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Suppressing the invasive common milkweed (*Asclepias syriaca* L.) saves soil moisture reserves

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Abstract Common milkweed (*Asclepias syriaca* L.) is a widespread invasive alien forb in dry sandy habitats of Central Europe. It adversely affects native plant and animal communities, but its ecosystem-level effects, particularly on hydrology, are little known. Since milkweed has an extensive, deep root system and large, broad leaves, we assumed a negative effect on the soil moisture content of the hosting ecosystem. Following the before-after control-impact protocol, we first compared the soil moisture content of the top 120 cm of the soil under seven milkweed stands to that of non-invaded reference sites. We then treated half of the stands by mechanically removing all aboveground milkweed biomass and repeated the comparative soil moisture measurements. We found that milkweed stands had significantly drier soils than reference grasslands during the growing season, but the soil under milkweed stands recharged to the level of the references in autumn and winter. However, the amount of moisture needed for this recharge was lost from deeper percolation to groundwater. Milkweed treatment prevented the depletion of moisture during the growing season, saving $21.6\,l\,m^{-2}$ of water on average. Treatment did not affect non-milkweed plant biomass, thus, moisture patterns could fully be attributed to the milkweed stands. Our results reinforce the importance of milkweed suppression in invaded grasslands, as, besides enabling the recovery of the native grassland ecosystem, it promotes groundwater recharge, which is particularly important in the dry regions of Central Europe, currently facing severe aridification due to climate change and unfavourable land use trends.

Keywords Ecosystem disservice · Experimental removal · Hydrology · Invasive species · Kiskunság · Sand soil · Transformer species · Water balance

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Introduction

Invasive alien plant species often suppress other plant populations by being more efficient competitors due to superior trait states or the lack of pathogens and consumers (Broadbent et al. 2018; Mathakutha et al. 2019). At the community level, these effects can result in declining species richness, changes in vegetation structure and shifts in trait compositions (Davies 2011; Hábenczyus et al. 2022). These changes modify ecosystem functions, compromising ecosystem services or delivering ecosystem disservices to human populations (Milanovic et al. 2020). For example, invasive annual grasses can increase fire hazard in arid shrublands (Bradley et al. 2018), while unpalatable invasive forbs can reduce pasture quality for the livestock (DiTomaso 2000).

The water regime of the host ecosystem is also frequently affected by invasive plant species. As high competitiveness often comes hand in hand with higher water consumption rates (Charles and Dukes 2007; Pejchar and Mooney 2009), negative effects are more common than positive ones (Pysek et al. 2020). The strongest drying effects are documented for woody invasive species with higher leaf area index and larger root systems than members of the native flora. Such species include, for example, pines, acacias and eucalypts in South-Africa (Richardson and Wilgen 2004; Dzikiti et al. 2016), and salt cedars (*Tamarix* spp.) in riparian communities of the American Southwest (Gordon 1998), where Zavaleta (2000) estimated a water loss of 1.4–3.0 million m^3 annually. The high water consumption of these invasive species can lead to significant reductions in streamflows and water table levels, which are particularly problematic in water-limited regions, where the rearrangement of evapotranspiration patterns may threaten the survival of the native flora and fauna, and the water security of human populations.

Beside biological invasion, water-scarcity can be aggravated by many other local to global synergistic factors, such as excessive afforestation, spontaneous woody encroachment (Farley et al. 2005), irrigation, and climate change (Overpeck and Udall 2020), leading to dramatic environmental changes. Central Hungary is one such region, where the water table declined in the past five decades up to seven meters and most lakes and wetlands vanished (Ladányi et al. 2010). There are at least five independent factors (climate change, afforestation, irrigation, drainage canals and mining) that have been confirmed as significant contributors (Tölgyesi et al. 2023), but biological invasion has never been tested in this respect.

