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ABSTRACT

Global climate change is gradually altering species distribution and spatial patterns of diversity. Yet, climatic factors influencing the local distribution and habitat preferences for southern African species remain largely unexplored. As such, predicting species distribution patterns and identifying environmental covariates that promote species range expansion will be critical in developing management protocols for biodiversity protection. Maxent, a species distribution model algorithm that applies a maximum entropy machine learning technique, is used in this study to map the geographical distributions of appropriate habitats for Colophospermum mopane (J. Kirk ex Benth.) J. Léonard in southern Africa under current and future climate change scenarios. We identified the highest contributors to the modelled distributions and calculated the range changes (expansion or loss) in southern Africa for C. mopane under three Representative concentration pathways (RCPs) for the 2050s and 2070s. Our results showed that the distribution of C. mopane was mainly influenced by solar radiation, annual temperature range, and annual precipitation. We also observe that C. mopane is distributed continuously in southern Africa, from southern Angola and northern Namibia to central-southern Mozambique, with a total occurrence area of 1,281,242 km². According to the species response curves, this species preferred habitats with annual precipitation of 130-200 mm, an annual temperature range of 22-28 °C, and elevations of about 500-1000 m above sea level. Under climate change scenarios, suitable habitat areas reduced significantly in the northern limits of the potential distribution areas while they expanded in the southern limits. Overall, the appropriate habitat areas will likely expand the least (4.08-4.46%) and decline the most (8.83-10.08%) under the extreme scenario of RCP8.5, depending on the year. Although there is a lack of consensus on the range changes in future distributions among the various RCPs, it is clear that solar radiation will significantly limit the distribution of C. mopane. This knowledge is important for landscape planners and rangeland managers working to safeguard biodiversity from extinction.

1. Introduction

Colophospermum mopane (J.Kirk ex Benth.) J. Léonard, typically known as the southern African Mopane, is a common woodland species belonging to the Ceasalpinoideae subfamily of Fabaceae (Moura et al., 2017). This species was introduced as *Copaifera mopane* J.Kirk ex Benth. but it is now widely known as *Colophosoermum mopane* (Léonard, 1949). In the late 20th century, Breteler et al. (1997) introduced the combination *Hardwickia mopane* (J.Kirk ex Benth.) Breteler by reducing the genus *Colophospermum* to a synonym of *Hardwickia* Roxb,—a genus occurring in India—by considering wood anatomy and pollen morphology. Nevertheless, Smith et al. (1998) argued strongly for retention of the genus *Colophospermum*, stating that the change would have resulted in more uncertainty over the classification of the species. Accordingly, in a vehement response to Breteler et al. (1997), Léonard (1999), rejecting their proposal and backing Smith et al. (1998) sentiments, opposed the name change.

Mopane is extensively distributed in the hot, low-lying areas of southern Africa's savannas, covering regions of about eight countries (Fig. 1) (Burgess et al., 2004; Maquia et al., 2019). Being a predominant native species, it forms the most important socio-economic and environmental vegetation in the area and a ready source of indigenous

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Fig. 1. Locations of occurrence records of *C. mopane* obtained from the Global Biodiversity Information Facility and Zambia Flora database.

woody products, food, and medicine for a large number of urban and rural residents highly reliant on these ecosystems (Dewees et al., 2010; Mojeremane and Lumbile, 2005; Rosenstock et al., 2019). As it is suited to a wide range of soil and microclimates, the plant takes on a variety of growth types, ranging from shrub-like to tall, slender trees with stunning leaf canopy. This dominant tree or multi-stemmed shrub in the Mopane woodlands is globally considered an ecosystem with irreplaceable species endemism, making it biologically unique. Besides, its leaves are a primary habitat for the caterpillar of the emperor moth *Gonimbrasia belina* (Westwood), which are utilized in the traditional South African cuisine as mopane worms. Collecting these insects as a food resource provide a major income to rural communities (Langley et al., 2020; Mojeremane and Lumbile, 2005).

