

# From salamanders to greenhouse gases: does upland management affect wetland functions?

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Although the effects of forest management on watershed hydrology are well recognized, little is known about how upland management affects the hydrology and functions of wetlands embedded within upland forests (hereafter, embedded wetlands). We simulated the effects of upland tree basal area (ie total cross-sectional area of trees per land area) and different upland management approaches on wetland hydrological, biogeochemical, and habitat functions. Increases in upland basal area and associated forest evapotranspiration reduced wetland inundation depth and duration. Wetland global warming potential decreased with higher upland basal area, driven by lower methane production in drier wetlands. Amphibian habitat suitability decreased with increasing basal area due to reduced wetland inundation. Simulations of three common 25-year management scenarios – namely, constant basal area, fire management, and pine plantation – highlighted impacts of forest structure that vary over time. Prescribed fires that recurred every 3 years generated cyclic patterns in wetland hydrology and function, whereas pine plantations transitioned from wet to dry regimes with stand growth. This work represents a first step to linking upland management, wetland hydrology, and wetland functions, highlighting opportunities for optimizing forest management to provide landscape-scale ecosystem services.

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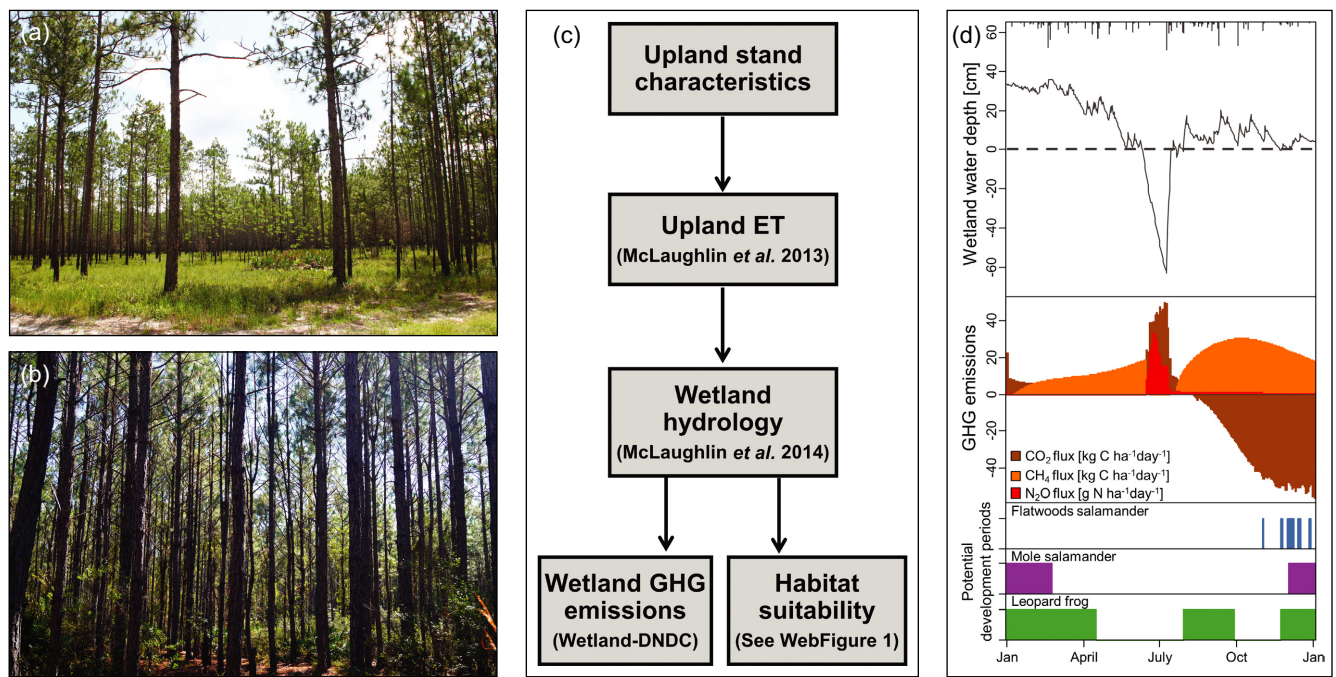
Upland forests are managed for a wide variety of functions, from timber production and carbon sequestration to habitat improvements and wildfire prevention. Informed forest management requires consideration of trade-offs among functions that are provided by different approaches (eg production forestry versus ecological forestry; Becknell *et al.* 2015), as well as the spatial and temporal scales over which different functions are realized. Forest management activities, such as tree thinning and prescribed fire, change forest structure and can yield both local effects (eg increased understory diversity; Belote *et al.* 2008) and larger-scale outcomes (eg regional stability of insect metapopulations; Tschardt and Brandt 2004). Specific management actions may therefore have both targeted and unintended impacts on ecological function at varying scales. For example, reductions in forest biomass for local habitat improvement may also decrease forest carbon storage, while at the same time decreasing forest water use (ie evapotranspiration; ET) and increasing water subsidies (via surface- and