The most abundant and wide-spread invasive species of the region is the common milkweed (*Asclepias syriaca* L.), which is a clonal forb of North-American origin. Its prevalence in open landscapes is extremely high; Botta-Dukát (2008) reported it from 75% of all sand grasslands and forest-steppes, where it often creates dense, homogeneous stands (Balogh et al. 2023). The native herbaceous vegetation of the region, due to the relative rarity of deep-rooted species, barely use soil moisture below 30–40 cm deep, as indicated by stable water contents throughout the year below this layer (Tölgyesi et al. 2020). In contrast, large clonal stands of milkweed, with their deep, rhizomatous root system (up to 1.5 m deep; Follak et al. 2021), potentially tap on moisture resources that are beyond the reach of most native herbaceous species. At the same time, milkweed has a considerably larger leaf area than the native plant species, which also enables high evapotranspiration rates (Szitár et al. 2018). Considering these traits of milkweed in conjunction with its high regional prevalence and abundance, we assumed that it may also have a significant negative effect on the input of soil moisture reserves of the region, even though it is not a woody species, like those for which negative hydrological effects have mostly been reported worldwide. Specifically, we hypothesised that (i) the soil under dense milkweed stands contains less moisture than under non-invaded control sites, and (ii) at least a partial restoration of the soil moisture reserves can be achieved by suppressing milkweed.

Materials and methods

Study region

The study was performed in the Kiskunság Sand Ridge of Central Hungary, East-Central Europe. It is an extensive, nearly 1-Mha sand region with subcontinental climate, characterized by warm summers and cold winters and an annual precipitation of 550–600 mm (Dövényi 2010). The soil of the region is coarse-grained, calcareous Arenosol with little humus content (Tölgyesi et al. 2016). The original

natural vegetation was forest-steppe, which is a mixture of dry steppe and deciduous woodland patches (Erdős et al. 2018), but large tracts of its territory have been transformed into either tree plantations or cropland (Biró et al. 2013a, b). Many croplands have since been abandoned and secondary succession towards sand steppe or forest-steppe vegetation could start (Csecserits et al. 2001, 2011).

Milkweed was introduced to the region in the eighteenth century deliberately (Bagi 2008). It was first planted for ornamental purposes, but agricultural usage was also tested for fibre and honey production (Follak et al. 2021). Its invasion became apparent only in the second half of the twentieth century and now it occurs in the entire region (Botta-Dukát 2008). The most abundant stands occur in abandoned croplands but tree plantations as well as primary forest-steppe fragments are also heavily infested (Szitár et al. 2018; Kapilkumar et al. 2019).

Data collection and analysis

We selected seven old (30 + years) abandoned croplands (Table S1), where milkweed stands and non-invaded reference patches could be found next to each other and references have already developed vegetation structure and composition patterns resembling native sand steppes. We chose abandoned croplands because they are among the most typical occurrences of the species and flat, homogenous soil surfaces were needed to ensure uniform micro-topographic positions, and hence identical a priori moisture and soil conditions in invaded and adjacent non-invaded reference patches.

In each field we selected two 5 × 5 m study plots in the milkweed stand and one 5 × 5 m plot in the non-invaded reference patch. In early July, 2021, we drilled two 1 m deep holes in each plot and measured soil moisture in every 20 cm as we proceeded downwards (i.e. 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, 80–100 cm and 100–120 cm). We used a portable soil moisture meter (FieldScout™ TDR 350) equipped with a 20 cm long probe. We made three measurements in every depth layer of every hole and used their average as data points in the subsequent calculations to reduce the effect of fine scale moisture heterogeneity; see also in Tölgyesi et al. (2020, 2023) for the same methodology. The date of the measurement was chosen to be July because it is the end of the main growing period of milkweed in the region. To follow up on soil moisture recharging after the active period of milkweed, we repeated the measurements at the beginning of the next growing season, in March, 2022.

We assessed the aboveground biomass (as a proxy of evapotranspiration capacity; Flanagan and Johnson 2005) of milkweed in the plots by clipping the stems in two randomly chosen 1 × 1 m quadrats in summer by cutting, drying at 50 °C for three days in a drying chamber, and gravimetrically measuring them. We collected two samples because this way we accounted for some of the within-plot variability (compared to a single sample) but had negligible consequences for the performance of milkweed in the following year (compared to a higher intensity of sampling).

