in the basin and on tributaries where gradients were low enough to permit appropriate duration floods (Figure 6). Most of this habitat for flood-dependent species is on point bars, in backswamps and oxbows as illustrated in Figure 7. Such frequently flooded geomorphic features have been referred to as the "floodplain under construction", which emphasizes the importance of the geomorphic processes such as lateral channel migration for the long term persistence of flood-dependent species (Shankman, 1993).

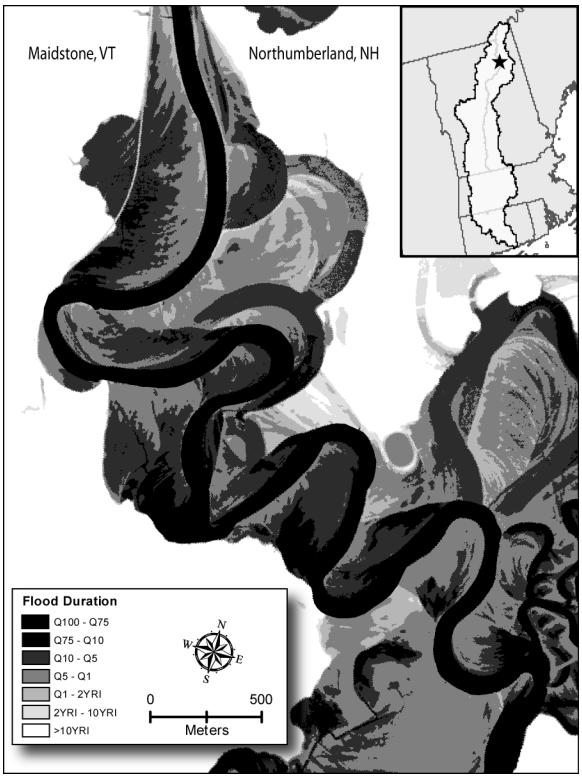

Figure 7

Map illustrating low floodplain habitat features at an example site.

The Connecticut River floodplain at the confluence of the Upper Ammonoosuc River shown here includes topographic features such as coves, oxbows, backswamps, swales and point bars with frequent and long duration flooding providing ample habitat for flood-dependent species. Note that the natural levees along the upstream banks of some of the meander bends are among the highest elevation features in the floodplain falling in the range of the 1.1 to 2 year recurrence interval flood stage, consistent with the conventional definition of "bankfull" flow. The watershed area upstream of the Upper Ammonoosuc River confluence is 3000 km^2 and is almost completely forested, had little development, and there are no upstream flood control dams. There is no evidence for a shift in hydrologic regime over the period of record for the two USGS stream gages in the area which go back to 1927 and 1930. See Maidstone Bends and Upper Ammonoosuc Confluence sites in Table S1 for details of measurement methods used in this reach.

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These results have important management implications. As Ogden et al. (2013) elucidate, environmental management in the Anthropocene demands novel forms of governance and institutional arrangements, ultimately requiring greater communication and cooperation between scientists and policy makers. Our results are important as they show that most of the appropriate floodplain tree species habitat is at or below the 2-year recurrence interval flood elevation; therefore flow prescriptions to maintain these habitats do not

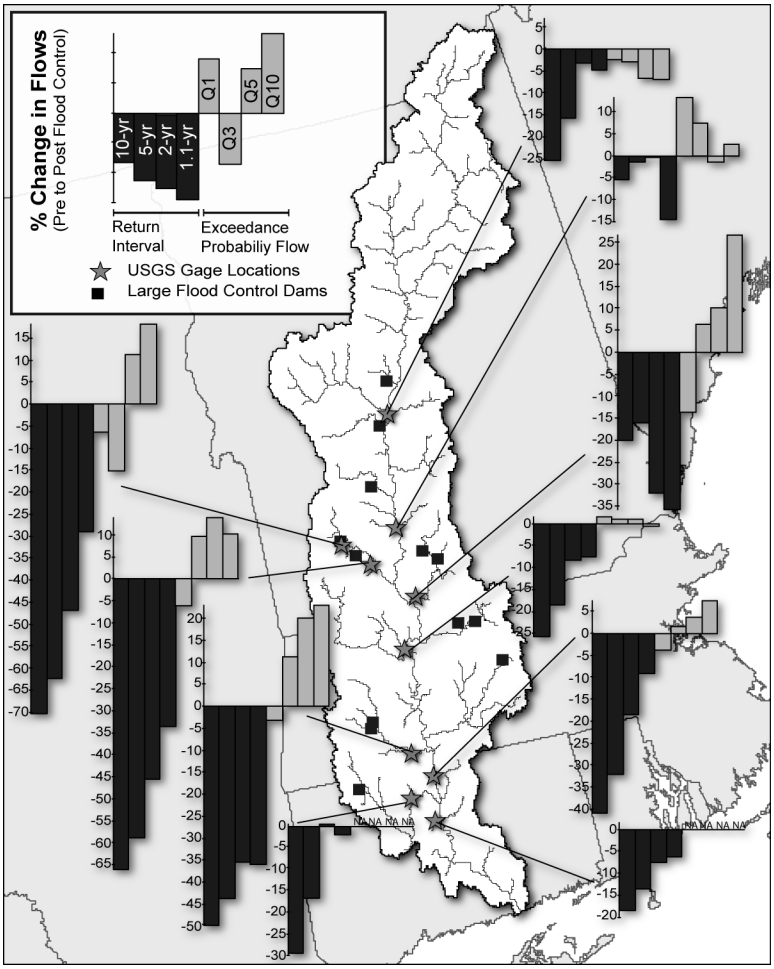

Figure 8

Map of Connecticut River watershed showing flood control dams and flow alteration at downstream gages.

