

Nutrient addition effects on tropical dry forests: a mini-review from microbial to ecosystem scales

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Humans have more than doubled inputs of reactive nitrogen globally and greatly accelerated the biogeochemical cycles of phosphorus and metals. However, the impacts of increased element mobility on tropical ecosystems remain poorly quantified, particularly for the vast tropical dry forest biome. Tropical dry forests are characterized by marked seasonality, relatively little precipitation, and high heterogeneity in plant functional diversity and soil chemistry. For these reasons, increased nutrient deposition may affect tropical dry forests differently than wet tropical or temperate forests. Here, we review studies that investigated how nutrient availability affects ecosystem and community processes from the microsite to ecosystem scales in tropical dry forests. The effects of N and P addition on ecosystem carbon cycling and plant and microbial dynamics depend on forest successional stage, soil parent material, and rainfall regime. Responses may depend on whether overall productivity is N- vs. P-limited, although data to test this hypothesis are limited. These results highlight the many important gaps in our understanding of tropical dry forest responses to global change. Large-scale experiments are required to resolve these uncertainties.

Keywords: tropical dry forest, nutrient limitation, ecosystem processes, carbon cycling, decomposition, nitrogen deposition, nitrogen cycling

Introduction

Not only have humans more than doubled the amount of reactive nitrogen (N) entering the global N cycle through industry, energy use, and agriculture (Vitousek, 1994; Galloway et al., 2004), we have also greatly accelerated the biogeochemical cycles of phosphorus (P) and metals (Smil, 2000; Rauch and Pacyna, 2009). While ecosystem processes in the temperate zone are thought to be primarily limited by the availability of N, a wide array of elements including N, P, and sodium (Na) can control tropical forest productivity, decomposition, and tree species distributions (Kaspari et al., 2009; Cleveland et al., 2011; Condit et al., 2013). The high biogeochemical heterogeneity of tropical forests (Townsend et al., 2008) challenges our ability to model ecosystem carbon (C) cycling and forest dynamics under rapidly changing climate and nutrient deposition regimes, and suggests that research from temperate forests may not apply in the tropics.

Ecosystem state factors including climate, parent material, topography, biotic organisms, and weathering affect the absolute and relative availabilities of different elements (Jenny, 1941).

In general, ecosystem processes (e.g., net primary productivity, NPP) are limited by N on geologically young soil substrates, such as recently glaciated soils in the temperate zone or recent lava flows in the tropics (Vitousek, 1999; Reich and Oleksyn, 2004). By contrast, older geologic substrates are depleted of rock-derived elements such as P and cations [e.g., calcium (Ca), potassium (K)]. As a consequence, it is generally thought that tropical forests, which tend to have more highly weathered soils, are primarily limited by P (Walker and Syers, 1976; Chadwick et al., 1999; Cleveland et al., 2011). Indirect evidence tends to support this generalization for tropical wet forests (Cleveland et al., 2011), although stand-level fertilization experiments demonstrate that N, P, and K additions all may influence tropical NPP (Wright et al., 2011; Alvarez-Clare et al., 2013). Additionally, previous land-use practices such as deforestation and burning may lead to N limitation of young secondary forests (Kauffman et al., 1993; Campo and Vázquez-Yanes, 2004; Davidson et al., 2007).

Tropical dry forests (TDFs) comprise more than 40% of the potentially forested area in tropical latitudes (Murphy and Lugo, 1986). In general, these forests have lower annual rainfall compared to moist or wet tropical forests, and experience a 3+ month dry season with little or no rainfall. As a consequence, many dry forest species have unique adaptations to seasonal drought such as deciduous leaf habits and deep roots (Eamus, 1999). Despite their large area, nutrient limitation and biogeochemical cycling in TDFs are relatively understudied (Gei and Powers, 2014). Further, there are reasons to expect that nutrient constraints and responses to anthropogenic nutrient deposition may differ in dry vs. wet tropical forests because of the strong water limitation and seasonally pulsed soil water availability in TDFs (Lambert et al., 1980; Read and Lawrence, 2006).

Here, we review the few studies that investigate how nutrient availability affects ecological processes in TDFs. Because of rapidly increasing rates of N deposition across the tropics (Hietz et al., 2011; Sullivan et al., 2014a), most of the studies included in our review focus on effects of N addition. We develop a conceptual model of how added N affects TDFs; because TDFs may be N- or P-limited, our model considers how responses to N addition may vary between forests with low or high P availability. We compare these hypotheses with what is known about these interactions in TDFs, integrate key lessons from temperate-zone research and draw contrasts with tropical wet forests. Further, when available, we point to studies that measure TDF ecosystem responses to the addition of P or other elements. We conclude by highlighting research gaps and priorities for future research.

