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1 Effects of phenology and meteorological disturbance on litter

2 rainfall interception for a *Pinus elliottii* stand in the Southeastern US

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8

9 Abstract

10 Litter layers develop across a diverse array of vegetated ecosystems and undergo significant 11 temporal compositional changes due to canopy phenological phases and disturbances. Past 12 research on temporal dynamics of litter interception have focused primarily on litter thickness 13 and leaf fall, yet forest phenophases can change many more litter attributes (e.g., woody debris, 14 bark shedding, and release of reproductive materials). In this study, weekly changes in litter 15 composition over 1 year were used to estimate litter water storage dynamics and model event-16 based litter interception. Litter interception substantially reduced throughfall (6-43%) and litter 17 water storage capacity ranged from 1-3 mm, peaking when megastrobili release and liana leaf 18 senescence occurred simultaneously during fall 2015. Tropical storm disturbances occurred 19 during the sampling period, allowing evaluation of how meteorological disturbances altered litter 20 interception. High wind speeds and intense rainfall from two tropical storms increased litter 21 interception by introducing new woody debris which, in this study, stored more water than the 22 pre-existing woody debris. After two extreme weather events, a third (Hurricane Hermine) did 23 not increase woody debris (or litter interception), suggesting that the canopy pool of branches 24 susceptible to breakage had been largely depleted. Needle and bark shedding had minor effects 25 on litter interception. Results suggest that the release of reproductive materials and 26 meteorological disturbances appear to be the major compositional drivers of litter interception 27 beyond their obvious contribution to litter thickness.

28 KEY WORDS. Forest litter, rainfall interception, *Pinus elliottii*, phenology, tropical storm.

30 INTRODUCTION

31 The latest global inventory of hydrologic flux rates found that >60% of terrestrial 32 precipitation is evaporated (Rodell et al., 2015). Some of the largest regional evaporative returns 33 of terrestrial precipitation are found in vegetated landscapes – most notably in forested areas 34 where annual precipitation reduction from the canopy, alone, can reach 50% (Carlyle-Moses and 35 Gash, 2011). This direct feedback of moisture to the atmosphere from forests' interception and 36 evaporation of precipitation supports continental rainfall (van der Ent et al., 2014) and regulates 37 storm water runoff responses (McPherson et al., 2016). When interception of rainfall by the 38 forest floor (its understory vegetation and litter layers) is added to canopy interception, total 39 intercepted rainfall becomes substantial (Tsiko et al., 2012), even double that of the more 40 commonly estimated canopy component (Gerrits et al., 2007; 2010). Although forest floor 41 rainfall interception has been long-recognized (e.g., Helvey, 1964; Helvey and Patric, 1965), it has received considerably less attention than canopy rainfall interception (Gerrits and Savenije, 42 43 2011). The litter layer's contribution to forest interception, in particular, has been understudied 44 compared to understory vegetation in recent decades (Black and Kelliher, 1989; Wedler et al., 45 1996; Suzuki et al., 2007; Allen et al., 2016).

46 Litter layers develop across a diversity of ecosystems, forming a barrier-dynamic in 47 both thickness and composition—between the mineral soil and any meteoric water supply. 48 Meteoric water may arrive to the forest litter (i.e. net rainfall) directly through canopy gaps, as 49 throughfall (droplets contacting the canopy that drip or splash to the surface), or as stemflow 50 (rain water funneled to the stem base). The degree of reduction in these "net" rainfall fluxes 51 during their infiltration through the litter layer has been found to vary mostly in response to litter 52 thickness and throughfall intensity (Sato et al., 2004; Guevara-Escobar et al., 2007; Gerrits and 53 Savenije, 2011). Litter layer structures also drastically alter the timing and intensity of litter 54 infiltration fluxes to the soil ecosystem (Dunkerley, 2015). Since measurement of litter storage, 55 drainage and evaporation processes in situ is difficult, a range of laboratory (Helvey, 1964; 56 Putuhena and Cordery, 1996; Guevara-Escobar et al., 2007) and only a few field methods 57 (Gerrits et al., 2007; Acharya et al., 2017) have been developed for litter interception monitoring. 58 These efforts have resulted in significant advancements in our understanding of litter interception 59 processes, yet little research has focused on characterizing spatiotemporal variability in litter

compositional influences. Few studies have, for example, measured spatial variability in litter to
scale litter water storage or evaporation (Putuhena and Cordery, 1996; Wedler et al., 1996;
Gerrits et al., 2010) or assessed whether temporal shifts in litter composition significantly
influence interception processes (Gerrits et al., 2010; Brantley et al., 2014).