groundwater flows) to adjacent water bodies (McLaughlin *et al.* 2013).

Here we focus on the potential for upland management actions that reduce forest biomass to influence hydrology and hydrologically mediated processes in wetlands embedded within upland forests (hereafter, embedded wetlands). Short-term increases in stream flow after intense forest harvesting have long been documented (Bosch and Hewlett 1982). However, recent research has identified the possibility for smaller but more sustained increases in water subsidies from forests maintained at consistently low levels of biomass (via thinning and prescribed fire; McLaughlin *et al.* 2013). Critically, this low tree basal area management strategy is widely applied to restore or maintain upland habitat quality (eg understory diversity, endangered species habitat; James *et al.* 2001), but its effects on unharvested, embedded wetlands are largely unknown. Increased water subsidies driven by reduced upland ET have the potential to increase inundation depth and duration in embedded wetlands, with cascading effects on biogeochemical cycling and habitat suitability.

The unique hydrological characteristics of wetlands support important ecosystem functions, which yield ecosystem services ranging from habitat provisioning to water-quality improvements to carbon storage. For instance, wetland-breeding insect and amphibian species often rely on inundation for reproduction and development, and changes to the hydrological regime can negatively affect sensitive species (Chandler *et al.* 2017). Wetland hydrology also drives biogeochemical cycling that can yield

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**Figure 1.** Example of (a) low basal area and (b) high basal area management typical of pine flatwoods systems in the southeastern US coastal plain. Basal area refers to the cross sectional area of trees 1.4 m above the ground in a given area, describing contributions of both tree sizes and stand density to forest biomass. (c) Model linkages used in this study. (d) Example of daily output from our series of linked models. Bars on lower panels of (d) represent the initial day of potential development periods for breeding amphibians, providing information on the number of times that inundation periods could allow development from egg through metamorphosis for each species.

water-quality improvements and regulate carbon sequestration rates, where prolonged inundation leads to soil redox conditions that promote denitrification and carbon storage (Morse *et al.* 2012). Likely connections among upland ET, wetland hydrology, and wetland functions suggest that there may be an opportunity to optimize wetland ecosystem services through upland management.

We explored the impact of upland forest management on embedded wetland hydrology and two attendant wetland functions (greenhouse-gas [GHG] emissions and amphibian development). We used a series of linked process-based and empirical models to (1) quantify the effects of upland forest biomass (via tree basal area) on wetland hydrological regimes and associated functions, and (2) simulate these effects for three common upland management scenarios: constant basal area, fire management, and pine plantation. These efforts are an important first step in understanding linkages among upland forest structure, wetland hydrology, and wetland functions, and highlight opportunities to optimize forest management for increased ecosystem services at landscape scales.