Considering the biomass and soil moisture data from 2021, we assigned one of the milkweed plots into a treatment group and a control group so that the averages of the two groups were as similar as possible in terms of the measured variables. In the treatment groups we manually removed all aboveground parts of milkweed stems three times during the growing season of 2022 (in late April, mid-May and mid-June) (Fig. 1). In total, we removed

Fig. 1 Native steppe vegetation with scattered woody vegetation on an old abandoned cropland in the Kiskunság Sand Ridge, Central Hungary (**A**). A 5 m × 5 m treatment plot within a common milkweed stand (**B**)

981 ± 248 (mean ± standard deviation) milkweed stems from the treatment plots. Milkweed stems in the control groups were left intact.

At the same time as moisture measurements and milkweed biomass collection in July 2021 and 2022, we also collected all aboveground biomass of non-milkweed vegetation, containing mostly native but also some other non-native species, from two 0.5 × 0.5 m plots. These non-milkweed biomass plots were selected in the reference study plots randomly, while in the invaded ones (treated and control study plots), they were placed within the milkweed biomass sampling plots. We used non-milkweed biomass samples as a proxy for their evapotranspiration capacity (Flanagan and Johnson 2005).

Soil moisture relations were analysed using linear mixed-effects models (LMM). We used plot type (three levels: treated milkweed stand, control milkweed stand and non-invaded reference vegetation) as the fixed factor and field identity as the random factor. We prepared separate models for the three dates (July 2021, March 2022 and July 2022) and for each soil layer (0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, 80–100 cm and 100–120 cm), making a total of 18 models. We also calculated average moisture content differences between the study plot types for later interpretation using the following equation: $D = (d_p/100)*1200 \ l \ m^{-2}$, where D is the difference in l m^{-2}, d_p is the difference of the average volumetric moisture content of two study plots types in percentages, and the factor of 1200 l m^{-2} refers to the volume of the soil layer covered.

We also prepared LMMs for the biomass of milkweed and the non-milkweed vegetation, using the same fixed and random effects as for soil moisture models. Model assumptions for normality were checked visually with QQ-plots. Data analysis was performed in an R 3.6.1 statistical environment (R Core Team 2019). We used the 'lmer' function of the *lme4* package (Bates et al. 2015) for preparing the models, the 'Anova' function of the *car* package (Fox and Weisberg 2019) to test the models for significance and the 'emmeans' function of the *emmeans* package (Lenth 2021) to perform pairwise comparisons among plot types.

Results

In July, 2021, soil moisture in the treatment and control milkweed plots did not differ from each other in either soil depth (Fig. 2, Table S2). Reference (i.e. non-invaded) plots had slightly drier soil in the top 20 cm than control and treatment plots, but below that until 1 m both the treatment and
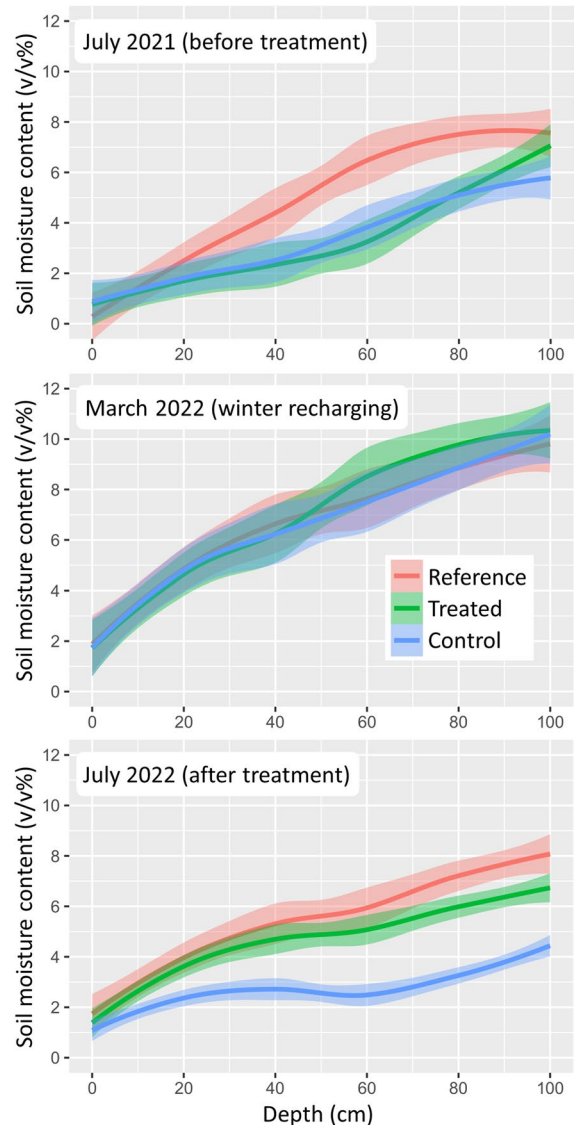