Conceptual Model of Nutrients and Ecological Processes in Tropical Dry Forest

Identifying which elements limit ecological processes in TDFs is a high priority for several reasons. First, ecosystem responses to nutrient enrichment and rising atmospheric CO₂ depend upon the identity of the limiting nutrient (Hall and Matson, 1999). For example, N deposition may increase productivity in N-limited forests, but have no effect in a P-limited forest. Second, because rainfall is highly seasonal in TDFs, documenting interactions

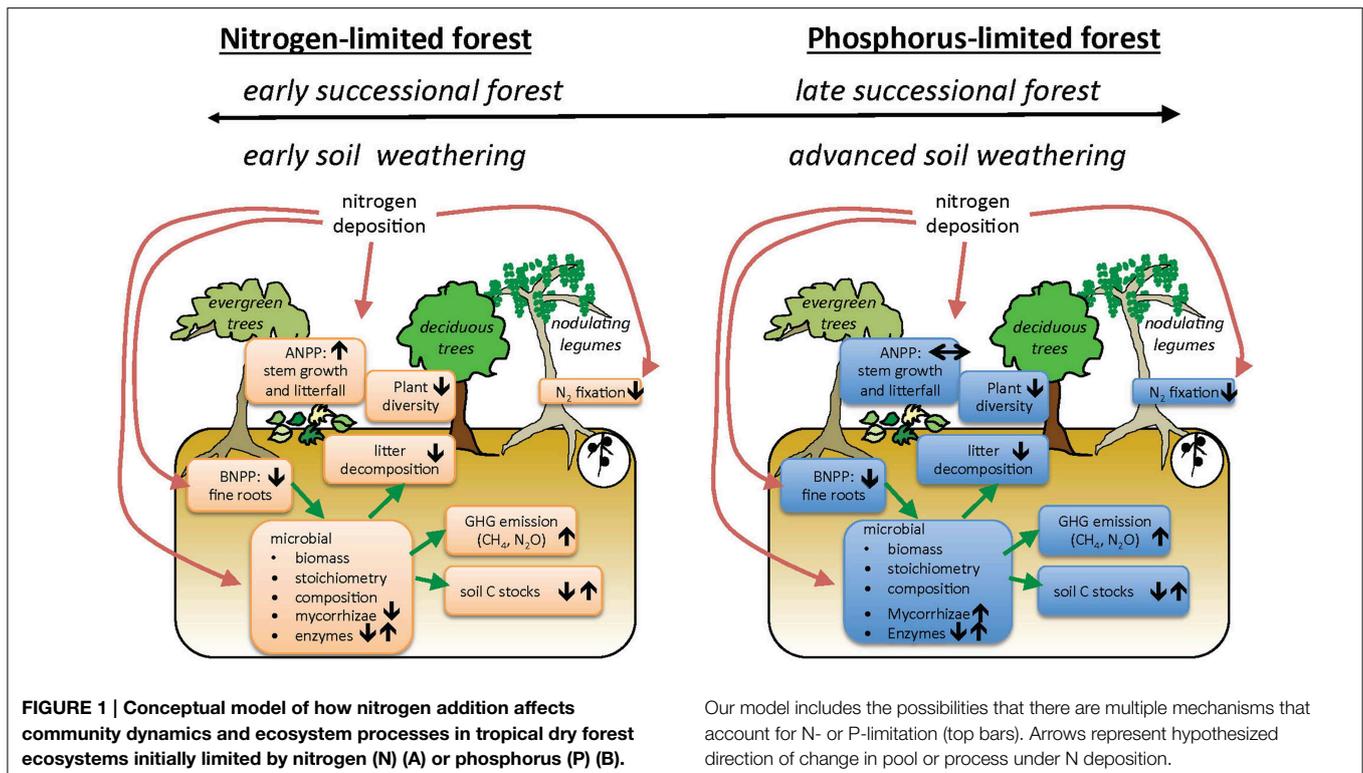
between water and nutrient availability may be crucial to accurately predict ecosystem responses to anthropogenic change. Understanding the relationship between precipitation pulses and element cycling poses a significant challenge for ecosystem modelers (Manzoni et al., 2014), and therefore responses of tropical wet forests to fertilization may not generalize to more seasonal ecosystems. Last, TDFs typically contain trees with diverse phenological strategies, from evergreen to drought-deciduous trees (Eamus, 1999), and these may respond differently to changing nutrient availability.

Our conceptual model of how increasing N deposition may affect key ecosystem processes in TDFs includes multiple levels of organization (**Figure 1**). This model summarizes hypotheses about how N deposition interacts with underlying nutrient limitation to generate a diversity of ecosystem responses. We emphasize here that different plant functional or phenological groups may vary in their responses to N deposition. Furthermore, TDFs are notable for the high abundances and diversity of legume trees that fix atmospheric nitrogen, and theory suggests legumes will be less affected by added N (Hedin et al., 2009). Because available evidence on TDF responses to water and nutrient availability is so limited, we treat **Figure 1** as a set of hypotheses, and throughout the review we evaluate the extent to which current literature for all biomes, and TDFs in particular, supports our conceptual model (**Table 1**).