## Methods

We based our study on the upland–wetland mosaic that typifies pine flatwoods of the southeastern US coastal plain. Uplands in pine flatwoods were historically characterized by low density, low basal area forests dominated by longleaf (*Pinus palustris*) and slash (*Pinus*

*elliottii*) pine, with an understory structured by frequent fire (Freeman and Jose 2009) (Figure 1a). A majority of these forests have been converted to monotypic production plantations, which are managed to maximize timber production (Figure 1b). Pine flatwoods are also defined by the widespread occurrence of embedded depressional wetlands, which often make up 30% of the landscape (McLaughlin *et al.* 2014; Chandler *et al.* 2017). Water-level variation in these wetlands is tightly linked to variation in upland water tables, which are largely influenced by upland ET (Crownover *et al.* 1995). Wetland hydrology not only supports numerous flora and fauna, including the endangered reticulated flatwoods salamander (*Ambystoma bishopi*) (Chandler *et al.* 2017; Figure 2), but also regulates nitrogen removal and carbon storage.

To connect upland ET, wetland hydrology, and wetland functions in these systems, we linked a series of process-based and empirical models (Figure 1c), including: (1) an empirical model to predict annual upland ET from forest stand characteristics (tree basal area and understory biomass) (McLaughlin *et al.* 2013); (2) a process-based hydrological model (McLaughlin *et al.* 2014) to simulate wetland water levels using upland and wetland daily water budgets; (3) the Wetland Denitrification-Decomposition (wetland-DNDC) model (Zhang *et al.* 2002) to simulate wetland GHG emissions (via carbon and nitrogen cycling); and (4) empirically derived habitat suitability models for development



periods of three amphibian species (southern leopard frog [*Lithobates sphenoccephalus*], mole salamander [*Ambystoma talpoideum*], and reticulated flatwoods salamander; WebFigure 1). We performed simulations using a daily time-step (Figure 1d), and results were aggregated annually. Model parameters (WebTable 1) were based on measurements from wetland sites at Eglin Air Force Base (Chandler *et al.* 2017), which is located in the Florida panhandle. Individual model components are described in greater detail in WebPanel 1.

Our series of linked models were applied in two steps. First, we simulated the effects of upland tree basal area (ie biomass metric that combines tree sizes and density) on wetland hydrology and function across a range of upland basal areas from low ( $8 \text{ m}^2 \text{ ha}^{-1}$ ) to high ( $25 \text{ m}^2 \text{ ha}^{-1}$ ). Lower basal areas are typical of historical pine uplands (Freeman and Jose 2009) and areas currently managed for conservation purposes (eg red-cockaded woodpecker [*Picoides borealis*] habitat; James *et al.* 2001; Figure 1a). Higher basal areas are representative of mature pine plantations managed for timber production (Ewel and Gholz 1991; Figure 1b). For each upland basal area, we conducted 1000 independent, one-year simulations to capture inherent climate variability and used annual means to compare outputs across simulations. Given that these one-year simulations do not account for stand growth patterns or management actions that vary over time, we next modeled the effects of temporal variation in biomass by simulating three common 25-year management strategies (as defined by McLaughlin *et al.* 2013): (1) constant low basal area management ( $14 \text{ m}^2 \text{ ha}^{-1}$ ) via frequent thinning; (2) low basal area management ( $14 \text{ m}^2 \text{ ha}^{-1}$ ) with prescribed fire to reduce understory biomass, and thus reduce ET, on a 3-year rotation; and (3) typical 25-year rotational timber production management from planting ( $0.5 \text{ m}^2 \text{ ha}^{-1}$ ) to maturity ( $25 \text{ m}^2 \text{ ha}^{-1}$ ). See WebPanel 1 for further descriptions of management scenarios. We conducted 1000 25-year simulations for each management scenario and compared mean annual and cumulative inundation duration, GHG emissions, and development periods across scenarios.