Mopane is thought to display gregariousness by suppressing other woody plants growth through various mechanisms, including the release of allelopathic compounds (Daru et al., 2016), making it a promising candidate for investigating landscape genomics. In addition, Mopane forms part of biodiversity that has a global impact on water carbon sequestration, as well as energy and water balances (Handa et al., 2020; Mlambo et al., 2005). Furthermore, the ecological dynamics of *C. mopane* have been reported to be considerably influenced by a combination of climate change and non-climatic factors such as fire (Kennedy and Potgieter, 2003), day length, and animal disturbances (Stevens et al., 2018, 2014). Also, the species' ecological niche is experiencing human population expansion, which exerts pressure on the woodlands through mining, farming, and clearing for infrastructure.

Even though Mopane is classified as Least Concern (LC) by the IUCN Red List (Hills, 2019) due to its widespread distribution in southern Africa (Makhado et al., 2014), its continued exploitation is causing patchy and scattered distributions. This situation creates a threat to the persistence of the species actual distribution, thus calling for urgent conservation management. In addition, with climate change, potentially increased and recurring drought seasons are expected in most parts of the world, resulting in desertification (Krug, 2017). Therefore, the distribution modelling and future predictions of drought-tolerant vegetation species such as Mopane become necessary.

Climate change has had significant effects on natural and human environments in recent decades. Regardless of their origin, these effects of climate change demonstrate the resilience of natural and human environments to changes in climatic systems' structure, interference between their elements, or changes in external factors, either spontaneously or due to anthropogenic causes (Ipcc, 2014). Climate is often related to the plants' global distribution as it reflects the availability of moisture and energy for plant growth, and therefore, forecasting species distribution is vital, particularly for ecologists and conservationists, in mitigating climate change. Undoubtedly, researchers and wildlife managers have placed high emphasis on understanding factors that impact species distributions and habitat selection.

One such approach is the use of statistical species distribution models (SDMs), which have been broadly utilized to forecast species distributions' potential changes under climate change (Austin and Van Niel, 2011). SDMs relate environmental variables to well-known species occurrence locations to establish abiotic conditions under which organisms will survive (Guisan and Thuiller, 2005). Maxent is a popular choice among the various tools used in SDMs since it is suited in circumstances when just presence data are available and produces high prediction performance (Phillips et al., 2006). Since its publication, Maxent has been broadly utilized in various fields, including ecology, conservation biology (Nzei et al., 2021) and soil mapping (e.g. Cama et al., 2020; Maerker et al., 2020), among others. As such, it is vital to understand the impact of environmental variables on species occurrence and distribution (Baldwin, 2009).

Many species' future distributions are increasingly being mapped using SDMs and ecological niche models (ENMs) (Fourcade et al., 2014). A modelling approach aims to estimate the ecological appropriateness of the ecosystem relative to environmental variables (Blanco et al., 2020; Phillips, 2008). In this study, we opted to predict the distribution patterns of *C. mopane* in response to climate change in the southern African region. As a result, this study aimed to (i) map the current distribution of *C. mopane*, and (ii) predict new distribution areas in the coming decades due to climate change under different representative concentration pathways (RCPs).

2. Materials and methods

2.1. Occurrence records

The distribution of *C. mopane* used in the present study was obtained from two sources: The Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) (759 records) and Zambia flora (122 records). GBIF platform provides basic data on biodiversity; we searched the keyword "*Colophospermum mopane*" on GBIF, accessed on 12th May 2020 and downloaded the data. We conducted initial filtering of the data by removing duplicated records, followed by spatial rarefying of the data performed on R package "spThin" v. 0.1.0 (Aiello-Lammens et al., 2015) to reduce the spatial autocorrelation between the points at each grid cell of 10 km². The remaining 367 records were used in the subsequent analyses (Fig. 1, Table S1).

2.2. Climate data and clipping

We obtained the climate data from the Worldclim database version 1.4 (Hijmans et al., 2005, http://www.worldclim.org). Nineteen bioclimatic variables, solar radiation variable and an elevation layer at a resolution of 2.5 arc-mic were used. In addition, we generated slope from the elevation raster using the spatial analyst tool in ArcGis v.10.5 and added it as a variable. To reduce collinearity, the 19 bioclimatic variables were subjected to Pearson's correlation at a threshold of 0.8 (Graham, 2003), implemented in ENMTools package in R, using the function *raster.cor.matrix* (Warren et al., 2019). ArcGIS v.10.5 was used to clip the study area, including the known ranges and the potential distribution regions for *C. mopane* in southern Africa. Eventually, eight variables were selected as representative of climate factors, as shown in Table S2.