Fig. 2 Soil moisture content under treated and non-treated control milkweed stands and under non-invaded reference plots. Thick lines are smoothed averages of measurements in every 20 cm section, while transparent bands are 95% confidence intervals

control plots were drier than the reference plots. At the deepest layer, the difference was smaller but still significant between the reference and the control plots, while there was no more difference between the reference and treatment plots.

In March, 2022, i.e. following soil moisture recharging in fall and winter and before the growing season of milkweed, soil moisture conditions did not have detectable differences among the plot groups in any of the soil layers (Fig. 2, Table S2). However, by July, 2022, control plots had become drier in all layers, including the top 20 cm, than the reference plots (Fig. 2, Table S2). Treatment, compared to the control, increased the soil moisture retention in all soil layers but the top 20 cm, and reached the level of reference plots in the 20–60 cm layers. Below that, the references were still moister, as well as in the top 20 cm, although the difference in the latter layer was rather small.

By summing up the average moisture differences we found that 29.2% of the moisture content (equalling 16.8 l m^{-2} water) was missing from the soil of invaded plots (treatment and control combined) compared to the non-invaded, reference plots in July, 2021. In July 2022, the difference between the control and reference plots was even greater and reached 49.2% (31.2 l m^{-2}) less in control compared to reference plots, while the measured difference between reference and treatment plots was only 14.6% (9.6 l m^{-2}). Thus, the treatment saved approximately 34.6% (21.6 l m^{-2}) of moisture in the soil.

Aboveground biomass of milkweed in the control and treatment groups before the treatment (in July 2021) was 294 ± 82 g m^{-2} (mean $\pm$ SD) and 302 ± 135 g m^{-2}, respectively, and they did not differ from each other statistically (LMM, t ratio $= 0.2$, $p = 0.843$) (Fig. 3A). In July 2022, following the removal rounds, only 10 ± 5 g m^{-2} milkweed regrew in the treatment plots, whereas the control groups had a significantly higher biomass, amounting to 392 ± 169 g m^{-2} (LMM, t ratio $= 10.09$, $p < 0.001$).

In 2021, reference non-milkweed biomass did not differ from the control and treatment groups ($F = 2.19$, $p = 0.128$; Fig. 3B). In contrast, treatment plots had 38.3% lower biomass in 2022 than the references (t ratio $= 3.08$, $p = 0.011$), while control plots had 43.4% lower biomass (t ratio $= 3.49$, $p = 0.0104$). Treatment and control plots did not differ statistically
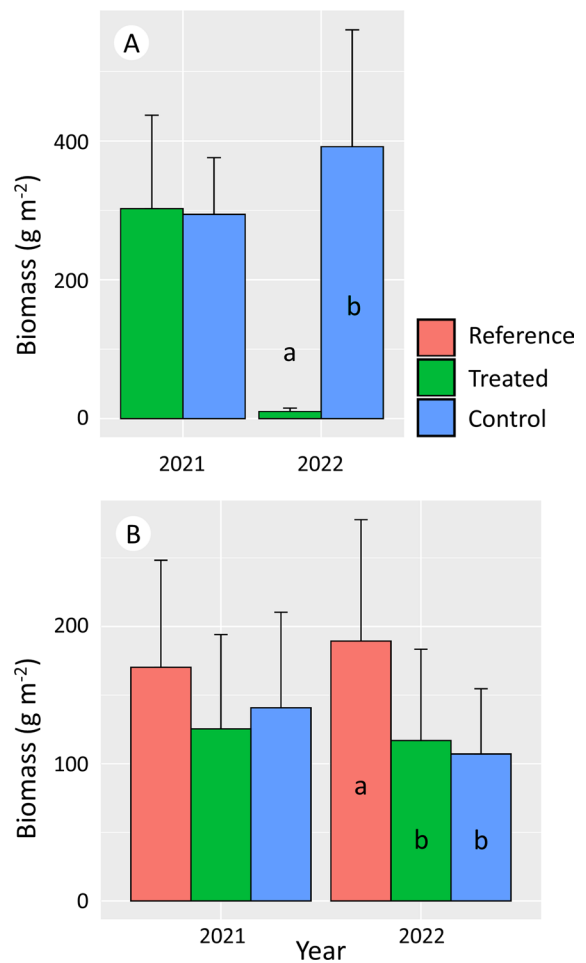