The bar graphs show the degree of high flow alteration at the stream gages as the percent change in the flows after the construction of the last upstream flood control dam compared with the flows prior to the construction of the first upstream flood control dam. Note that the reduction in peak flows has been most severe for the 5-year discharge and higher, as the system was designed to do because these rare events can cause serious damage. The 1.1-year to 2-year discharges and in many cases even the Q1 have also been reduced despite being of little threat. The Q3, has changed relatively little while the Q5 to Q10 has tended to increase because the water held back by the flood control dam during the flow peak is subsequently released at these lower flow rates.

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necessarily conflict with the protection of human infrastructure (roads and buildings). Further efforts at modifying large dam operations could be focused more on duration than on magnitude of prescribed flows. An important consideration, however, is the extent to which the higher magnitude floods that have been most modified by flood control dam operations (see Figure 8) may be necessary for the formation of low floodplain features such as bars, oxbows, swales and backswamps. Likewise, the preoccupation of channel restoration practitioners with channel stability minimizes the natural geomorphic processes that form these crucial habitats. Improved river restoration designs should include bars, channel shelves, backswamps and even oxbows wherever appropriate to provide habitat for a broader range of species. Such riparian wetland areas also contribute disproportionally to important ecosystem functions like the removal of excess nitrogen (Craig et al., 2008). By quantifying the flood regime for floodplain tree species, this work informs both management strategies and our basic region-specific understanding of the structure and function of floodplain forests.

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Contributions

- Contributed to conception and design: COM, KHN, FJM
- Contributed to acquisition of data: COM, KHN, FJM
- Contributed to analysis and interpretation of data: COM, KHN, FJM
- Drafted and/or revised the article: COM, KHN, FJM
- Approved the submitted version for publication: COM, KHN, FJM

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Competing interests

We are not aware of any competing interests.

Supplemental material

- **Table S1: List of field sites and methods used to model flood regime at the site.** doi:10.12952/journal.elementa.000031.s001
- **Table S2: Distribution of tree species with respect to amount of flooding.**
  Species are sorted in order from the one experiencing the most flooding to the one experiencing the least flooding. The distribution of a species is described by the percent of the year that the 10th percentile, median and 90th percentile individuals of that species experience flooded conditions. For example, half of all *Salix nigra* individuals experience flooding more than 19.3% of all days, while the other half experience less than that. Only 10% of *S. nigra* individuals experience flooding less than 8.7% of all days, while 90% of individuals experience flooding less than 23.9% of all days. Species habitat classifications are based on the floodplain forest community ecology literature cited in the methods. Habitats include: low floodplain forest (F), swamps (S), rich high terrace floodplain forest (R), upland forest (U), disturbed areas (D), non-native invasive (I). Trees are defined as individuals with circumference 10 cm or greater. Only species with a number of 50 or more occurrences are listed (N). (DOC) doi: 10.12952/journal.elementa.000031.s002
- **Table S3: Distribution of woody species in the shrub and seedling layer with respect to amount of flooding.**
  Species are sorted in order from the one experiencing the most flooding to the one experiencing the least flooding. The distribution of a species is described by the percent of the year that the 10th percentile, median and 90th percentile occurrence of that species experience flooded conditions. For example, half of all *Cephalanthus occidentalis* individuals experience flooding more than 20.2% of all days, while the other half experience less than that. Only 10% of *C. occidentalis* individuals experience flooding less than 7.0% of all days, while 90% of individuals experience flooding less than 66.3% of all days. Only species with a number of 50 or more occurrences are listed (N). (DOC) doi: 10.12952/journal.elementa.000031.s003
- **Table S4: Distribution of dominant species in the herb layer with respect to amount of flooding.**
  Species are sorted in order from the one experiencing the most flooding to the one experiencing the least flooding. The distribution of a species is described by the percent of the year that the 10th percentile, median and 90th percentile location where that species is dominant is flooded. For example, half of the studied locations where *Cephalanthus occidentalis* is dominant experience flooding more than 25% of all days, while the other half experience less than that. Only 10% of *C. occidentalis* dominated locations experience flooding less than 9.3% of all days, while 90% of *C. occidentalis* dominated locations experience flooding less than 99.7% of all days. Only species that were dominant in the herb layer in at least 50 locations are listed (N). (DOC) doi:10.12952/journal.elementa.000031.s004

Data accessibility statement

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.jn3rr
- Transect vegetation data in the form of an MS Access database
- HEC-RAS hydraulic model files for research sites
- Stage data from data loggers for research sites

These data will not only allow other researchers to replicate and expand upon our analyses, but the HEC-RAS models in particular will be a useful base upon which to build further river research.

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