2.3. Model building and evaluation of SDM performance

The maximum entropy algorithm implemented in Maxent v.3.3 k was used to develop the current SDMs for *C. mopane* by allowing the transformations of covariates utilizing the software's default parameters, except the following: number of background points = 10^4 , and the

number of iterations = 5000. Eighty percent of the localities for model training, and the remaining 20% for testing. The model validation involved conducting 10 replicated run models for C. mopane, applying the threshold rule of maximum training sensitivity plus specificity (MTSS). MTSS is recommended as a conservative approach that minimizes commission and omission errors (Guisan et al., 2017; Liu et al., 2016). Jackknife tests were used on each of the ten replicated models to assess the most important variables contributing to Maxent's final model (Phillips et al., 2006). The performance of models was evaluated by the area under the curve (AUC) values of the receiving operator characteristics (ROC) (Mas et al., 2013; Phillips and Dudík, 2008). AUC values were examined using the test points. AUC values less than 0.8 indicate poor performance of the model, AUC values between 0.8 and 0.9 moderate performance, while AUC values above 0.9 are considered excellent (Thuiller et al., 2005). The presence of C. mopane was projected geographically by driving the probability of occurrence in four categories as follows: values below MTSS threshold "no data", "low" threshold–0.3, "medium" 0.3–0.6, and "high" >0.6. The logistic output was used to generate the final models, where the MTSS was used to define the presence-absence binary data.

To assess the probable future distribution in *C. mopane* ranges, we utilized the climate projections from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Collins et al., 2014). We considered three RCP scenarios for the Community Earth System Model (CCSM4) (Gent et al., 2011). The stringent mitigation scenario RCP2.6 aims to keep global warming under 2.0 °C under pre-industrial temperatures by 2010 (Collins et al., 2014). Under the intermediate scenarios, the global mean surface temperatures are projected to rise by 1.5–3.2 °C and the CO2 concentrations to 850 ppm in RCP4.5. For the RCP8.5 pessimistic scenario, global mean surface temperatures will possibly increase by 2.6–4.8 °C, while the concentration of CO2 will approximately be 1350 ppm by 2100.

2.4. Changes in potential distributions

The binary maps were used to determine the absolute area changes in habitat suitability for *C. mopane* between the present and the 2050s or 2070s under the three future scenarios (RCP2.6, RCP4.5, and RCP8.5). Using the SDM toolbox (Brown, 2014) in ArcGIS v.10.5, the range changes were analyzed with respect to the present period.

3. Results

3.1. Variable importance and climatic preference

Eight variables were retained after the correlation analyses following their multicollinearity (Table S2). The model tunings test for C. mopane produced satisfactory outcomes for the current and future scenarios with high AUC scores = 0.941-0.942 (Table 1). These results signified the high reliability of the models in habitat suitability modelling for C. mopane in southern Africa. The most significant variables for the current distribution of C. mopane were solar radiation (relative contribution: 41.8%), Bio12 (annual precipitation - relative contribution: 16.9%), and Bio7 (annual temperature range - relative contribution: 15.9%), contributing to 74.6% of the maxent model (Table 2). In addition, for all the future scenarios, the same variables remained the most influential variables limiting Mopane distribution. Jackknife tests showed that when used in isolation, Solar radiation, Bio12 (annual precipitation), and Bio7 (annual temperature range) had the highest gain and were considered the most informative (Fig. 2). When solar radiation was omitted, the gain was reduced the most, indicating that this variable had most information absent in other variables.

The current distribution models showed that *C. mopane* has a potentially broader distribution in Botswana and lower elevations from approximately 15S to 25S and 11E to 35E (Fig. 3). Besides, the current model's habitat suitability revealed low suitability for *C. mopane* in



Fig. 2. Jackknife analysis of test gain for ten runs of the current distribution model for *Colophospermum mopane*.

