

RESEARCH ARTICLE OPEN ACCESS

Upland Afforestation Desiccates Downslope Wetlands on Sandy Soil

Csaba Tölgyesi¹  | László Szél² | Luca Sára Kukla³ | Alida Anna Hábcenyus¹  | András Kelemen³ | Kata Frei³ | Zoltán Bátori³ | Viktória Tóth³  | László Erdős^{4,5}  | Péter Török^{5,6,7} 

¹MTA-SZTE 'Momentum' Applied Ecology Research Group, University of Szeged, Szeged, Hungary | ²Hortobágy National Park Directorate, Debrecen, Hungary | ³Department of Ecology, University of Szeged, Szeged, Hungary | ⁴HUN-REN Centre for Ecological Research, Institute of Ecology and Botany, Lendület Seed Ecology Research Group, Vácrátót, Hungary | ⁵HUN-REN-UD Functional and Restoration Ecology Research Group, Debrecen, Hungary | ⁶Department of Ecology, University of Debrecen, Debrecen, Hungary | ⁷Polish Academy of Sciences, Botanical Garden - Center for Biological Diversity Conservation in Powsin, Warszawa, Poland

Correspondence: Csaba Tölgyesi (tolgyesi.csaba@szte.hu)

Received: 23 September 2025 | **Revised:** 12 March 2026 | **Accepted:** 23 May 2026

Keywords: deep infiltration | evapotranspiration | forest thinning | lateral water flow | *Robinia pseudoacacia* | soil moisture | wetland

ABSTRACT

Afforestation of formerly open, water-limited habitats is a globally widespread form of land conversion, driven by the need for timber and non-timber forest products, and capturing atmospheric carbon. However, increased tree cover can adversely affect hydrological cycles by increasing evapotranspiration and reducing downslope water yield, threatening agricultural production and water-dependent habitats. Here, we assessed the effect of afforestation with the non-native *Robinia pseudoacacia* in dry sandy upland areas of Hungary on the water supply of adjacent wetlands, and experimentally tested whether forest thinning can restore the hydrologic regime. We found that little moisture seeped down to the subsoil of plantations due to increased precipitation interception and transpiration, compared with grassy uplands. The lack of deep infiltration precluded lateral moisture seepage across the upland–wetland ecotone during the growing season. Conversely, we detected no notable interruption of lateral flows from grassy upland areas. Forest thinning (approx. 40% of the basal area) did not meaningfully improve water availability, probably because the effects of lower interception and transpiration were offset by the disruption of the understorey microclimate and the quick recovery of the canopy cover. We conclude that the afforestation of upland areas is an important contributor to wetland loss in the region and partial solutions are of limited effectiveness. We recommend a landscape-wide reconsideration of forestry strategies on uplands and planning alternative land use types to support soil moisture infiltration. One possible approach is to restore the original open ecosystems, but supporting solar developments in these marginal areas is also a viable option.

1 | Introduction

Afforestation, as opposed to reforestation or forest restoration, is the action of increasing tree cover in areas where historically open ecosystems prevailed due to climatic, edaphic or long-term natural or anthropogenic disturbances (Erdős et al. 2022). Trees in afforested areas may require intensive forestry interventions to establish and persist, as conditions are often beyond their limit of tolerance (Yildiz et al. 2018). Alternatively, planting

non-native trees that are more adapted to stressed conditions (e.g., having better drought tolerance) than trees in the native species pool is also a frequently used option (Reisman-Berman et al. 2019). Although man-made, these plantations can also provide various ecosystem services, such as timber and non-timber forest products, but nowadays, they are also held in high esteem due to their potential role in climate change mitigation by capturing carbon in their biomass (McEwan et al. 2020; Quiroz Dahik et al. 2021; Yamaura et al. 2021).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2026 The Author(s). *Ecohydrology* published by John Wiley & Sons Ltd.

Exceeding historical tree cover, however, has its downside, including several unexpected ecosystem disservices. In polar and high-montane areas, trees decrease surface light reflectance, called the albedo effect, which leads to warming, potentially overriding the climate change mitigating effect of carbon capture (Kristensen et al. 2024). Further problems include the loss of biodiversity associated with the previous open ecosystem (Veldman et al. 2019) and adverse effects on water regimes. Although afforestation may protect the soil from erosion and reduce flash flood amplitudes after heavy rains (Jin et al. 2020), there is a growing consensus that afforestation reduces water yield in downstream parts of catchments, threatening wetland ecosystems, irrigation-dependent crop production and water sources for other human needs (Farley et al. 2005; Huang et al. 2020; Valente et al. 2021).

The reason for the negative shift in the water balance after afforestation mostly lies in the increased evapotranspiration of forests compared to open ecosystems (Farley et al. 2005; Tölgyesi et al. 2020). A considerable share of the precipitation is held back by the canopy of trees and evaporates without reaching the ground. Moisture reaching the soil surface can evaporate more easily in open sites due to greater insolation but, in forests, a higher proportion is absorbed and transpired by the trees than by the grasses of open ecosystems. Although in moist tropical regions the water returned to the atmosphere by the trees has been shown to increase precipitation (Ruiz-Vásquez et al. 2020), water recycling in more arid areas is assumed to be less effective (Durigan and Honda 2024). Nevertheless, scientific evidence related to the vegetation–precipitation nexus is far from complete.

In water-limited regions, where afforestation can be expected to exacerbate water loss, the establishment of new forest plantations may need to be reconsidered by comparing potential benefits with drawbacks, and even existing forest cover may need to be reduced (Buisson et al. 2019), contrary to the current global popularity of tree planting schemes. If climate change is expected to increase aridity, planners also need to look into the future, as tree planting is a long-term endeavour and the balance between future pros and cons should also be taken into account (Mátyás et al. 2018). Because of the apparent trade-offs in such arid lands and the global pro-forest attitude, we need solid evidence on the hydrologic benefits of lower tree cover to discourage afforestation and specific case studies that directly show the effects of tree removal. Available studies are scarce and often inconclusive (Acharya et al. 2018).

In this study, we compared the water supply dynamics of wetlands adjacent to recently afforested versus natural, open upland areas, and tested whether partial tree removal (40% removal of the basal area) in the afforested uplands can have any positive effect on the water supply. Specifically, we measured moisture input by collecting precipitation in open, grassy uplands, under the canopy of forest plantations, and under the canopy of freshly thinned forest plantations over 16 months, monitored subsoil moisture content and microclimate relations, and measured subsoil moisture fluxes across the ecotone between the upland areas and the neighbouring wetlands. We assumed that evapotranspiration is lower in the open upland areas; therefore, more moisture infiltrates their subsoil, leading to greater lateral

moisture fluxes and a better water supply to the neighbouring wetlands than in the case of afforested uplands. We also expected a partial recovery of the moisture dynamics following forest thinning.