Fig. 3 Biomass of above-ground vegetation (mean and standard deviation) besides common milkweed in the studied plot types in 2021 and 2022. Plot types did not differ significantly in 2021, while types identified by different lower case letters in the 2022 dataset were significantly different ($p < 0.05$)

from each other regarding non-milkweed biomass (t ratio $= 0.41$, $p = 0.911$).

Discussion

Woody invasive species have often been found to have negative effects on local to regional scale water balance, evidenced by decreasing water table or streamflow following the invasion of pines, salt cedars, acacias, and *Melaleuca* species (Gordon 1998, Zavaleta 2000, Charles and Dukes 2007, Pejchar et al. 2009, Pysek et al. 2020). In contrast, studies on the

hydrological effects of invasive herbaceous species are scarce and not so easy to generalize. For example, an invasive forb, spotted knapweed (*Centaurea maculosa*) can increase runoff by more than 50% in the American southwest (Lacey et al. 1989), and short-lived invasive annual grasses also use less moisture than native perennial bunchgrass prairie (Pejchar et al. 2009). However, when these grasses are displaced by yellow starthistle (*C. solstitialis*), a perennial invasive forb, the water balance recovers (Gerlach 2004). Thus, unlike in the case of invasive woody species, it is probably not enough to consider the leaf area index or the size of the root system, but, due to shorter life cycles, the overlap between the active period of the plants and the seasonality of water availability may also have a decisive role. Therefore, a rigorous assessment of the hydrological effects of each potentially problematic invasive species may be needed.

Here, we studied the effects of an invasive clonal forb, common milkweed, in comparison with non-invaded references, and we also tested whether mechanical removal of milkweed stems can restore the water content of the soil, if needed. We found that the native dry sand steppe vegetation had slightly drier topsoil than the invaded patches in one of the study years, but we detected a remarkable reduction of the soil moisture below 20 cm of depth under milkweed stands. The moister topsoil is likely explained by the high shading capacity of milkweed due to its broad leaves and dense foliage. The importance of this is highlighted by Szitár et al. (2018), who found that the germination of native graminoid species can be facilitated by milkweed, although this nursing effect turns into a competitive interaction as the native species reach their mature stages and compete for light and other resources with milkweed (Kelemen et al. 2016). This eventual competition was also partially confirmed by the non-milkweed biomass data in our study, as they were lower in the invaded plots than in the reference grasslands in the second study year.

During the off-season months, deep soils recharged both under the milkweed stands and the non-invaded reference grasslands, and reached identical levels, indicating that there is no significant a priori hydrological difference between the invaded and non-invaded plots. The removal of milkweed shoots reduced the water loss in the deeper soil layers. A total restoration of the water content was probably not possible because the young stems we removed were also attached to the deep root network and used some moisture before removal, and the intact stems outside the 5×5 m treated plots could also have some lateral moisture depleting effect. A complete eradication of the clones in larger patches would likely have resulted in a more complete restoration of the moisture reserves. Such successful interventions have already been documented after the clearing of woody invasive species, such as salt cedars in the US (Gordon 1998), so it is also likely for milkweed.

Another factor to be considered in relation to the recovery of moisture reserves is that after milkweed removal, the non-milkweed vegetation may theoretically be released from the competitive pressure, resulting in higher growth rate and biological activity, which may partially offset the effect of milkweed removal. However, we did not detect such effect in the short term; the release of the non-milkweed vegetation did not result in a temporary biomass surplus reaching or potentially exceeding that of the reference grasslands, but remained at the same low level. So, the release of the non-milkweed vegetation has a longer time lag or does not occur at all, maybe because milkweed also used up soil resources other than moisture. However, to understand the long-term response of the non-milkweed vegetation to milkweed removal needs further, longer-term studies.