## Results and discussion

### Effects of upland basal area

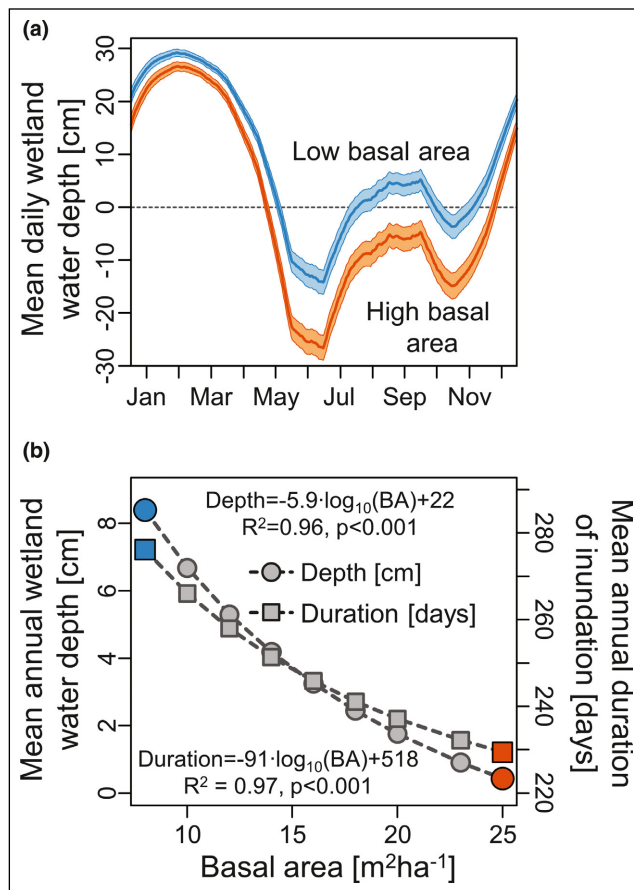
Our conceptual model posits that higher upland basal area, and thus higher upland ET, decreases water subsidies to embedded wetlands, affecting the depth, duration, and timing of inundation. Our simulation results are in agreement with this prediction, with higher basal area uplands associated with reduced depth and duration of wetland inundation as compared with lower basal area uplands (Figure 3a–b). Across simulations, wetland water level and inundation duration exponentially declined with increasing upland basal area (Figure 3b).

As predicted, changes in upland basal areas and wet-



**Figure 2.** (a) Example of historical pine flatwoods habitat characterized by low density pine forests, frequent fire, and high density of embedded wetlands. Many wetland species, including (b) the endangered reticulated flatwoods salamander (*Ambystoma bishopi*), rely on this unique habitat for breeding and development.

land hydrology influenced wetland carbon, nitrogen, and cumulative GHG emissions. Increases in upland basal area (ie reduced wetland inundation duration) increased wetland carbon dioxide ( $\text{CO}_2$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ) emissions but lowered methane ( $\text{CH}_4$ ) production (Figure 4a). Higher  $\text{CO}_2$  emissions with shorter inundation duration can be explained by more frequent aerobic conditions that speed organic matter decomposition (Altor and Mitsch 2006); higher  $\text{N}_2\text{O}$  emissions can be explained by paired nitrification–denitrification induced by increased hydrological variability (eg Firestone and Davidson 1989). Reduced inundation duration also inhibited methanogenesis due to less frequent low-redox conditions (Altor and Mitsch 2006). To quantify the cumulative effect of these fluxes, we calculated the global warming potential (GWP) for each simulated basal area (positive GWP indicates a net source of GHG emissions). GWP is defined as the radiative forcing of GHG fluxes normalized to  $\text{CO}_2$  equivalents, where  $\text{CH}_4$  and  $\text{N}_2\text{O}$  decay are considered across 20-, 100-, and 500-year reference frames (as defined by Whiting and Chanton 2001). Wetlands served as GWP sources across all simulations under 20- and 100-year reference frames; however, GWP decreased with increasing basal area (Figure 4b) due to lower  $\text{CH}_4$  emissions, despite higher



**Figure 3.** (a) Simulated mean daily wetland water level (over 1000 simulations) under low ( $8 \text{ m}^2 \text{ ha}^{-1}$ ) and high ( $25 \text{ m}^2 \text{ ha}^{-1}$ ) basal area management. (b) Simulations across upland basal areas for wetland hydrology: mean annual water level and inundation duration.