64 Research on seasonal variability of litter interception attributable to compositional 65 changes has exclusively focused on leaf senescence and subsequent breakdown in deciduous 66 hardwood stands (Gerrits et al., 2010; Brantley et al., 2014). However, there are a multitude of 67 other processes that may alter litter composition enough to significantly influence the 68 interception of net rainfall. No work known to the authors, for example, has focused on the 69 impact of different biomass materials related to phenological phases in coniferous stands, like 70 needles, megastrobili (cones), bark, or branches (Dougherty et al., 1994)-each differing in their 71 water storage capability—on litter rainfall interception. As the only study on rainfall interception 72 by reproductive materials (like fruiting heads) shed from forest canopies has shown them capable 73 of storing >500% of their oven-dried weight in water (Levia et al., 2004), the dropping of cones 74 to the litter of coniferous forests is especially likely to increase litter interception. Coniferous 75 forest litter may also receive leaf senescence materials from deciduous vines, or liana (Leicht-76 Young et al., 2010). In addition to phenological phases, meteorological disturbances (like 77 hurricanes and ice storms) can introduce significant amounts of woody and foliar debris to the 78 litter layer (Scatena et al., 1996; Vanderwel et al., 2013), yet the authors are unaware of any 79 work examining how these disturbance-related alterations to litter composition affect litter 80 interception. The aim of this study is, therefore, to provide the first assessment of hypotheses 81 regarding the influence of phenology and meteorological disturbances (tropical storms) over 82 coniferous litter composition and related litter rainfall interception.

We hypothesized that both (1) phenologically-driven inputs of material (particularly cone production) and (2) tropical storm-related inputs of aboveground biomass will produce significant momentary increases in litter water storage, ultimately increasing total litter interception. These hypotheses were tested by analysis of weekly litter compositional elements (needles, woody debris, bark, cones, and broadleaves) and water storage measurements (per litter element) alongside hydrometeorological observations collected over one year in a *Pinus elliottii* stand with deciduous liana cover (*Berchemia scandens* and *Vitis* spp.). Lastly, a model of litter 90 rainfall interception was generated that considered the observed water storage dynamics of each
91 litter element over the study period.

92 MATERIALS AND METHODS

93 *Study site*

94 Our study was conducted at the Oliver Bridge Wildlife Management Area (OB-WMA) 95 located along the Ogeechee River in southeast Georgia, USA (32.4910 N, 81.5615 W; Figure 1). 96 Monitoring equipment was installed in a stand composed of *Pinus elliottii* (Englem., slash pine) 97 with some deciduous liana cover: Berchemia scandens ((Hill) K. Koch, rattan vine) and at least 98 one Vitis species. These liana are common in pine stands (Shelton and Cain, 2002). Stand density 99 was 1060 trees ha⁻¹ and the stand is evenly aged. Thus, all trees were the same diameter at breast 100 height (DBH), varying only ± 5.4 cm (standard deviation) around the mean DBH of 21.8 cm. Site 101 climate is humid subtropical with no distinct dry season (Köppen Cfa) and, according to the 102 nearest long-term meteorological record (12.8 km away in Statesboro, Georgia), its mean annual (1925-2014) rainfall is 1170 mm year⁻¹ (University of Georgia Weather Network, 2016). The 103 104 dominant precipitation form is rainfall and it accounts for all precipitation observed during the 105 study period. Mean minimum monthly temperatures stay above freezing all year (3.5 °C low in 106 January), snowfall is negligible (University of Georgia Weather Network, 2016). Mean 107 minimum and maximum yearly temperatures are 12.4 °C and 25.2 °C, respectively, with the 108 mean maximum monthly temperature reaching 33.4 °C in July (University of Georgia Weather 109 Network, 2016). Mean monthly rainfall is relatively even from September through May (60-100 110 mm month⁻¹), then increase to 110-150 mm month⁻¹ for June, July, and August due to frequent 111 convective thunderstorms (University of Georgia Weather Network, 2016). The average number 112 of rainy days per annum over the historical record was 98 (University of Georgia Weather 113 Network, 2016).