2 | Materials and Methods

2.1 | Study Area

The study area is located in the Nyírség region, North-East Hungary (Figure 1). Climate is semi-humid sub-continental, with a mean annual precipitation and temperature of 550–650 mm and 9°C–11°C, with a clear aridification trend in recent decades (Zoltán 2019). The soil is coarse-grained sand with low humus content and water-holding capacity (Lovas-Kiss and Süveges 2022). The region has diverse topography featuring large sand dunes and alluvial-aeolic depressions separating them with an elevation difference of over 10 m (Novák et al. 2014). The potential natural vegetation on upland areas was forest-steppe composed of broadleaf forest patches (mostly *Quercus robur*) embedded in a matrix of dry bunchgrass steppe. Depressions used to receive lateral water flows from adjacent upland areas (Simon et al. 2023), giving rise to permanently damp, peat-forming fens, hosting many endangered, cold-adapted relict plant and animal species (Kevey et al. 2017; Demeter 2022). Traditional land use forms included extensive forestry and grassland management, but recently, this has changed to intensive forestry by afforesting open sites and changing the native forest stands to non-native plantations, mostly composed of black locust (*R. pseudoacacia*) (Rédei et al. 2014). Combined with climate change and groundwater extraction for irrigation and communal water use, the increased evapotranspiration of forest plantations has led to extensive groundwater decline (Quang et al. 2022; Simon et al. 2023), and many wetlands of high conservation importance dried up.

2.2 | Study Design and Data Collection

We selected two middle-aged (approx. 25 years old), approx. 2-ha *Robinia* plantations located on sand dunes adjacent to wetlands. We thinned about half of each plantation, following standard forestry protocols in February 2021, including the removal of all spontaneously established woody species (e.g., the invasive *Prunus serotina*) and some planted black locust trees to reach a 40% reduction in basal area. This was the maximum value that the management plan of the forests allowed. Higher values, even if permission had been granted, would have had lower practical relevance due to limited applicability elsewhere. Resprouting of woody species was prevented by brush cutting twice in 2021.

The wetlands were currently desiccated and overgrown by *Urtica dioica* and *Sambucus nigra*, but components of the original fen vegetation (e.g., *Carex elata* and *Thelypteris palustris*) were still present in low abundance. In the vicinity of the plantation–wetland complexes, we also selected two areas with similar topography but grassland cover in upland position (dominated by *Corynephorus canescens*) and more intact wetland vegetation in the neighbouring depressions featuring *Carex elata*, *Frangula alnus*, *Juncus inflexus*, etc.

After the canopy thinning, in February 2021, we installed two precipitation collection tubes at a height of 1 m in the thinned and intact sections of both plantations and in the open areas (Figure 2). Each tube was equipped with a funnel and a container at the bottom, from where evaporation was limited. We monitored precipitation until May 2022 by regularly emptying and measuring the accumulated water in the tubes. To keep track of canopy cover (i.e., a proxy for precipitation interception and a measure of transpiration), we took five photographs of the canopy in each forest section using a 55-mm lens camera from a height of 1.5 m holding the device in an upright position. Canopy photos were processed in GIMP 2.10.28 GNU Image Manipulation Program by turning them grey-scale and

then black-and-white using manual thresholding, where canopy components (leaves, twigs and branches) were black and the background, representing open sky, was white. The percentage of black pixels, a proxy for canopy cover, was used for further data analysis.

In August 2021, we deployed an ADL-THP1 (Optin Kft.) microclimate sensor capable of recording air temperature and relative humidity to each habitat of the two study sites. The sensors were fixed on 50 cm high posts and covered by plastic caps to avoid direct insolation and precipitation. The sensors recorded data at 5-min intervals for 7 days during an average warm and dry summer period.

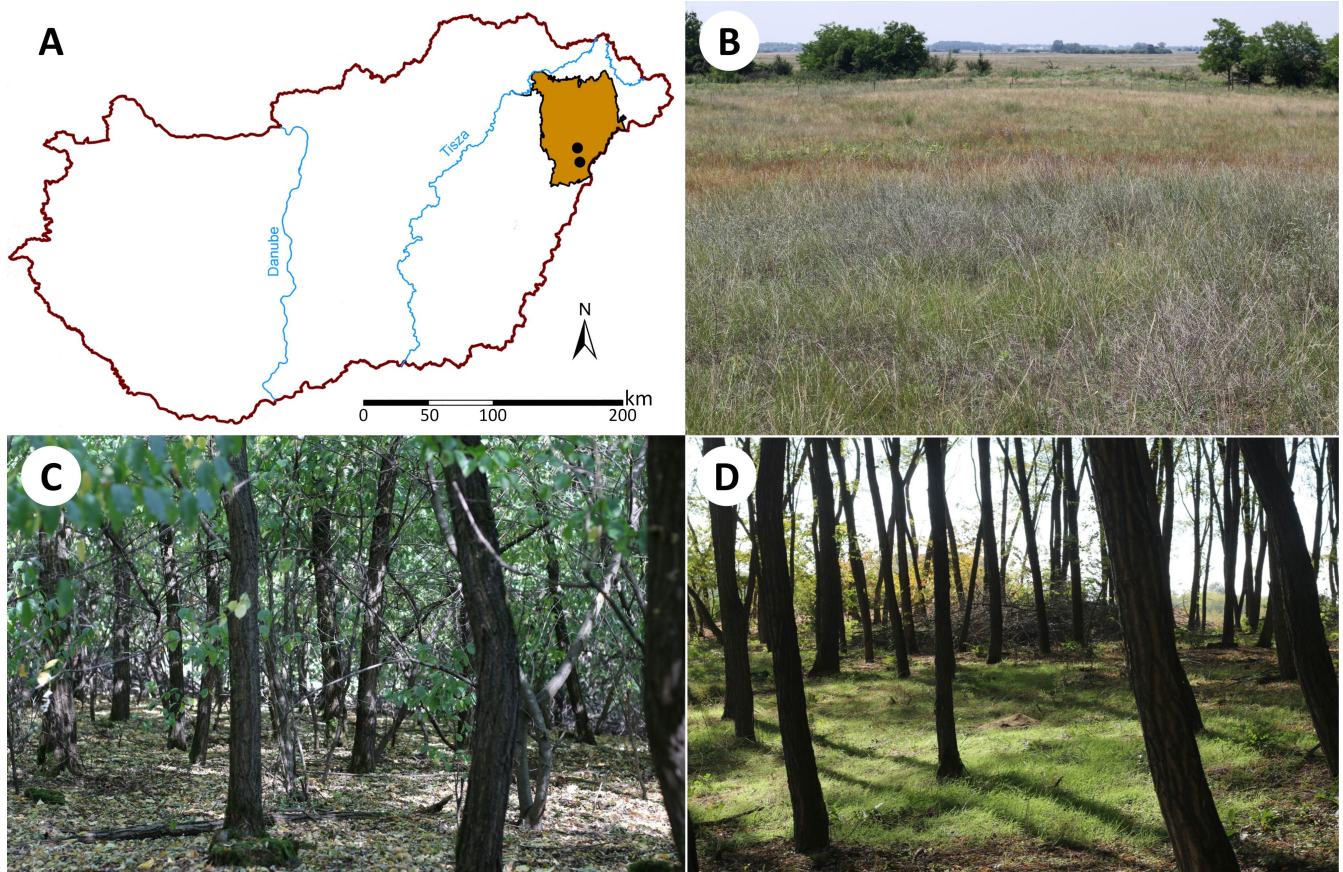


FIGURE 1 | Location of the Nyírség region in North-East Hungary (brown area) and the two study sites (black dots) (A). Each study site had three habitat settings, including, in upland position, naturally grassy sand dunes (B), thick forest plantation (C) and thinned forest plantation (D).