$\text{CO}_2$  and  $\text{N}_2\text{O}$  emissions (Figure 4a). Differences in GWP among simulated basal areas were insignificant at the longest reference time frames.

Potential development periods (from egg through metamorphosis) of the three representative wetland-breeding amphibian species also varied with increasing upland basal area. We used two metrics to predict how wetland hydrology affects amphibian development: (1) the mean annual number of potential development periods (Figure 4c) and (2) the proportion of years with adequate hydrological conditions for development (ie the percentage of simulated years with at least one potential development period; Figure 4d). Potential development periods represent explicit inundation events that satisfy the *timing* and *duration* requirements for both egg and larval stages (WebFigure 1). Periods may overlap and signify the total number of possible development windows in each year based solely on hydrological regime (Figure 1d). All three species demonstrated sensitivity to changes in upland basal area. Across the gradient from low to high upland basal area, the annual number of potential development periods decreased for all taxa (Figure 4c): leopard frogs

(184 to 130, a 29% decrease), mole salamanders (64 to 46, a 28% decrease), and flatwoods salamanders (20 to 15, a 25% decrease). Likewise, as basal area increased, the proportion of years with adequate hydrological conditions decreased but remained >90% in all cases (Figure 4d). Among the modeled species, the reticulated flatwoods salamander has the most complicated and restrictive hydrological requirements. Nevertheless, across all species, the model results suggest that reduced upland basal area has the potential to improve amphibian development success.

### Effects of 25-year management scenarios

Simulated temporal variation in inundation duration fluctuated considerably across the three 25-year management scenarios (Figure 5a). Constant, low basal area management resulted in relatively consistent annual flooding duration, whereas fire management created cyclic inundation patterns, mirroring fire (ie sudden reduction of upland ET) and understory regrowth (ie slow increase in upland ET) cycles. In the pine plantation scenario, wetland hydrological regime transitioned from wet to relatively dry conditions as the pine plantation matured. Across the 25-year simulations, cumulative inundation was similar for constant basal area and pine plantation management scenarios and higher in landscapes under fire management ( $P < 0.01$ , pairwise Wilcoxon test; Figure 5b). In agreement with hydrological variation, GWP and potential development periods were consistent for constant basal area scenarios, were cyclic with the addition of fire, and decreased with pine plantation maturity (Figures 5c–e). Cumulative GWP (Figure 5d) was similar between the constant basal area and pine plantation scenarios and greater under the fire management scenario ( $P < 0.01$ , pairwise Wilcoxon test); for the flatwoods salamander, cumulative potential development periods were different among all scenarios and highest under fire management (Figure 5f;  $P < 0.01$ ).