114 Hydrometeorological monitoring

Rainfall, throughfall, and in situ litter water storage measurements were taken during a 116 12-month study period, beginning 7 Sep 2015 and ending 12 Sep 2016. For rainfall and 117 meteorological conditions controlling evaporation, a continuously recording meteorological 118 station was situated in a clearing within the OB-WMA, immediately nearby the forest plot, and 119 equipped with 3 tipping bucket gauges (TE-525MM, Texas Electronics, Dallas, TX, USA), a 120 pyranometer (CMP6, Kipp & Zonen, Delft, The Netherlands), a 2-axis ultrasonic wind 121 speed/direction sensor (WindSonic, Gill, Hampshire, UK), and an air temperature/relative 122 humidity probe (HMP155, Vaisala, Vantaa, Finland). All meteorological station sensors were 123 interfaced with a datalogger (CR1000, Campbell Scientific, Logan, UT, USA) to record 124 observations at 5-minute intervals. Automated throughfall monitoring was performed using ten 125 3.048-m long and 10.16 cm diameter PVC troughs oriented at a moderate slope, with a 5.08 cm 126 slot cut lengthwise for collection and drainage of throughfall to a Texas Electronics (Dallas, Texas, USA) TR-525I tipping bucket gauge, resulting in 1.65 m^2 of collection area. Tipping 127 128 bucket gauges and their associated troughs were randomly placed within a 0.25 ha plot and 129 recorded every 5 minutes by a CR1000 datalogger. All throughfall trough angles were measured 130 with a digital clinometer to correct computations of trough area receiving throughfall. Trough 131 and tipping bucket assemblies were field tested to ensure accuracy (\pm 5%) under storm 132 conditions typical for the region (Van Stan et al., 2016a). 68 discrete storm events totaling 1528 133 mm occurred during the study period (Figure 2), where an event was defined as any rainfall >1134 mm proceeded by a minimum inter-event time of 12 hours. Rarely did any storm event generate 135 throughfall intensities that resulted in significant gauge undercatch. These few occurrences of 136 extremely high throughfall intensity (as high as 10 mm in 5 minutes) occurred under tropical 137 storm conditions—specifically during Tropical Storms Bonnie (29 May 2016), Colin (6 Jun 138 2016) and Hurricane Hermine (2 Sep 2016) (indicated in Figure 2). These meteorological 139 disturbances not only brought substantial rainfall (195.3 mm, 69.8 mm, and 113.5 mm; Figure 2), but produced frequent 5-minute sustained wind gusts over 13 m s⁻¹, 15 m s⁻¹, and 17 m s⁻¹ for 140 141 Bonnie, Colin, and Hermine, respectively. Stemflow was ignored in this study as it represented 142 <0.1% of rainfall in a nearby (28 km away) similar pine stand for 22 storms (data collection is 143 ongoing). Stemflow so far has also never exceeded a funneling ratio of 0.8—meaning near-stem 144 soils receive <80% of rainfall compared to the open (data not shown). Since stemflow is 145 negligible, canopy rainfall interception was computed as the difference between rainfall and 146 throughfall.

147 Litter sampling, sorting and water storage measurements

148 Litter samples were collected on a weekly basis with collection gaps occurring twice in 149 the study period: (1) during the month of December 2015 and (2) for two weeks in the summer 150 from 11-25 July 2016. A litter sampling event consisted of gathering 30 separate samples of 20 151 cm diameter areas to whatever depth the Oi horizon terminated (generally 5-15 cm). Sampling 152 locations each week were chosen at random within the hectares of forest surrounding the 153 monitoring site, and previous sampling locations were avoided. Care was taken to ensure, at least 154 visually, that the randomly selected locations for litter sampling represented the overall litter 155 composition that week. Because litter depth and composition varied between samplings, the 156 oven-dried biomass of all samples collected during a single weekly sampling ranged from 230-157 690 g.

158 Immediately after sampling, the litter was manually sorted into its compositional elements (needles, woody debris, bark, cones, and broadleaves), total weight of each litter 159 160 element was recorded, and then all litter elements were placed in a drying oven at 100 °C for 72 161 h. Field water storage for each litter element was calculated as the difference between the oven-162 dried weight and the initial field weight (S_L [L]). (Conversion of volumetric water storage 163 capacity to depth equivalent was done by dividing by the total area sampled each week (314.2 $cm^2 \times 30$ locations = 9,426 cm^2)). After oven-dried litter elements were weighed, they were 164 completely submerged in water for 96 h and weighed while saturated. The difference between 165 166 each litter element's saturated weight and their oven-dried weight was their volumetric water 167 storage capacity ($S_{L,max}$ [L]).

168 Total litter rainfall interception (I_L [L T⁻¹]) was computed as the summation of litter 169 storage (S_L [L]) and evaporation (E_L [L T⁻¹]) as represented by the balance between throughfall 170 (T_f [L T⁻¹]) and infiltration (F [L T⁻¹]):

(1)
$$I_L = \frac{\partial S_L}{\partial t} + E_L = T_f - F$$

171 S_L of litter before a storm begins (t = 0) was determined by regression formulas relating 172 field water storage to the days (*D*) since any previous storm exceeding weekly litter water 173 storage capacity ($S_{L,max}$), with α and β being regression coefficients unique to each litter element 174 determined from lab measurements per Bulcock and Jewitt (2012):

(2)
$$S_L(t=0) = \alpha (D)^{-\beta}$$

The threshold of the litter storage "reservoir" ($S_{L,max}$) varied each week in accordance with the lab-derived water storage capacity. Water exceeding $S_{L,max}$ was assumed to enter the soil as *F* since the soils at the site are classified as Bladen fine sandy loam with high infiltration rates possible (National Resources Conservation Service-Web Soil Survey, 2017).

 E_L (m s⁻¹) was the sum of within-storm and between-storm evaporation estimates. 179 Within-storm E_L was determined per the Renner et al. (2016) formulation which stems from 180 recent findings that, due to the thermodynamic limits of convection, vapor pressure deficit and 181 182 wind speed (as is classically used to estimate potential evaporation: Brutsaert, 1982) are driven 183 by land-atmosphere interactions with locally absorbed solar radiation (Kleidon and Renner, 184 2013a). This concept was successfully applied to assess hydrologic sensitivity to global climate change (Kleidon and Renner, 2013b), estimate global-scale annual average terrestrial 185 186 evaporation (Kleidon et al., 2014), and estimate forest stand-scale potential evaporation (Renner 187 et al., 2016). As rain water on the litter is stored on the same materials as in the canopy (leaves, 188 branches, bark, etc) and wind speed is very low at the forest floor, we apply the Renner et al. (2016) formula to estimate E_L solely based on absorbed solar radiation (R_{sn} , W m⁻²) and 189 190 temperature data:

(3)
$$\rho E_L = \frac{1}{\lambda} \frac{s}{s+\gamma} \frac{R_{sn}}{2}$$

191 where ρ is density of water (kg m⁻³), λ is the latent heat of vaporization (J kg⁻¹), γ is the 192 psychrometric constant (kPa C⁻¹), and *s* is the slope of the saturation vapor pressure curve (kPa 193 C⁻¹) determined from air temperature (*T* in K) from Bohren and Albrecht (1998):

(4)
$$s = 6.11 \cdot 5417 \cdot T^{-2} \cdot e^{19.83 - \frac{5417}{T}}$$

194 R_{sn} at the litter was computed from incident radiation (I_0 , W m⁻²) measured by the gap 195 weather station multiplied by an estimate of albedo (a = 0.18) representative for *P. elliottii* 196 forests (Gholz and Clark, 2002) after being reduced using a species-specific extinction 197 coefficient (k = 0.35, Gholz et al., 1991) and site-specific Leaf Area Index (LAI = 5.7). The 198 Beer-Lambert law was modified per Gholz et al. (1991) to include the fraction of canopy gap (F_o 199 = 0.34) and cover ($F_f = 0.66$):

(5)
$$R_{sn} = (1-a) I_0 (F_o + F_f e^{-k \cdot LAI})$$

Canopy gap fraction and LAI were determined using an LAI-2200TC plant canopy analyzer (LiCOR, Lincoln, NE, USA) where one of two wands was leveled in the open, logging each minute to correct manual measurements made by the second wand. Estimates of E_L between storms were determined using litter drying curves developed from field water storage measurements (as described earlier) plotted against days since rainfall.

205 Data analysis

Descriptive statistics were compiled for all hydrometeorological and litter compositional variables. Regressions were performed to generate drying curves for each litter element, and for testing correlation strength and significance between litter elements and water storage. All statistical work was accomplished in Statistica 12 (Statsoft, Tulsa, OK, USA).

210

211 **RESULTS**

212 *Litter composition and elemental drying curves*

213 Litter sampling resulted in the collection, sorting, and lab submersion testing of over 14.5 214 kg of oven-dried weight (Table 1). Total litter composition from all sampling events consisted 215 primarily of needleleaves and cones – each representing just under a third of the total oven-dried 216 biomass (Table 1). The remaining third of oven-dried litter biomass was composed mostly of 217 bark flakes (18%) and woody debris (16%), leaving about 2% for broadleaves from the 218 deciduous lianas (Table 1). Cones exhibited the greatest variation in oven-dried biomass (Table 219 1) since P. elliottii cone drop at our site was seasonally concentrated between October and 220 March, whereafter cone biomass contributions from the canopy ceased (Figure 3). Needleaves 221 within the litter also exhibited high variability in oven-dried biomass (Table 1), but this 222 variability was observed throughout the study period (Figure 3). The greatest coefficient of 223 variation (77%) in oven-dried biomass for any litter element was for broadleaves (Table 1). High 224 variability in broadleaves' oven-dried biomass reflects leaf abscission from lianas in the fall of 225 2015 (exceeding 20 g), which eventually decayed to minimal proportions (<1 g) in the late 226 summer (Figure 3). Contributions to the litter from bark flakes had the lowest variability

compared to the mean oven-dried biomass (<25%; Table 1) and were the most temporally consistent, showing little-to-no seasonal trends (Figure 3). Although the range of oven-dried biomass observations for woody debris in the *P. elliottii* litter was smaller than observed for bark flakes, the standard deviation was larger (Table 1). The relatively larger standard deviation in oven-dried woody debris biomass in the litter can be, in part, explained by the large jump in woody debris in late May through June 2016 (Figure 3) after arrival of TS Bonnie and TS Colin (Figure 2).

234 Maximum time since saturation for all litter sampling events was 12 days, and neither 235 the litter nor any litter element dried completely within that time (Figure 4). Nevertheless, all 236 litter elements dried out relatively quickly within the first 3 or 4 days, then slowly thereafter 237 depending on conditions driving evaporation (Figure 4). Equations for each regression shown in 238 Figure 4 are provided in Table 2. Total litter water storage immediately after storms achieved 239 just over 2 mm (Figure 4), and average $S_{L,max}$ throughout the study was 1.7 mm (Table 2). The 240 greatest water storage immediately after rainfall was observed for broadleaves (just over 3 mL g 241 ¹), but when this is converted to depth equivalent, the in situ, post-storm S_L and mean $S_{L,max}$ for 242 broadleaves throughout the study were low (< 0.1 mm; Table 2 and Figure 4) due to its small 243 biomass contribution (Table 1). Cones and woody debris stored 0.6 mm and 0.3 mm immediately 244 after rainfall (Figure 4), yet accounted for more of the litter composition (Table 1) allowing for > 245 7 and 4 times larger average $S_{L,max}$ estimates than broadleaves, respectively (Table 2). 246 Needleleaves and bark flakes generally stored the least water per oven-dried biomass after storms (~1 mL g⁻¹), but since needleaves composed a large proportion of the litter oven-dried 247 biomass (Table 1), they were able to average 0.5 mm of $S_{L,max}$ (Table 2) and sometimes exceed 248 249 0.6 mm of storage immediately after a storm (Figure 4). For all litter elements, the regression α 250 coefficients derived from field water content data (column 2 of Table 2) are smaller than the lab-251 derived $S_{L,max}$ (column 3 of Table 2), indicating that saturation via submersion achieved greater 252 water storage than field conditions allowed and/or that the litter lost water within the ~24 h 253 between field saturation and sampling.