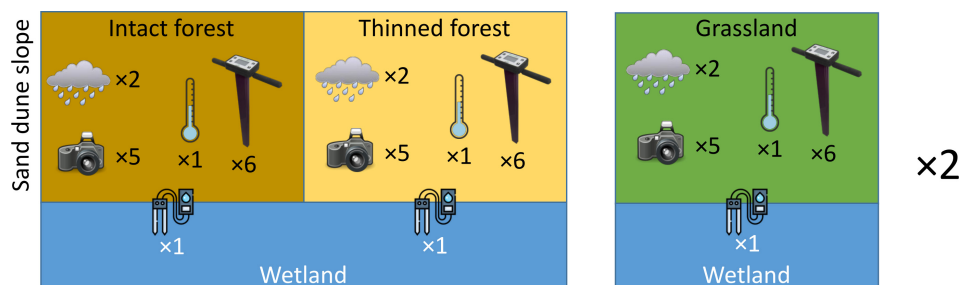


FIGURE 2 | Study design, with measurements on dune slopes with three types of habitat settings (intact forest, thinned forest and open grassland) adjoining wetlands in the dune slacks. In each habitat, we had two precipitation collectors, took five canopy photos, had one microclimate sensor, measured soil moisture with a portable meter in six localities and installed a permanent soil moisture meter in the ecotone between the slope and the wetland. We had two spatial replicates for the entire measuring design.

We measured soil moisture in the middle of the sand hill slopes at a depth of 70 cm using a portable FieldScout TDR 350 soil moisture meter (Spectrum Technologies Inc.) equipped with a pair of 4.8-in. vertical probes. We made six measurements in each stand in February, July and October 2021.

After the thinning, we deployed an ADL-SM1 (Optin Kft.) soil moisture meter to the foot of the sand dunes, in the upland-wetland ecotone, a few meters from the edge of the forest plantation. The sensors were inserted in the soil in a horizontal position, approx. 70 cm below soil surface, and measurements were intended as a proxy for lateral seepage across the ecotone. We chose the depth of 70 cm because the topsoil until approx. 50 cm deep is affected by insolation and the herbaceous flora (Tölgyesi et al. 2020), but we also wanted to avoid direct contact with the water table (often rising up to 90–100 cm in the ecotones), because sensors immersed in groundwater are no more sensitive to further increases of water availability. The case of the devices was placed 20 cm deep, so we could recharge the batteries in September 2021 without stopping the measurements. We removed the devices in September 2022, but most of them terminated measurements due to battery failures back in May 2022, so we trimmed all recordings accordingly.

2.3 | Data Processing

Data processing and analysis were performed in R version 4.2.2 (R Core Team 2024). Because of the absence of normality, we compared canopy cover percentages between the thinned and intact sections of the plantations with two-sample Wilcoxon test using the built-in ‘wilcox.test’ function. We averaged the two precipitation records per study site type (thinned and intact sections of the plantations, and open sites) and calculated canopy interception as the percentage loss of precipitation reaching the ground of the plantations compared to the open habitats.

For characterizing daily air temperature and relative humidity relations, we averaged the two recordings per habitat type (thinned and intact sections of the plantations, and open habitats), and fitted a generalized additive model (GAM) on the three categories separately using time (the 24-h period of the day with a 5-min resolution) as the fixed effect and air temperature or relative humidity (seven records for each time point due to the 7-day recording period) as a response variable. We used the fitted models and their 95% confidence intervals for statistical inferences. Non-overlapping stretches of the bands were considered significantly different, while overlapping ones were regarded as indistinguishable. For calculating the models, we used the ‘gam’ function of the *mgcv* package (Wood 2011), while for visualization, we used the ‘ggplot’ function of the *ggplot2* package (Wickham 2016).

Soil moisture measurements made with the portable device were compared across study site types with linear mixed-effects models, using study site as the random term and habitat type as the fixed effect. We prepared separate models for the three measurement dates, using the ‘lmer’ function of the *lme4* package (Bates et al. 2015). We tested the models for significance with the generic ‘anova’ function, assisted by the *lmerTest* package (Kuznetsova et al. 2017). We used the ‘emmeans’ function of the

emmeans package (Lenth 2023) for *post hoc* pairwise comparisons if the model was significant. Continuous soil moisture recordings at the upland-wetland ecotones were averaged across the two sites in every habitat type (thinned and intact sections of the plantations, and open sites), plotted against time and visually assessed.

3 | Results

According to our collecting tubes in the open sites, the precipitation of the February 2021–May 2022 period (16 months) was 582.5 mm. In the intact plantations, we collected 374.1 mm, which indicates an interception loss of 35.8%. In the thinned plantations, the precipitation value was 404.5 mm, corresponding to a loss of 30.6%.

Thinned plantations had on average 40.2% lower canopy cover in the beginning of the growing season of 2021 than intact plantations; this difference was statistically significant ($W=0$, $p<0.001$; Figure 3). Later on during the season, in July, the canopy of the thinned plantations exhibited fast expansion and reached a level comparable to the intact plantations, shrinking the average difference to a non-significant level (4.3%; $W=29$, $p=0.123$; Figure 3).

Regarding microclimate, open grassland sites were overall 4.1°C warmer and 5.5% drier than thinned plantations, and 5.6°C warmer and 10.9% drier than intact plantations during the day. All differences were statistically acceptable with a 95% confidence (Figure 4). At night, open grassland sites were 2.5°C colder and 8.6% more humid than thinned plantations, and 2.3°C colder and 5.1% more humid than the intact plantations. These differences were also acceptable with a 95% confidence. Thinned plantations were 1.6°C warmer and 5.4% drier than intact ones during the day, and their confidence bands did not overlap. Conversely, the average night-time temperature of thinned plantations was only 0.2°C warmer than that of the intact ones, and the confidence intervals largely overlapped. Despite this, relative humidity was still significantly lower—by 3.5% on average—in the thinned plantations than in the intact plantations at night.