### Implications for management and science

#### Trade-offs in functions

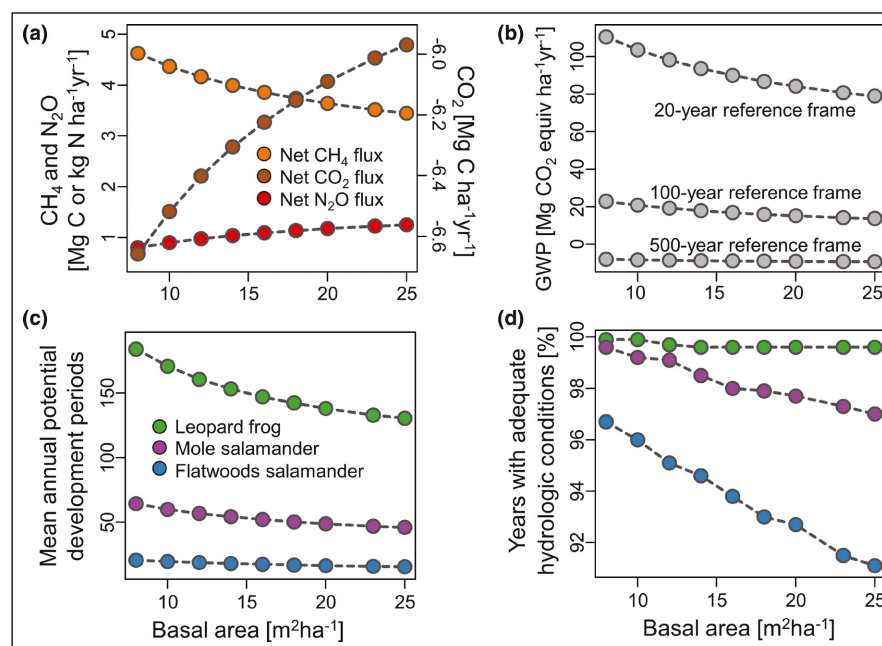
Our modeling study highlights the opportunity for upland forest management to enhance specific wetland functions but also points to potential trade-offs among functions in both uplands and embedded wetlands. At the highest basal areas, pine plantation management emphasizes merchantable timber and increases forest carbon sequestration (Ewel and Gholz 1991) but also lowers the probability of development of wetland-breeding amphibians (Figures 4c–d and 5e–f). By contrast, low basal area management with prescribed fire encourages wetland amphibian development, in addition to improved upland habitat (Freeman and Jose 2009). However, this management strategy also potentially

increases wetland CH<sub>4</sub> emissions and associated GWP (Figures 4a–b and 5c–d). Increasingly, ecosystem science is recognizing trade-offs among ecosystem services and in a variety of settings (eg wetlands [Doherty *et al.* 2014], grasslands [Kim *et al.* 2016], and mixed land-use watersheds [Nelson *et al.* 2009]). Optimizing these trade-offs is essential for managing a landscape portfolio of functions using different strategies specific to different ecosystem units (Doherty *et al.* 2014). Notably, our work highlights off-site effects of upland management actions, representing an important consideration for future optimization of landscape functions.

### Time and space considerations

Management of landscapes for a portfolio of ecosystem services can be enhanced by incorporating temporal and spatial variation in ecosystem functions. Our 25-year management scenarios were intended to account for temporal variation in management actions and stand growth. From a cumulative accounting perspective, constant low basal area and pine plantations had similar inundation duration, GWP, and potential development periods for the flatwoods salamander (Figure 5b, d, f). However, over the course of the 25-year management period, differences in temporal variation for each output were evident (eg wet to dry conditions in the pine plantation; Figure 5a, c, e). Temporal variation in GHG emissions is inconsequential for overall system GWP over relevant time periods (and thus cumulative GHG emissions are a useful management metric). By contrast, sustained success of amphibian populations relies on a predictable interannual wetland hydrologic regime to allow at least one successful breeding event within the species' breeding life span (eg 4–5 years for the flatwoods salamander; Snodgrass *et al.* 2000). Spatial diversity in management goals (conservation versus plantation) and time histories (clear-cut versus mature plantation) within a habitat range thus represents a possible strategy to optimize both timber production and wetland amphibian habitat.

Wetland morphology also influences hydrological regime and can determine hydrological response to landscape drivers. Within this context, we further suggest that the management scale should shift from focusing on individual wetlands to a larger system that encompasses a mosaic of wetlands with varying sizes and shapes. Although a complete sensitivity analysis of model parameters was