254 Effects of phenology and meteorological disturbance on litter water storage capacity

The percentage representation of $S_{L,max}$ by different litter elements (Figure 5a) and the magnitude of $S_{L,max}$ (Figure 5b) varied markedly throughout the study period. Values of $S_{L,max}$

257 ranged from 0.8 mm in early April to a maximum that was 4 times greater than the minimum 258 (3.2 mm) in mid-October (Figure 5b). Maximum $S_{L,max}$ closely corresponded to a maximum in 259 cone biomass (Figure 3) and the cones' proportion of $S_{L,max}$ (Figure 5a). Broadleaf inputs to the litter from the deciduous lianas also briefly, but measurably, contributed to the elevated $S_{L,max}$ 260 261 values from September through November 2015-during the same time as cone drop (Figures 3 and 5a). Although small magnitudes were measured in some weeks, $S_{L,max}$ rarely fell below 1 mm 262 263 (Figure 5b). In fact, 1 mm marks the 10 percentile boundary and the interquartile range of $S_{L,max}$ 264 is 1.2 - 2.1 mm. The early April minimum in $S_{L,max}$ occurred when overall litter biomass was low (Figure 3) and the dominant contribution to $S_{L,max}$ (~40%) was from needleaves (Figure 5a). 265

266 Soon after the measurement of minimum $S_{L,max}$ in April, meteorological disturbances (TS 267 Colin and Bonnie) supplied the litter with fresh woody debris. This woody debris increased 268 woody debris contributions to $S_{L,max}$ by 10% compared to all weeks previous (~25% versus 15%: 269 Figure 5a). The highest woody debris contribution to S_{Lmax} was measured at nearly 30% shortly 270 after TS Colin during the month of June (Figures 2 and 5a). The result of this supply of fresh 271 woody debris to the litter was that $S_{L,max}$ increased by 40-50% of its magnitude during the 272 preceding weeks (Figure 5). However, it is interesting to note that trends in $S_{L,max}$ for woody 273 debris (Figure 5b) corresponds well with trends in its oven-dried biomass (Figure 3) for the 274 entire study period.

Univariate regressions were performed to assess the strength of relationships between individual litter elements' oven-dried biomass and $S_{L,max}$ during times where these litter elements appeared to drive $S_{L,max}$. A significant correlation was only found for oven-dried cone biomass during the cone drop period: about 12 weeks after the start of the study on 7-Sep-2015 (Figure 6). Oven-dried cone biomass exerted a strong positive linear influence over $S_{L,max}$ until the spring of 2016 (Figure 6). After March 2016 no significant correlation could be found between any individual litter element and $S_{L,max}$.

282 Total canopy rainfall partitioning and litter rainfall interception

The majority of rainfall events during the study period ranged in magnitude between 4 and 40 mm (Table 3), with only eight storms exceeding 50 mm (Figure 2). Four of these eight storms exceeded 100 mm (02-Feb-2016, TS Bonnie, TS Colin, and Hurricane Hermine; Figure

286 2), with TS Bonnie producing the greatest storm magnitude measured during the study year (195.3 mm; Table 3). Although significant 5-minute rainfall intensities were observed (as 287 mentioned in Section 2.2), hourly rainfall intensity rarely exceeded 1 mm h⁻¹, maximizing around 288 8 mm h⁻¹ (Table 3). Throughfall represented 64.5% of rainfall per storm on average, with an 289 290 interguartile range between 40-81% of rainfall (Table 3). These relative throughfall proportions 291 corresponded to an average throughfall receipt at the litter of 23 mm storm⁻¹ (Table 3). The litter 292 intercepted a significant quantity of throughfall, reducing throughfall amounts to the soil surface 293 by 23% on average (Table 3). Modelled litter interception exceeding 1/3 of throughfall was 294 relatively common, being within the interguartile range of 68 measured storms (Table 3). During 295 large magnitude storms with high rainfall intensity and low radiation receipt (due to dense cloud 296 cover), litter interception was minimized—i.e., the minimum 0.6% reduction in throughfall was 297 observed during TS Bonnie (Table 3). Smaller magnitude, low intensity storms resulted in the 298 litter being able to store and evaporate all throughfall (Table 3). The largest storm magnitude 299 where 100% of throughfall was intercepted by the *P. elliottii* litter at this site was 3.6 mm at an 300 intensity of 0.72 mm h^{-1} .