In February 2021, the soil moisture content of the three habitat types (thinned and intact plantations, and grasslands) did not differ from each other ($F=1.13$, $p=0.335$) (Figure 5). In July, habitat type explained a significant proportion of soil moisture variation ($F=52.80$, $p<0.001$). Both thinned and intact plantations had drier soils than the grassland sites (t ratio >8.12 , $p<0.001$), while thinned and intact plantations had similar soil moisture contents (t ratio $=1.39$, $p=0.356$). By October, the differences had disappeared again ($F=1.08$, $p=0.351$).

Continuous measurements at the upland-wetland ecotones showed that the soil was similarly rich in gravitational water (approx. 30 V/V%) at all three habitat settings at the beginning of the growing season, indicating similar water fluxes from the sand dunes towards the wetlands (Figure 6). However, as the canopy of the forests developed during May, the moisture content dropped by around 15%, and remained more or less constant (probably equalling the field capacity) until late fall and early

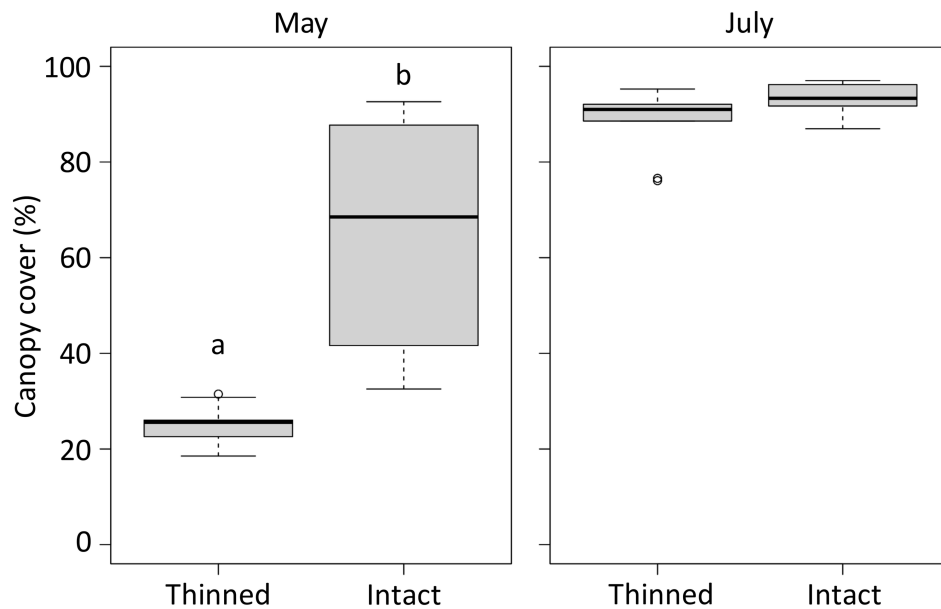


FIGURE 3 | Canopy cover of the thinned and intact sections of forest plantations at the beginning of the growing season (in May) and in the middle of it (in July). Values derive from digital photographs taken by 55-mm lens camera from a height of 1.5 m. Lowercase letters above the boxes identify significantly different groups ($p < 0.05$).

winter, when seeping water arrived and the values returned to pre-growing season levels. There seemed to be little difference between the path of the soil moisture curves of the thinned and intact plantations, although intact ones started to dry up 3 weeks earlier and recharge similarly later than the thinned ones. Conversely, moisture content in the soil of the ecotones where the upland areas were covered by open grassland barely decreased during the growing season ($< 5 \text{ V/V\%}$), suggesting a year-round, mostly uninterrupted lateral moisture flow from the uplands towards the wetlands.

4 | Discussion

In this study, we aimed to assess the effects of afforestation of upland sand dunes on the seeping water supply of adjacent low-lying wetlands, and experimentally tested to what extent forest thinning can restore the original hydrologic regime characteristic of original open upland conditions. Although our study lasted for less than 2 years, and therefore could not appropriately account for potential effects of inter-annual weather variations, we found that the only external water input of the upland areas (i.e., precipitation) was markedly reduced by forest cover. Canopy interception amounted to over one-third of the precipitation. This value is somewhat higher than, e.g., in Ma et al. (2019), who found interceptions for *Robinia pseudoacacia* below 20%, and is comparable to scores typical of pines (Le Maitre et al. 1999). The difference might be related to the thick shrub layer in the intact forest stands or differences in the within-year distribution of the precipitation, as higher scores can result from more precipitation during the growing season and less intensive individual precipitation events. Furthermore, our method was not suitable to measure stemflow (i.e., the fraction of precipitation running off tree trunks and eventually reaching the ground), but this is usually just a few percent of the total precipitation (Crockford

and Richardson 2000). So, it is clear that a notable fraction of the precipitation does not reach the soil surface of the forested sand dune slopes as compared with the open ones. Forest thinning could be expected to considerably reduce canopy interception, but the canopy exhibited a quick recovery, rendering the overall reduction of interception rather modest.

Concerning the moisture reaching the soil surface, certain amounts are lost to evaporation and transpiration. The microclimate moderating effect of the canopy was apparent in our case, leading to cooler and moister daytime values, and therefore lower evaporation, consistent with many other studies on forest vs. open habitats (e.g., Noretto et al. 2005; D'Odorico et al. 2013). However, this could not compensate for the moisture loss due to interception and transpiration, as less moisture could get below the main root zone of the trees (being the top 0–60 cm zone; Tölgyesi et al. 2020) during the growing season than in the open sand dune slopes.

Interestingly, forest thinning did not help let more moisture through into the subsoil of the dune slopes. Although transpiration after thinning can be assumed to be lower than that of intact forests due to the lower cover of active canopy (Jiménez et al. 2008; Iida et al. 2024), the disruption of their stable daytime microclimate could lead to higher evaporation during the day (Ma et al. 2010). Furthermore, higher air turbulence after forest thinning can increase moisture loss (Russell et al. 2018; Burns et al. 2025), which is consistent with the drier air of our thinned stands during the night (despite the low temperatures). More stable and prolonged soil moisture retention could probably have been achieved by a more extensive thinning, where the effect of unfavourable microclimate on moisture retention could be offset by the lack of remaining or expanding trees (Yang et al. 2012; Wang et al. 2018; Kovács et al. 2020). The contribution of shrub clearing to the findings is not clear, as they ensure a stable, moist microclimate but