Table 1Model performance for *C. mopane.*

Period	AUCtrain	AUCtest	MTSS
Current	0.950	0.941	0.1927
RCP 2.62050	0.949	0.942	0.1830
RCP 4.52050	0.950	0.941	0.1879
RCP 8.52050	0.949	0.942	0.1984
RCP 2.62070	0.949	0.942	0.1860
RCP 4.52070	0.949	0.942	0.1808
RCP 8.52070	0.948	0.942	0.2075

AUC, Area Under Curve; MTSS, Maximum training sensitivity plus specificity.

Lesotho. The simulations mainly covered areas in Botswana and Zimbabwe, with central Zimbabwe, southern Mozambique, northern Namibia, and southern Zambia having the most favourable conditions. Similar high habitat suitability was also observed in northern parts of S. Africa. These high habitat suitability areas correspond with the abundant occurrences of *C. mopane*. Lower habitat suitability for *C. mopane* was observed in Madagascar, although no real observations confirm its presence.

3.2. Future predictions and ranges change

The specifics of the projections differed slightly among the three simulated scenarios for future periods, but their overall behaviour was largely similar (Fig. 4; Table 3). The rates of range loss are greater than the rates of range increase in all scenarios and years. We also observe that the intermediate scenario RCP4.5 had the highest range expansion of 5.65% (72,334.27 km²) and 6.09% (78,027.53 km²) for the 2050s and 2070s, respectively (Table 3). In addition, there is a latitudinal shift in the suitable areas for Mopane in all the predicted scenarios. Specifically, we observe that in the northern limits, potential areas reduce while they increase towards the southpole (Fig. 5). In all scenarios, the potential distribution of Mopane in the western areas, including regions in Angola and Namibia, reduce while they shift Eastwards in Mozambique and Zimbabwe (Fig. 5).

4. Discussion

Correlative and predictive SDMs have frequently been used to produce predictions of potential species richness changes and the influence of climate change on biodiversity. Such predictions have been made for different groups of species across the planet. For example, Thuiller et al. (2005) estimated the potential loss of plant species across Europe to vary between 27% and 42% by the end of the 21st century.

As a result of temporal mismatches between species occurrence localities and current bioclimatic data, assessing SDMs in versatile geographical areas like southern Africa poses a significant challenge for model accuracy. Undeniably, previous studies assessing the distribution

Table 2

Percent contributions (%) of the variables to the distribution of C. mopane according to Maxent Modelling (bold values are the most important variables).

Variable	Description	Current	2050			2070		
			RCP2.6	RCP4.5	RCP8.5	RCP2.6	RCP4.5	RCP8.5
Bio1	Annual temperature	5.8	3.5	3.2	4.5	3.0	5.9	4.3
Bio5	Max temperature of warmest month	7.7	6.5	3.8	5.7	6.8	8.3	8.0
Bio7	Annual temperature range	15.9	16.0	13.2	14.3	16	16.3	13.3
Bio11	Mean temperature of coldest quarter	2.7	2.3	4.3	2.2	2.6	2.5	2.1
Bio12	Annual precipitation	16.9	19.1	24.1	19.1	18.9	15.7	19.1
Bio15	Precipitation seasonality	2.5	1.9	1.0	1.4	1.8	2.0	1.5
Bio17	Precipitation of driest quarter	0.6	0.8	0.7	0.6	0.7	1.0	0.8
Bio19	Precipitation of coldest quarter	1.3	3.6	3.7	4.3	3.7	3.8	4.2
Elevation	Height above sea level (m)	3.3	4.2	3.6	5.0	4.4	3.9	5.6
Slope	The degree of inclination (decimal degrees)	1.5	0.6	0.5	0.7	0.6	0.9	0.8
Solar radiation	-	41.8	41.5	41.9	42.0	41.4	39.6	40.3



Fig. 3. Current potential distribution map of *Colophospermum mopane*. Suitability classification: 0-MTSS = No data; MTSS- 0.3 = Low; 0.3-0.6 = Medium; 0.6-1 = High.

of mopane under different climate change scenarios have traditionally focused on a smaller portion of the mopane's range, such as national parks, rather than its entire distribution (Stevens et al., 2014, 2018). In this study, we used the entire distribution of ranges Mopane in southern Africa, which helped us use most occurrence-environment data while avoiding errors caused by temporal mismatches.