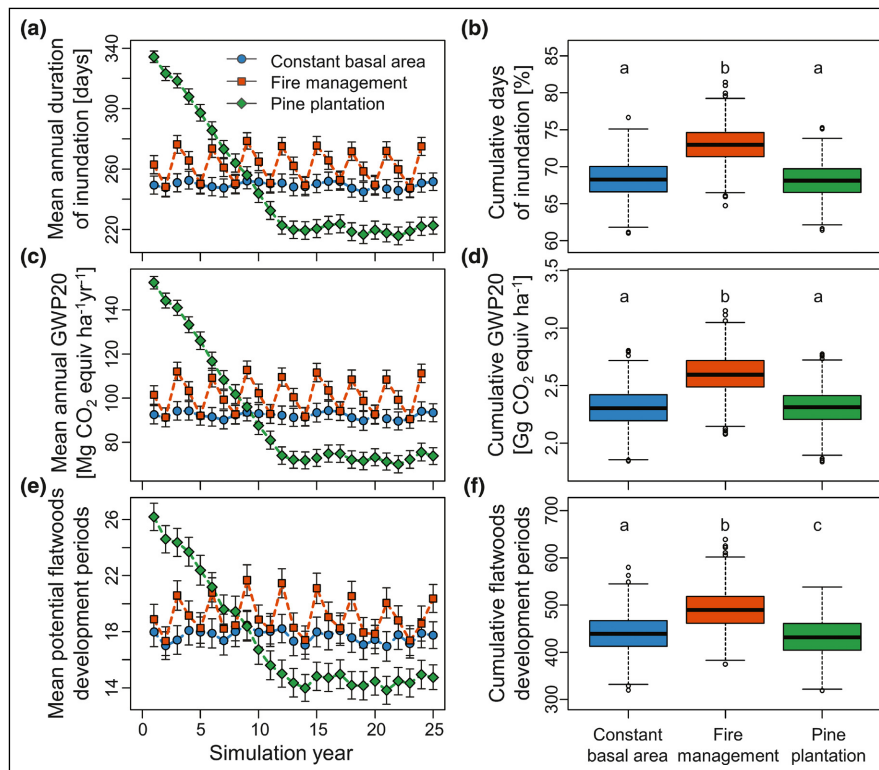
**Figure 4.** Simulations across upland basal areas for wetland functions: (a) mean greenhouse-gas fluxes; (b) mean global warming potential (GWP) for different reference time frames; (c) mean annual potential development periods for amphibian reproduction; and (d) percentage of years with adequate hydrological conditions for amphibian development (species indicated by same colors as in [c]).

beyond the scope of this work, we did explore the influence of wetland size on model results. In general, the hydrology of smaller wetlands was more sensitive to shifts in upland basal area, with associated changes in GWP and amphibian development predictions. For instance, when transitioning from low to high basal area (14 to 25 m<sup>2</sup> ha<sup>-1</sup>), a 50% reduction in wetland size yielded a 21% further reduction in mean annual inundation duration (data not shown). Heterogeneity in wetland size could thus be used to target different wetland functions and potentially balance opposing objectives through a combination of upland and wetland management.

### Challenges for management and science

Our modeling exercise clearly highlights linkages among upland management, wetland hydrology, and wetland function. However, the magnitude, and even direction, of effects likely vary with other environmental drivers, requiring coupled adaptive management and monitoring efforts to effectively implement upland management for wetland functions. For example, site-specific variables play an important role in both wetland hydrology (eg soil type, topography; McLaughlin *et al.* 2014) and GHG emissions (eg soil carbon, nitrate availability; Zhang *et al.* 2002). Moreover, our work focused on only three amphibian species, but because wetland hydrology often controls the success of many flora and fauna (Snodgrass *et al.* 2000), upland management likely influences a variety of other wetland species. While





**Figure 5.** Mean annual and cumulative (a–b) inundation duration, (c–d) wetland GWP for 20-year reference frame, and (e–f) flatwoods salamander development periods simulated for three management scenarios: constant low basal area (blue), fire on a 3-year recurrence interval (orange), and 25-year rotation pine plantation (green). Error bars represent standard error around annual means. Scenarios are representative of frequent stand thinning, regular prescribed fire, and typical pine plantation management, respectively. Statistical differences between simulations are denoted by alphabetic groups. Differences in annual patterns (left) can be important, even when cumulative values (right) are comparable.

our modeling study strengthens the plausibility that effects of upland management cascade to valued wetland functions, empirically evaluating these linkages should be a primary focus of future science and management aimed at optimizing landscape functions.

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## Supporting Information

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