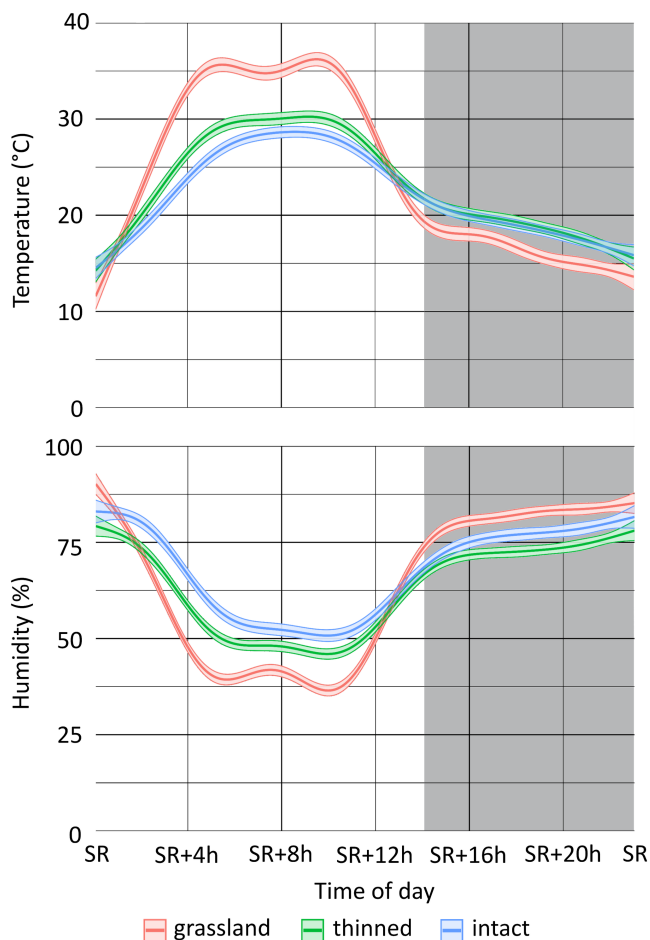


FIGURE 4 | Daily microclimatic relations of the thinned and intact forest plantations and adjacent open grassland sites. Thick curves are fitted values of GAM models, while the lighter bands indicate their 95% confidence intervals. Non-overlapping stretches of the bands are considered periods of the day exhibiting significantly different microclimates. Loggers were fixed on 50-cm high posts and measurements were done in 5-min intervals. SR: sunrise; grey shading: night time.

can lead to a net moisture loss if expanding after tree canopy reduction (Prévosto et al. 2020).

Finally, consistent with our first hypothesis, the higher loss of moisture via the combination of evaporation and transpiration in the forested dune slopes was associated with a drop of moisture influx to the wetland via the dune slope–wetland ecotone. Although a direct measurement of lateral flow with, e.g., tracer experiments, would have resulted in more direct evidence, we can reasonably assume that our proxy, soil moisture content dynamics, also supports the outlined flow pattern changes, particularly because lateral flows from the dunes towards the downslope wetlands have formerly been confirmed in the area (Simon et al. 2023). The lack of moisture discharge towards the wetland was not restricted to the growing season, but lasted further into the autumn, and the amount of moisture started to increase again from the intact forest only in December. This is expectable, as evapotranspiration drops once the leaves start to senesce in late September to early October but the moisture that arrives afterwards first needs to recharge the dry zone in the subsoil of the dune slopes to field

capacity before any gravitational water could seep on towards the wetland.

Thinning delayed the drop of moisture content in the ecotone in spring but as the canopy recovered, through-flow decreased similar to the intact sections of the forests. Recharge started slightly earlier too, probably due to the lack of shrubs, which usually shed their leaves later than black locust, a species with one of the shortest annual canopy lifetimes among woody species in the region (Tölgyesi et al. 2020). Nevertheless, this slight effect of thinning is unlikely to sustain better water supply in the long run, i.e., in subsequent springs, as the recovery of the canopy cover was complete. In drier years or with an overall drying of the climate, such recovery may be hindered, supporting moisture recharge, but in such a scenario, the overall moisture input of the wetlands would probably still decline, although less so than without tree removal.

So, for an effective restoration of wetland water supply, larger gaps or a complete removal of the forest plantations might be considered, but the exact proportions that can be allowed by the law should be established by future research. Nevertheless, to further illustrate the importance of scale in this matter, a 700.000-ha deforestation in the Murray–Darling Basin could lead to considerable groundwater level rise in Australia (Jackson et al. 2000), while a 20% thinning in a forest of the Rocky Mountains of the US had no detectable effect on annual stream flows (Stednick 1996). However, large-scale conversion of non-native tree plantations to more natural open habitats must be carefully planned to avoid adverse effects, such as flash floods and soil erosion (Jin et al. 2020).

Inter-annual variation of the weather in the region is large (Izsák et al. 2022), so a longer monitoring period could have lent higher robustness to the findings. However, the overall climatic moisture deficit is expected to increase, which, according to Farley et al. (2005), can increase the proportionate effect of afforestation on runoff. Thus, our results, coming from a period with average weather, provide useful evidence for the negative effects of upland afforestation on deep infiltration and the water supply of adjacent, low-lying wetlands (see also, e.g., Schwärzel et al. 2020).

The desiccation trend of these wetlands is thus at least partially attributable to the unnaturally high forest cover, exceeding the potential woody cover of the original forest-steppe vegetation (Rédei et al. 2014; Tölgyesi, Hábcenyus, et al. 2023). Unfortunately, a slight thinning does not necessarily solve this issue; therefore, we recommend revisiting afforestation strategies that target water-limited, low-productivity uplands in this and similar regions worldwide. Other regions, where landscape-scale moisture regimes are not compromised, should be favoured for forest expansion. For example, floodplains surrounding the Nyírség region used to be wide and rich in woody vegetation but are now squeezed within narrow strips of land bordered by tall artificial dykes. The rehabilitation of these floodplains, which is now prescribed by the Nature Restoration Law of the EU (Stoffers et al. 2024), would offer vast areas for reforestation, while a simultaneous reduction of tree cover in sandy uplands would also provide many new land use and restoration opportunities. The reduction of