Climate change is a major factor limiting the species' distributions (Parmesan, 2006) and is expected to intensify in the future leading to global warming (Walther et al., 2002). In this study, SDMs were utilized to identify the current and future habitat suitability of *C. mopane*. In estimating *C. mopane* distribution in southern Africa, our SDMs showed considerable results, supported by validation results. AUCs, such as those we obtained (>0.941), are among the highest values for reported models and have high habitat suitability predictive capacities (Elith et al., 2010).

For the current distribution of *C. mopane*, MaxEnt projections showed that this species, in general, occurs in the warm, dry, low-lying regions. Therefore, the MaxEnt models accurately predicted the current species distribution of mopane as it tends to prefer lowland and drier habitats compared to highlands (Burgess et al., 2004; Maquia et al., 2019). Our model predicted high suitability for this species throughout northern and eastern Botswana, southern Zimbabwe, southwestern Mozambique, and northern parts of South Africa bordering Zimbabwe and Mozambique. High habitat suitability was also observed in the northern parts of Zimbabwe bordering Zambia and northwestern Angola. In addition, the current model also detected moderate habitat



Fig. 4. Future climatic projections of *Colophospermum mopane* in the 2050s and 2070s under different RCPs scenarios. Suitability classification, similar to Fig. 2 above; MTSS values are shown in Table 1.

suitability of Mopane in southern Mozambique, southern Namibia, eastern Angola, and southern Zambia. These regions are characterized by extensive miombo strands and savanna ecosystems (Bruschi et al., 2017; Khavhagali and Ligavha-Mbelengwa, 2009). The predicted habitat suitability for Mopane is consistent with previous reports that have assessed the distribution and expansion of Mopane, e.g., in Kruger national park (Stevens et al., 2014, 2018).

Solar radiation, annual temperature range, and annual precipitation contributed considerably to the model of the current distribution of Mopane. Water availability and ambient temperatures are essential factors that support plant growth (Marshall, 1988). However, *C. mopane* has been observed to tolerate low nutrient conditions, moisture pressures, and even disruptions caused by fire, ability to resist drought, and browsing by large herbivores, making the species able to conquer the low-lying regions of southern Africa's savannas (Gandiwa and Zisadza, 2011; Makhado et al., 2014).

Table 3

Loss and gain of suitable areas in southern Africa for *C. mopane* under stringent mitigation (RCP2.6), intermediate (RCP4.5) and high (RCP8.5) greenhouse gas emission scenarios for the 2050s and 2070s.

Scenario	Stable		Range expansion		Range contraction	
	km ²	%	km ²	%	km ²	%
Current	1,281,242	-	-	-	-	-
RCP2.6	1,191,568	93.00	68,978.25	5.38	89,673.72	6.99
2050s						
RCP2.6	1,187,113	92.65	67,500.00	5.23	94,128.44	7.35
2070s						
RCP4.5	1,187,133	92.65	72,334.27	5.65	94,108.47	7.34
2050s						
RCP4.5	1,192,866	93.10	78,027.53	6.09	88,375.26	6.89
2070s						
RCP8.5	1,152,055	89.92	57,152.27	4.46	129,186.90	10.08
2050s						
RCP8.5	1,168,096	91.17	52,218.11	4.08	113,145.90	8.83
2070s						



Fig. 5. Potential changes in suitable areas for *Colophospermum mopane* considering different RCPs in the future. Changes in distribution highlighted in different colors; for Gain (Range expansion)- Red, Loss (Range contraction)-Blue, Unsuitable-Beige, and Stable – Grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mopane grows in a tropical savanna climate with distinct geological and hydrological features that are ideal for the survival of Mopane strands (Moura et al., 2017). As a result, environmental conditions play an essential role in the distribution of Mopane. Previous studies showed that mopane's distribution correlated with humidity levels and temperature (Makhado et al., 2014; Stevens et al., 2014, 2018). Using the niche models, we were able to obtain concurrent research findings, demonstrating that temperature and precipitation can significantly impact Mopane's niche distribution. Notably, since precipitation is a plant growth prerequisite, it may facilitate the growth of Mopane, resulting in the expansion/loss of its natural populations, depending on its availability in the future.