301

302 DISCUSSION

303 Litter interception is generally neglected by past forest ecohydrological research (Gerrits 304 and Savenije. 2011), yet our findings align well with past work showing large litter water storage capacities ($S_{L,max} = 0.8-3.2$ mm) that can consistently and significantly reduce through fall (9-305 306 46%) reaching the soil surface (Table 3). Throughfall reductions of this magnitude have been 307 reported in other forests: 22% for temperate Fagus sylvatica (L., European beech) in 308 Luxembourg (Gerrits et al., 2010), 20% for Brachystegia spiciformis (Benth., Msasa) savannah 309 in Zimbabwe (Tsiko et al., 2012), 16-18% for maritime Picea abies (L., Norway spruce) forests 310 in Scotland (Miller et al., 1990), and 8-12% in Himilayan forests (Pathak et al., 1985). The annual range in $S_{L,max}$ observed for *P. elliottii* litter in this study (Table 2; Figure 5) spans the 311 312 range of observations from past research. For instance, litter $S_{L,max}$ from the broadleaved 313 Lithocarpus edulis (Makino, Japanese stone oak) and Asperulo-Fagetum forests maximized 314 around 3 mm (Thamm and Widmoser, 1995; Sato et al., 2004), yet needleleaf litter from Pinus 315 sylvestris (L., Scots pine) and Cryptomeria japonica (L.f., Japanese cedar) typically stored less

than 1.7 mm (Walsh and Voigt, 1977; Sato et al., 2004). Diminished water storage for 316 317 needleleaves compared to broadleaves was also observed between *Cedrus atlantica* (Endl., blue 318 cedar) and European beech, with cedar litter storing half as much water as beech (Gerrits, 2010). 319 Our results agree with these findings as water storage per oven-dried mass was greater for broadleaves than for needleleaves (3 mL g⁻¹ versus 1 mL g⁻¹). Despite this difference in water 320 321 storage per dry mass needleleaves stored more total water (Table 2 and Figure 4) as a result of 322 needleleaf contributions from the P. elliottii canopy exceeding the liana broadleaf contributions 323 (Table 1; Figure 3).

324 The timing of leaf senescence from broadleaved lianas hosted by P. elliottii coincides 325 with the tree canopies' cone drop (Figure 5). Since liana broadleaves can store double the amount of water per dry mass compared to most other litter elements (\sim 3 mL g⁻¹ for broadleaves 326 versus 1 mL g⁻¹ for needleaves or bark flakes), they likely enhance the elevated $S_{L,max}$ effect 327 produced by the contribution of new cones (Figure 6). This intersection of liana and P. elliottii 328 329 phenophases resulting in both significant broadleaf and cone biomass contributions is not 330 unusual. The phenophase where P. elliottii drops cones typically occurs every 3-4 years (after 331 nearly a year of cone development) for mature stands (Dougherty et al., 1994), typically 332 beginning in October and ending as late as March or April for the southeastern US (Moore and 333 Wilson, 2006). Meanwhile, the lianas (B. scandens and Vitis spp.) senesce their leaves each year, 334 beginning in late October to early November (per observations at site). Many previous studies 335 have discussed reasons undergirding the significant water storage of broadleaves (e.g., Walsh 336 and Voigt, 1977; Sato et al., 2004; Gerrits, 2010; Gerrits and Savenije, 2011), but to the 337 knowledge of the authors, only two studies have examined the role of any type of reproductive 338 materials in enhancing $S_{L,max}$ (Levia et al., 2004) and litter interception (Levia et al., 2005)—and 339 these studies focus on one species, Liquidambar styraciflua L. (sweetgum). These two studies 340 found that empty fruiting heads with complex morphological structures (numerous openings, ledges, and roughly-textured surfaces) and a large surface area are not only capable of storing 341 342 nearly 5 mm of rainfall (Levia et al., 2004), but can evaporate that storage at rates similar to 343 those found for saturated canopies under favorable meteorological conditions (Levia et al., 344 2005). Storage by P. elliottii cones in this study was not as high as observed for L. styraciflua 345 fruiting heads, but both were capable of storing as much water as all the leaf litter elements 346 (Figure 5; Levia et al., 2004). As such, we echo the call from Levia et al. (2004; 2005) that future

work is needed on throughfall interception from reproductive materials in other forest systems with morphologically complex reproductive materials. This includes a vast array of tree species around the globe: *Magnolia*, *Platanus*, *Liriodendron*, *Picea*, etc. Perhaps the historical neglect of litter rainfall interception by forest ecohydrological studies is, in part, a result of past litter interception studies' focusing on the more temporally consistent (but lower water storage) elements (like leaves).