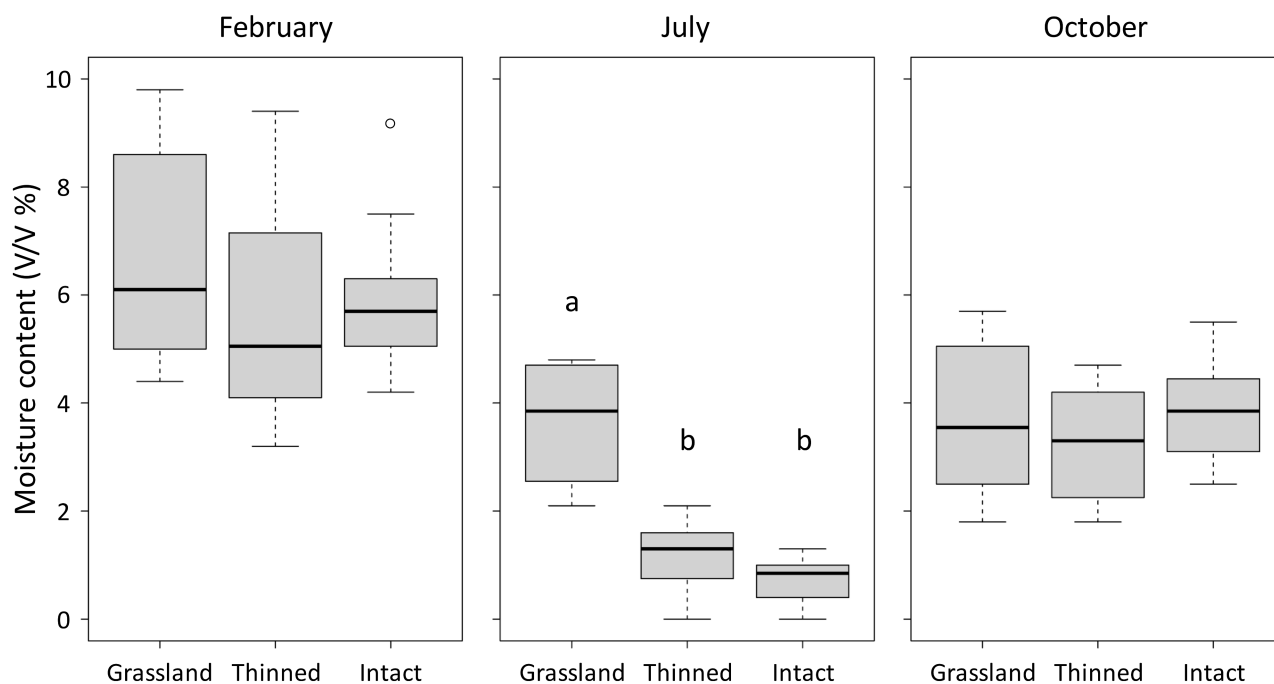


FIGURE 5 | Soil moisture relations of the studied habitat types at a depth of 70 cm, at the time of the thinning intervention (February), the middle of the growing season (July) and after the growing season (October). Different lowercase letters indicate significantly different groups ($p < 0.05$).

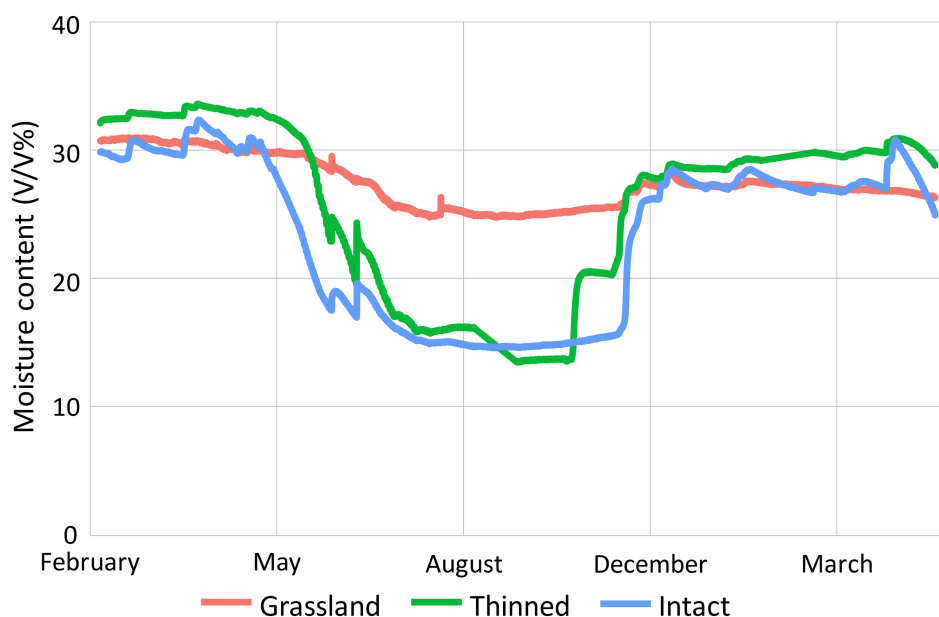


FIGURE 6 | Volumetric water content of the subsoil of upland–wetland ecotones, with the upland sides covered by open grassland or forest plantations (thinned or intact stands). Measurements were performed 70 cm deep (somewhat above the fluctuating groundwater level). The curves show the average of two spatially independent measurements.

tree cover in upland areas would directly contribute to wetland restoration in low-lying areas but would also enable the restoration of forest-steppe vegetation in the uplands. Both of these would mean a significant leap in biodiversity and ecosystem services. The only drawback would be the locally reduced timber production rate, which has to be taken into consideration during decision-making. Another important ecosystem service of black locust is its contribution to honey production (Ábri et al. 2023); but given the huge amount of *Robinia* plantations in the Nyírség (approx. 22,700 ha; Rédei

et al. 2014) and its uncontrolled invasion outside plantations (Puchałka et al. 2021), the nectar supply far exceeds the demand. Furthermore, native herbs of the steppe component, such as *Vicia* species, can also partially substitute *Robinia*.

The restored wetlands and forest-steppes can be utilized by extensive grazing, which is a strongly subsidized, sustainable form of agricultural production in the EU (Jones et al. 2016). However, sand dunes are prone to degradation and soil erosion if overgrazed (Provoost et al. 2011); therefore, alternative options

should also be taken into consideration. For example, the EU's Nature Restoration Law prescribes the restoration of Habitats of Community Importance, and both components of the former forest-steppe vegetation (Pannonic Sand Steppes and Euro-Siberian steppe oak woods with *Quercus* spp.) correspond to such habitats (Biró et al. 2018) and require no active forestry or grassland management for long-term sustainability. However, if land owners require a higher local economic return, investment into green energy production, such as solar development, could also be an option after a careful examination of potential negative environmental impacts and how to alleviate them (Tölgyesi, Bátori, et al. 2023; Sturchio and Knapp 2023).

Author Contributions

C.T. and L.S. conceived the study, C.T., L.S. and P.T. acquired funding, C.T., L.S., L.S.K., A.A.H., A.K., Z.B., and V.T. collected and processed the data, C.T. led the writing of the manuscript, and all authors critically contributed to the final version.

Acknowledgements

The authors are grateful to the Hortobágy National Park Directorate for helping in study site selection, implementing the forest thinning and granting access to their protected areas. We thank the support of the National Research, Development and Innovation Office (Grant IDs: K 146137, KKP 144068, and FK 142428).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data that support the findings are available from the corresponding author upon request.

Funding

This work was supported by Nemzeti Kutatási Fejlesztési és Innovációs Hivatal, K 146137, KKP 144068, FK 142428.