The fact that the soil is drier under milkweed stands and this can be reversed by milkweed removal confirms that the moisture patterns do not only correlate with the presence of milkweed but milkweed has a causative role. Thus, we confirmed that milkweed invasion reduces soil moisture reserves, and the amount needed to reach the moisture level of the reference grasslands is definitely lost from groundwater recharge. The average loss in the two study years was 24 l m^{-2}. This does not seem a lot compared to the annual precipitation of 550–600 mm (equalling $550–600 \text{ l m}^{-2}$), but most of that is lost through evapotranspiration. According to Szilágyi et al. (2012), an average of only 75 l m^{-2} percolates to deeper soil layers and reaches the groundwater annually in the study region; so, compared to this, milkweed causes a 32% loss of groundwater recharge. This figure may, of course, change with varying milkweed density, although other studies also encountered very high local densities of milkweed clones in old-fields. For instance, Kelemen et al. (2016) reported a 40% average cover, while the study sites of Szitár et al. (2018)

were characterized by around 50% cover scores, which are comparable to our stand densities.

Milkweed has long been considered a noxious invasive species in many European countries due to its unfavourable effects on native ecosystems. Milkweed has been shown to decrease the cover of native grassland plant species (Kelemen et al. 2016), and change their compositional patterns (Bakacsy 2019). Milkweed invasion can affect higher trophic levels as well, indicated by lower functional diversity and altered species composition of arthropods compared to non-invaded reference habitats (Gallé et al. 2015; Kapilkumar et al. 2019). Owing to these unfavourable effects, milkweed is included in the List of Invasive Alien Species of Union Concern, so its eradication is compulsory for EU member states (European Commission 2017). Unfortunately, milkweed has a massive underground bud bank in its root system, so mechanical removal, like in the present study, has little long-term effect (Bakacsy and Bagi 2020). Herbicide treatment is the most commonly used solution, although a single application is usually not enough (Csecserits et al. 2020). Although it kills most stems and greatly reduces regrowth the following year, it can also damage the native vegetation (Crone et al. 2009), and milkweed clones can recover later on. In addition, milkweed is often among the first plants to recolonize a patch (Ricono et al 2020), where the herbicide treatment created available substrates due to its good dispersal abilities (Follak et al. 2021; Berki et al. 2023) and the commonly occurring native propagule limitation of areas subject to biological invasion (MacDougall and Turkington 2005). To sum this up, a single treatment of milkweed without post-treatment interventions such as native propagules introduction has little chance to undo the negative effects of milkweed on the plant and animal communities, which may discourage conservation practitioners. However, our newly described ecosystem disservice of milkweed, the reduction of soil moisture reserves and the consequential hindering of groundwater recharge, offer a more reliable and quantifiable outcome of milkweed treatment, which may increase interest and help raise funding for milkweed treatment.

Monetization of ecosystem services and disservices is a difficult task, but it is a powerful tool to convince decision makers (Bunse et al. 2015). According to the Hungarian practice, the treatment of dense milkweed stands requires approx. 15 l ha^{-1} herbicide (typically glyphosate), costing 450 USD, and average accessory costs (travelling and daily allowance of workers, etc.) of 1030 USD (Takács et al. 2015). If a single treatment makes the site mostly milkweed-free for at least two years (see also Bakacsy and Bagi 2020), that results in preserving approx. 480 m^3 ha^{-1} of soil moisture, costing 820 USD according to the current prices of the regional water utility corporation (Bácsvíz Zrt.), which bases its water provision on underground resources. So, the costs of the herbicide are completely offset and even the accessory costs are somewhat compensated for. In light of these, we encourage milkweed treatment in invaded areas, even if repeated treatments cannot be ensured due to project timelines or the unpredictability of funding resources both in Hungary and other European countries, where milkweed invasion takes place. Nevertheless, this rough calculation does not consider the long-lasting negative effects of herbicide application, such as chemical residues remaining in the soil or contaminating groundwater resources. Thus, developing methods that are similarly cost-effective to glyphosate, but have no adverse effects, should also be encouraged.

Data availability All source data will be stored in the Dryad Data Repository upon acceptance of the manuscript.

Declarations

Conflict of interest The authors have no relevant financial or nonfinancial interests to disclose.

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