353 Average $S_{L,max}$ for *P. elliottii* bark flakes was low (0.27 mm; Table 2) compared to bark 354 water storage capacities measured in the lab using intact bark sampled from the stems of rough, 355 thick-barked tree species, being 1-2.7 mm (Levia and Herwitz, 2005; Van Stan et al., 2016b). 356 Water storage experiments performed on the bark of in situ *P. elliottii* trunks by others in nearby 357 North-Central Florida (USA) were closer to our estimate (0.5 mm), but still nearly double the 358 magnitude of bark flakes sampled from the litter at our study site (Liu, 1998). It may be that the 359 flakes from bark shedding are much thinner than the bark on tree stems, with bark flakes 360 collected from the litter being only 2-10 mm thick compared to the 15-25 mm bark thicknesses 361 measured on tree stems by a Haglöf Barktax (Stockholm, Sweden) bark thickness gauge. As the 362 lowest $S_{L,max}$ estimate for stem bark is double that of bark flakes in the litter at our site, the 363 difference in thickness does not entirely reconcile the two values. Recent work indicates that 364 significant inter- and intraspecies variability in "interception surface" morphology can alter the 365 ability of bark surfaces to retain water (Ilek and Kucza, 2014). Pinus species shed "flakes" of 366 bark during trunk growth (in a process called periderm shedding) which produces thin, flat bark 367 flakes. It is likely that the flatter interception surface morphology of these bark flakes compared 368 to the rougher trunk bark reduces $S_{L,max}$ by preventing water retention on the surface of this litter 369 element.

370 Few studies examine the role of woody debris in the storage and evaporation of water 371 (Unsworth et al., 2004; Sexton and Harmon, 2009), and only one quantifies the reduction of 372 throughfall by woody debris-specifically logs (Sexton and Harmon, 2009). The absorption and 373 evaporation of throughfall by logs was 47-70% for Oregon forests (Sexton and Harmon, 2009). 374 This finding indicates that litter interception by woody debris at our site was likely greater as we 375 did not measure water dynamics for whole logs, and these are observable at the site. However, 376 woody debris in our P. elliottii stand after meteorological disturbances appear to more markedly 377 affect contributions to $S_{L,max}$ than previous pulses of woody debris inputs (Figure 5). This may be

378 a result of a change in the quality of the woody debris. Winds and heavy rainfall from TS Bonnie 379 and TS Colin resulted in a sudden increase in fresh branches to the litter layer. It is likely that the 380 relatively intact bark on fresh branches stores more water compared to shed bark flakes (see 381 discussion point above). In addition, the clumps of fresh needles attached to these branches were 382 not separated from the freshly deposited woody debris to keep litter elements as intact as 383 possible, and these have been shown to efficiently intercept and store rainfall in the canopy by 384 others (Keim et al., 2006). It is probable that needles attached to fresh branches similarly store 385 significant water at the forest floor. A third quality of the freshly deposited branch materials that 386 may increase water storage include the broken ends of the branches, which may permit 387 significant water absorbance into internal structures. No significant woody debris drop after 388 Hurricane Hermine (Figure 5) suggests that the "pool" of canopy materials to be contributed to 389 the litter layer was depleted by the previous two storms.

390 Although $S_{L,max}$ varied weekly with litter composition in our litter rainfall interception 391 estimates, some parameters in the litter interception process did not. Specifically, infiltration 392 processes are expected to change with litter composition, as was found by sprinkler experiments 393 (Guevara-Escobar et al., 2007). This could have allowed the litter to retain more water in some 394 instances (perhaps due to water pooling in the proximal area of pine cones' ovuliferous scales) 395 and less water in other cases (perhaps water drains more rapidly along the hydrophobic cutin 396 layers of a needleaf-dominated litter: Dufrenoy, 1918; Hansel et al., 2008). Canopy traits 397 controlling receipt of radiation were also held constant, yet the LAI and fraction of canopy gap 398 (F_o) will change with phenological shifts in *P. elliottii* stands (Gholz et al., 1991; Gholz and 399 Clark, 2002) and, likely, after meteorological disturbance due to downed branches. LAI 400 variability also affects throughfall (Dietz et al., 2006), yet the throughfall was measured directly 401 over time (i.e., across LAI conditions) in this study.

402

403 CONCLUSIONS

404 Our findings from a *Pinus elliottii* stand in the southeastern US not only show substantial 405 rainfall interception by the litter layer (2-32%), but indicate that the effects of different biomass 406 materials related to phenological activity and meteorological disturbances on the temporal 407 variability of litter composition can significantly alter litter interception processes. The

408 magnitude of litter rainfall interception observed in this study was similar to the few previous 409 estimates in other forests, but exceeded those that solely considered the water storage and 410 evaporation of individual litter elements. Pine cones (and likely reproductive materials from 411 other tree species as well) were capable of storing significant quantities of water compared to 412 other litter elements. In forests where multiple phenophases from different canopy plants 413 coincide, the substantial biomass contributions may result in a seasonal spike of litter rainfall 414 interception. A spike in litter interception at our site occurred during the concurrent pine cone 415 release and liana leaf senescence that tripled litter water storage (from ~1 mm to 3 mm). Per 416 these findings and the current underrepresentation of litter rainfall interception, we recommend 417 future forest ecohydrological research measure its magnitude, underlying processes and temporal 418 dynamics, as failure to do so may introduce significant uncertainties into soil hydrological (and 419 related biogeochemical) processes.