References

- Ábri, T., K. Cseke, Z. Keserű, A. Porcsin, F. M. Szabó, and K. Rédei. 2023. "Breeding and Improvement of Black Locust (*Robinia pseudoacacia* L.) With a Special Focus on Hungary: A Review." *iForest - Biogeosciences and Forestry* 16: 290–298.
- Acharya, B. S., G. Kharel, C. B. Zou, B. P. Wilcox, and T. Halihan. 2018. "Woody Plant Encroachment Impacts on Groundwater Recharge: A Review." *Water* 10, no. 10: 1466.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1–48.
- Biró, M., J. Bölöni, and Z. Molnár. 2018. "Use of Long-Term Data To Evaluate Loss and Endangerment Status of Natura 2000 Habitats and Effects of Protected Areas." *Conservation Biology* 32, no. 3: 660–671.
- Buisson, E., S. Le Stradic, F. A. Silveira, et al. 2019. "Resilience and Restoration of Tropical and Subtropical Grasslands, Savannas, and Grassy Woodlands." *Biological Reviews* 94, no. 2: 590–609.
- Burns, S. P., V. Humphrey, E. D. Gutmann, M. S. Raleigh, D. R. Bowling, and P. D. Blanken. 2025. "Using GNSS-Based Vegetation Optical Depth, Tree Sway Motion, and Eddy Covariance to Examine Evaporation of Canopy-Intercepted Rainfall in a subalpine forest." *Biogeosciences* 22, no. 20: 5741–5769.
- Crockford, R. H., and D. P. Richardson. 2000. "Partitioning of Rainfall Into Throughfall, Stemflow and Interception: Effect of Forest Type, Ground Cover and Climate." *Hydrological Processes* 14, no. 16–17: 2903–2920.
- Demeter, L. 2022. "A Dél-Nyírség páfrányflórája (Pteridopsida)." *kitabelia* 27: 162–182.
- D'Odorico, P., Y. He, S. Collins, S. F. De Wekker, V. Engel, and J. D. Fuentes. 2013. "Vegetation–Microclimate Feedbacks in Woodland–Grassland Ecotones." *Global Ecology and Biogeography* 22, no. 4: 364–379.
- Durigan, G., and E. A. Honda. 2024. "Ecological Restoration and Water-Related Ecosystem Services, One Step Ahead: A Reply to Dib et al. (2023)." *Restoration Ecology* 32, no. 4: e14113.
- Erdős, L., P. Török, J. W. Veldman, et al. 2022. "How Climate, Topography, Soils, Herbivores, And Fire Control Forest–Grassland Coexistence in the Eurasian Forest–Steppe." *Biological Reviews* 97, no. 6: 2195–2208.
- Farley, K. A., E. G. Jobbágy, and R. B. Jackson. 2005. "Effects of Afforestation on Water Yield: A Global Synthesis With Implications for Policy." *Global Change Biology* 11, no. 10: 1565–1576.
- Huang, Z., W. J. Yang, Y. Liu, W. Shen, M. López-Vicente, and G. L. Wu. 2020. "Belowground Soil Water Response in the Afforestation–Cropland Interface Under Semi-Arid Conditions." *Catena* 193: 104660.
- Iida, S. I., S. Noguchi, D. F. Levia, et al. 2024. "Effects of Forest Thinning on Sap Flow Dynamics and Transpiration in a Japanese Cedar Forest." *Science of the Total Environment* 912: 169060.
- Izsák, B., T. Szentimrey, M. Lakatos, and R. Pongrácz. 2022. "Extreme Months: Multidimensional Studies in the Carpathian Basin." *Atmosphere* 13, no. 11: 1908.
- Jackson, R. B., H. J. Schenk, E. G. Jobbágy, et al. 2000. "Belowground Consequences of Vegetation Change and Their Treatment in Models." *Ecological Applications* 10, no. 2: 470–483.
- Jiménez, E., J. A. Vega, P. Pérez-Gorostiaga, et al. 2008. "Effects of Pre-Commercial Thinning on Transpiration in Young Post-fire Maritime Pine Stands." *Forestry* 81, no. 4: 543–557.
- Jin, Z., L. Guo, Y. Yu, D. Luo, B. Fan, and G. Chu. 2020. "Storm Runoff Generation in Headwater Catchments on the Chinese Loess Plateau After Long-Term Vegetation Rehabilitation." *Science of the Total Environment* 748: 141375.
- Jones, N., F. Duarte, I. Rodrigo, A. van Doorn, and J. de Graaff. 2016. "The Role of EU Agri-Environmental Measures Preserving Extensive Grazing in Two Less-Favoured Areas in Portugal." *Land Use Policy* 54: 177–187.
- Kevey, B., L. Papp, and G. Lendvai. 2017. "A Nyírség gyertyános-tölgyesei (Convallario-Carpinetum Kevey 2008)." *Botanikai Közlemények* 104, no. 1: 147–164.
- Kovács, B., F. Tinya, C. Németh, and P. Ódor. 2020. "Unfolding the Effects of Different Forestry Treatments on Microclimate in Oak Forests: Results of a 4-yr Experiment." *Ecological Applications* 30, no. 2: e02043.
- Kristensen, J. Å., L. Barbero-Palacios, I. C. Barrio, et al. 2024. "Tree Planting is No Climate Solution at Northern High Latitudes." *Nature Geoscience* 17, no. 11: 1087–1092.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82, no. 13: 1–26.
- Le Maitre, D. C., D. F. Scott, and C. Colvin. 1999. "A Review of Information on Interactions Between Vegetation and Groundwater." *Water SA* 25: 137–152.