Under climate change, the forecasted loss of potentially suitable areas for C. mopane intensified from best to worst scenario (RCP2.6-6.99% [89,673.72 km²], RCP4.5-7.34% [94,108.47 km²], and RCP8.5-8.83% [113,145.90 km²], respectively) in the 2050s, while in the 2070s, the intermediate scenario (RCP4.5-6.89% [88,375.26 km²]) had the smallest range loss, followed by the stringent scenario (RCP2.6–7.35% [94,128.44 km²]) and the extreme scenario having the greatest loss (RCP8.5-8.83% [113,145.90 km²]) (Table 3). Comparatively, we observe the ranges expansions of mopane having the lowest gains in the extreme scenarios of RCP8.5 (4.46 and 4.08% [57,152.27 and 52,218.11 km²], for the 2050s and 2070s, respectively). Thus, given that C. mopane has a large potential distributional region in southern Africa, it is noted that ideal areas for this species will not adversely change in the coming years (the 2050s and 2070s). Furthermore, it is projected that future excellent potential regions in northern Namibia, northern Botswana, and the region bordering Zimbabwe, South Africa, and Mozambique would not change considerably and will be identical to those of the current period. Previous studies have demonstrated that global climate changes will reduce species ranges in future periods (Bellard et al., 2012; Saiz et al., 2021), with some moving polewards and to higher elevations (Lenoir et al., 2008; Parmesan and Hanley, 2015; Saiz et al., 2021). In the case of *C. mopane*, past studies have shown that its ranges will increase and shift westwards with increases in global warming (Stevens et al., 2018). Similarly, our findings have demonstrated that the habitat suitability of the study species will shift polewards, and parts of the ranges will remain unchanged with climate change.

ENM findings can also help determine a species' physiological tolerances, which, when combined with knowledge of life history, physiological and behavioural characteristics, could help select the most plausible predictions (Escobar and Craft, 2016). As demonstrated in this and other studies, climate change is influencing mopane populations, raising concerns about the future of woodlands in southern Africa (Stevens, 2021). Fortunately, more research is being conducted on the use of species distribution models to predict future distributions of biodiversity under climate change scenarios in diverse African regions.

We choose Maxent because it consistently outperforms other predictive precision approaches, and the program is relatively user-friendly (Merow et al., 2013; Terribile and Diniz-Filho, 2010). It has been widely used to model species distributions since its publication in 2004 (Phillips et al., 2006; Elith et al., 2011). Several experiments have been carried out to compare Maxent's findings with other models, and Maxent has been observed to predict better areas for the use of expert landscape classification than regularized logistical regressions (Dicko et al., 2014) and has been used to forecast the distribution of *C. mopane* in southern Africa (Stevens et al., 2018).

The shortcomings of our research should be noted in this article; i) the data comes from GBIF and online databases, resulting in publication bias; ii), the precision of the geographic coordinates of *C. mopane* we obtained is limited; and iii), the distribution modelling does not take into account other factors influencing local adaptation and microclimates for Mopane. Regrettably, we could not collect complete and up-to-date data on these factors, which should be deliberated in future research.

5. Conclusions

In this study, the distribution of *C. mopane* was assessed using environmental covariates and projected its future distribution under different RCPs using the current data as the baseline data. Our findings indicate that, although *C. mopane* is a semi-arid species at present living at its biological limits (Makhado et al., 2014), it may not be adversely affected by climate change, like other organisms have been shown to (Parmesan, 2006). Even so, this has not always been the scenario. In reality, certain organisms may even be able to respond to shifting local environments by phenotypic plasticity (Donelson et al., 2019). However, most plants are far more likely to shift their range and then go into extinction in response to temperature increases and shifts in rainfall (Dyderski et al., 2018; Williams and Blois, 2018). To introduce the most ambitious adaptation policies proposed by Yalcin and Leroux (2017), we will need accurate estimates of the potential climate change impacts on biodiversity.

Finally, evaluating which climatic factors have the most significant influence on Mopane distribution is critical for supporting suggestions for future conservation management under a climate change context. However, ecological systems are complicated, and a variety of other factors can impact species distributions. As a result, more research is required to refine species ecological behaviour by modelling present and appropriate future habitats, then combining this knowledge with processes like disturbance, as suggested by Stevens (2021).

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Declaration of Competing Interest

The authors declare no conflict of interest.

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