420

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578 **Figure captions**

- 579 Figure 1. Site location within the Oliver Bridge Wildlife Management Area (WMA) in 580 southeastern Georgia (USA) and orientation of the 10 trough-based automated 581 throughfall gauges.
- Figure 2. Daily rainfall amount throughout the study period with the tropical storms (TS) andhurricane disturbances highlighted.
- Figure 3. Weekly oven-dried biomass for all litter compositional elements during the 20152016 study period. Lines with asterisks indicate when TS Bonnie and then TS Colin
 occurred.
- Figure 4. Scatterplots showing field water content of litter elements with increasing days (D)
 since the last storm that exceeded weekly litter water storage capacity. Regression
 equations in Table 2.
- Figure 5. Total weekly litter water storage capacity ($S_{L,max}$) plotted atop (a) the proportion (%) each litter element contributed as percentage and (b) the actual depth equivalent of each litter element.

593 Figure 6. During the \sim 3 months long period of cone drop from *Pinus elliottii* canopies, total 594 weekly litter water storage capacity ($S_{L,max}$) significantly and positively correlated 595 with oven-dried cone biomass.

596 Tables

597 **Table 1.** Total oven-dried biomass (g m⁻² ground area) for all compositional elements and full

598 litter samples across the study period alongside descriptive statistics (where CV indicates

599 coefficient of variation).

	Percentile							
Element	Mean	CV	25%	75%	Min	Max		
Cones	116.9	0.50	80.3	148.2	20.4	288.8		
Needleleaves	115.0	0.37	88.1	143.2	42.3	251.5		
Broadleaves	6.6	0.81	3.5	8.1	0.8	21.6		
Wood	56.9	0.33	42.5	73.3	24.2	88.7		
Bark	64.8	0.25	55.6	75.5	20.3	96.1		
Litter (all)	360.1	0.27	291.7	404.2	242.2	729.9		

- 601 **Table 2.** Drying curve regression equations for determination of pre-storm field water storage
- $(S_L \text{ [mm]})$ from days (D) since the last storm exceeding weekly litter water storage capacity
- $(S_{L,max})$ and mean $S_{L,max}$ for all litter compositional elements derived from laboratory
- 604 experiments. Data plotted in Figure 4.

		Mean (SD) $S_{L.max}$
Element	Drying curve equation	(mm)
Cones	$S_L = 0.512 (D)^{-0.7362}$	0.57 (0.44)
Needleleaves	$S_L = 0.420 (D)^{-0.5449}$	0.51 (0.16)
Broadleaves	$S_L = 0.061 (D)^{-1.0103}$	0.07 (0.05)
Wood	$S_L = 0.229 (D)^{-0.6844}$	0.30 (0.13)
Bark	$S_L = 0.190 (D)^{-0.6128}$	0.27 (0.06)
Litter (all)	$S_L = 1.607 (D)^{-0.7362}$	1.73 (0.65)

	Percentile						
Variable	Mean	SD	25%	75%	Min	Max	
Rainfall (<i>R</i>)							
Amount (mm)	28.8	37.7	4.6	36.9	1.0	195.3	
Intensity (mm h ⁻¹)	0.82	0.95	0.27	1.02	0.05	8.14	
Throughfall (T_f)							
Amount (mm)	23.1	32.8	1.8	30.0	0.4	168.2	
$T_f: R (\%)$	64.5	17.9	40.2	81.3	13.1	87.7	
Canopy interception (I_c)							
Amount (mm)	5.6	5.0	2.7	6.9	0.6	27.0	
$I_c: R(\%)$	35.5	18.0	18.7	59.8	12.3	86.9	
Litter interception (I_L)							
Amount (mm)	5.3	6.5	0.2	9.8	0.1	16.7	
$I_L: T_f(\%)$	23.3	24.0	6.4	43.2	0.6	100.0	
$I_L: R (\%)$	17.8	17.2	1.9	31.8	0.1	56.6	

Table 3. Descriptive statistical summary of event-based rainfall, throughfall, and litter

607 interception (sum of storage and evaporation components) during the 2015-2016 study period.



Figure 1. Site location within the Oliver Bridge Wildlife Management Area (WMA) in
southeastern Georgia (USA) and orientation of the 10 trough-based automated
throughfall gauges.



614 Figure 2. Daily rainfall amount throughout the 2015-2016 study period with the tropical storms615 (TS) and hurricane disturbances highlighted.



Figure 3. Weekly oven-dried biomass for all litter compositional elements during the 20152016 study period. Lines with asterisks indicate when TS Bonnie and then TS Colin
occurred.



621Figure 4.Scatterplots showing field water content (S_L) of litter elements with increasing days622(D) since saturation (i.e., the last storm that exceeded weekly litter water storage623capacity). Regression equations in Table 2.



625Figure 5.Total weekly litter water storage capacity $(S_{L,max})$ plotted as (a) the proportion (%)626each litter element contributed as percentage and (b) the actual depth equivalent of627each litter element. Lines with asterisks indicate when TS Bonnie and then TS Colin628occurred.





630Figure 6.During the \sim 3 months long period of cone drop from *Pinus elliottii* canopies, total631weekly litter water storage capacity ($S_{L,max}$) significantly and positively correlated632with oven-dried cone biomass.