- Lenth, R. 2023. *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.8.4–1. <https://CRAN.R-project.org/package=emmeans>.
- Lovas-Kiss, Á., and K. Süveges. 2022. "Adatok a Dél-Nyírség és peremterületei flórájához." *Kitaibelia* 27, no. 1: 68–85.
- Ma, C., X. Li, Y. Luo, M. Shao, and X. Jia. 2019. "The Modelling of Rainfall Interception in Growing and Dormant Seasons for a Pine Plantation and a Black Locust Plantation in Semi-Arid Northwest China." *Journal of Hydrology* 577: 123849.
- Ma, S., A. Concilio, B. Oakley, M. North, and J. Chen. 2010. "Spatial Variability in Microclimate in a Mixed-Conifer Forest Before and After Thinning and Burning Treatments." *Forest Ecology and Management* 259, no. 5: 904–915.
- Mátyás, C., I. Berki, A. Bidló, et al. 2018. "Sustainability of Forest Cover Under Climate Change on the Temperate-Continental Xeric Limits." *Forests* 9, no. 8: 489.
- McEwan, A., E. Marchi, R. Spinelli, and M. Brink. 2020. "Past, Present and Future of Industrial Plantation Forestry and Implication on Future Timber Harvesting Technology." *Journal of Forestry Research* 31, no. 2: 339–351.
- Nosetto, M. D., E. G. Jobbágy, and J. M. Paruelo. 2005. "Land-Use Change and Water Losses: The Case of Grassland Afforestation Across a Soil Textural Gradient in Central Argentina." *Global Change Biology* 11, no. 7: 1101–1117.
- Novák, T., G. Négyesi, B. András, and B. Buró. 2014. "Alluvial Plain With Wind-Blown Sand Dunes in South Nyírség, Eastern Hungary." In *Soil Sequences Atlas*, edited by M. Switoniak and P. Charzynski, 181–197. Nicolaus Copernicus University Press.
- Prévosto, B., M. Helluy, J. Gavinet, C. Fernandez, and P. Balandier. 2020. "Microclimate in Mediterranean Pine Forests: What is the Influence of the Shrub Layer?" *Agricultural and Forest Meteorology* 282: 107856.
- Provoost, S., M. L. M. Jones, and S. E. Edmondson. 2011. "Changes in Landscape and Vegetation of Coastal Dunes in Northwest Europe: A Review." *Journal of Coastal Conservation* 15, no. 1: 207–226.
- Puchałka, R., M. K. Dyderski, M. Vitková, et al. 2021. "Black Locust (*Robinia pseudoacacia* L.) Range Contraction and Expansion in Europe Under Changing Climate." *Global Change Biology* 27, no. 8: 1587–1600.
- Quang, H. T., Z. Z. Fehér, N. Túri, and J. Rakonczai. 2022. "Climate Change as an Environmental Threat on the Central Plains of the Carpathian Basin Based on Regional Water Balances." *Geographica Pannonica* 26: 184–199.
- Quiroz Dahik, C., P. Crespo, B. Stimm, et al. 2021. "Impacts of Pine Plantations on Carbon Stocks of Páramo Sites in Southern Ecuador." *Carbon Balance and Management* 16, no. 1: 5.
- R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Rédei, K., I. Csiha, Z. Keserű, J. Rásó, Á. Kamandiné Végh, and B. Antal. 2014. "Growth and Yield of Black Locust (*Robinia pseudoacacia* L.) Stands in Nyírség Growing Region (North-East Hungary)." *South-East European Forestry* 5, no. 1: 13–22.
- Reisman-Berman, O., T. Keasar, and N. Tel-Zur. 2019. "Native and Non-Native Species for Dryland Afforestation: Bridging Ecosystem Integrity and Livelihood Support." *Annals of Forest Science* 76, no. 4: 114.
- Ruiz-Vásquez, M., P. A. Arias, J. A. Martínez, and J. C. Espinoza. 2020. "Effects of Amazon Basin Deforestation on Regional Atmospheric Circulation and Water Vapor Transport Towards Tropical South America." *Climate Dynamics* 54, no. 9: 4169–4189.
- Russell, E. S., H. Liu, H. Thistle, B. Strom, M. Greer, and B. Lamb. 2018. "Effects of Thinning a Forest Stand on Sub-Canopy Turbulence." *Agricultural and Forest Meteorology* 248: 295–305.
- Schwärzel, K., L. Zhang, L. Montanarella, Y. Wang, and G. Sun. 2020. "How Afforestation Affects the Water Cycle in Drylands: A Process-Based Comparative Analysis." *Global Change Biology* 26, no. 2: 944–959.
- Simon, S., J. Déri-Takács, M. Sziájtó, L. Szél, and J. Mádl-Szőnyi. 2023. "Wetland Management in Recharge Regions of Regional Groundwater Flow Systems With Water Shortage, Nyírség Region, Hungary." *Water (Basel)* 15, no. 20: 3589.
- Stednick, J. D. 1996. "Monitoring the Effects of Timber Harvest on Annual Water Yield." *Journal of Hydrology* 176, no. 1–4: 79–95.
- Stoffers, T., F. Altermatt, D. Baldan, et al. 2024. "Reviving Europe's Rivers: Seven Challenges in the Implementation of the Nature Restoration Law to Restore Free-Flowing Rivers." *WIREs Water* 11, no. 3: e1717.
- Sturchio, M. A., and A. K. Knapp. 2023. "Ecovoltaic Principles for a More Sustainable, Ecologically Informed Solar Energy Future." *Nature Ecology & Evolution* 7, no. 11: 1746–1749.
- Tölgyesi, C., Z. Bátor, J. Pascarella, et al. 2023. "Ecovoltaics: Framework and Future Research Directions to Reconcile Land-Based Solar Power Development With Ecosystem Conservation." *Biological Conservation* 285: 110242.
- Tölgyesi, C., A. A. Hábczyus, A. Kelemen, et al. 2023. "How to Not Trade Water for Carbon With Tree Planting in Water-Limited Temperate Biomes?" *Science of the Total Environment* 856: 158960.
- Tölgyesi, C., P. Török, A. A. Hábczyus, et al. 2020. "Underground Deserts Below Fertility Islands? Woody Species Desiccate Lower Soil Layers in Sandy Drylands." *Ecography* 43, no. 6: 848–859.
- Valente, M. L., J. M. Reichert, R. B. L. Cavalcante, J. P. G. Minella, O. Evrard, and R. Srinivasan. 2021. "Afforestation of Degraded Grasslands Reduces Sediment Transport and May Contribute to Streamflow Regulation in Small Catchments in the Short-Run." *Catena* 204: 105371.
- Veldman, J. W., J. C. Aleman, S. T. Alvarado, et al. 2019. "Comment on 'The Global Tree Restoration Potential'." *Science* 366, no. 6463: eaay7976.
- Wang, Z., Q. He, B. Hu, X. Pang, and W. Bao. 2018. "Gap Thinning Improves Soil Water Content, Changes the Vertical Water Distribution, and Decreases the Fluctuation." *Canadian Journal of Forest Research* 48, no. 9: 1042–1048.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.
- Wood, S. N. 2011. "Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models." *Journal of the Royal Statistical Society (B)* 73, no. 1: 3–36.
- Yamaura, Y., Y. Yamada, T. Matsuura, et al. 2021. "Modeling Impacts of Broad-Scale Plantation Forestry on Ecosystem Services in the Past 60 Years and for the Future." *Ecosystem Services* 49: 101271.
- Yang, L., W. Wei, L. Chen, and B. Mo. 2012. "Response of Deep Soil Moisture to Land Use and Afforestation in the Semi-Arid Loess Plateau, China." *Journal of Hydrology* 475: 111–122.
- Yildiz, O., E. Altundağ, B. Çetin, Ş. Teoman Güner, M. Sarginci, and B. Toprak. 2018. "Experimental Arid Land Afforestation in Central Anatolia, Turkey." *Environmental Monitoring and Assessment* 190, no. 6: 355.
- Zoltán, M. M. 2019. "Climate Analysis of Nyírség And Upper-Tisza Region." *Légekör* 64: 105–108.