Communities: Microbial Composition and Function

Because bacteria and fungi mediate soil element cycling, microbial responses to N and P inputs may drive ecosystem-scale responses to nutrient enrichment. For example, resource stoichiometry influences microbial growth rates (Rousk and Baath, 2007), substrate use efficiency (Sinsabaugh et al., 2013), and the production of extracellular enzymes that degrade soil organic matter (Mooshammer et al., 2012). In turn, these microbial traits and processes affect soil C storage (Cotrufo et al., 2013) and the availability of nutrients to plants. Across the globe, the C:N:P ratio of microbial biomass is fairly well-constrained despite substantial variation in the environmental availability of these elements (Cleveland and Liptzin, 2007). Therefore, background nutrient limitation will determine microbial responses to nutrient enrichment in TDF. The addition of limiting nutrients should augment the size and/or growth efficiency of the microbial biomass (Schimel and Weintraub, 2003; Geisseler and Scow, 2014), which in turn may alter soil C storage (Bradford et al., 2013; Frey et al., 2014).

Limited evidence suggests that microbial biomass tends to be more P-limited in tropical soils (Cleveland et al., 2002, 2003; Waring et al., 2013; Turner and Wright, 2014; Warren et al., 2015). Consistent with this hypothesis, P but not N addition increased microbial biomass in a TDF in southern China (Li et al., 2015a). However, because diffusion and osmotic stress constrain microbial growth under dry conditions (Manzoni et al., 2014), nutrient uptake is strongly mediated by water availability. The handful of studies that have examined microbial nutrient limitation in TDF soils report that microbial responses to labile C



(Montano et al., 2007), N, and P (Galicia and Garcia-Oliva, 2004) are dependent upon season and the intensity of plant-microbe competition.

Mycorrhizal fungi deserve special mention. Mycorrhizae live in close symbiosis with plants and their responses to nutrient addition depend partially upon plant nutrient status as well as background nutrient limitation (Treseder, 2004). N deposition decreases arbuscular mycorrhizal biomass in both temperate and tropical forests (Johnson et al., 2003; Treseder, 2004; Camenzind et al., 2014; Krashevskaya et al., 2014; Wurzbürger and Wright, 2015), but responses to N and P addition are context-dependent. Ecological relationships between plants and their mycorrhizae depend both upon soil C:N:P stoichiometry (Johnson et al., 2015) and mycorrhizal type (e.g., arbuscular, ectomycorrhizal, etc). Theory predicts that N deposition may lead to increased mycorrhizal biomass and more parasitic phenotypes under N-limitation and decreased biomass/more mutualistic phenotypes under P-limitation (Johnson et al., 2015). Finally, because mycorrhizae may enhance plant water uptake to different degrees depending on nutrient availability and mycorrhizal type (Auge, 2001, 2004; Lehto and Zwiazek, 2011), any change in mycorrhizal colonization or composition related to nutrient deposition may affect plant water relations during drought, potentially leading to differential feedbacks on evergreen and deciduous species in TDFs.

Communities: Plants

N deposition may reduce plant diversity in a number of ecosystems (Bobbink et al., 2010). While large-scale studies

addressing this in TDFs are rare, a number of seedling pot experiments have tested how particular functional groups respond to increased nutrient availability (Lawrence, 2003). In general, higher N availability enhances biomass and relative growth rates and decreases root: shoot ratios (Huante et al., 1995a; Mendieta-Araica et al., 2013). The response to elevated nutrient availability is higher in light-demanding species compared to shade-tolerants (Huante et al., 1995a), in small-seeded species compared to those with larger seeds (Huante et al., 1995b), in slow-growing compared to fast-growing species (Khurana and Singh, 2004; Tripathi and Raghubanshi, 2014), and in non-legumes compared to legumes (Tripathi and Raghubanshi, 2014). However, not all of these generalizations are consistent among studies.

In field fertilization experiments in TDFs, seedling growth and survivorship in fertilized plots was higher than controls overall, but this effect was species- and site-specific (Salinas-Peba et al., 2014). Additionally, seedling responses tended to be higher for N vs. P addition (Salinas-Peba et al., 2014), suggesting that ANPP may be N-limited, at least for young plants. Fertilization of regenerating TDFs in Mexico led to higher seedling recruitment, survival and growth (Ceccon et al., 2003, 2004), increases in herbivory, and increased leaf P or N content in trees (in young and old sites, respectively) (Campo and Dirzo, 2003). In this experiment, responses to fertilization were higher in young forests with high light availability, but again, these depended on particular species (Ceccon et al., 2003).

Altered nutrient availability may also impact the intensity of interspecific competition, generating shifts in community composition over time. Six years of fertilizing an abandoned

TABLE 1 | List of processes, hypothesized changes under nitrogen deposition in tropical dry forests, and whether this change is supported by the literature, along with key references.

Process	Hypothesized response to nitrogen deposition	Support for hypothesis	Important mediating ecosystem state factors	Relevant literature
Microbial biomass	Increase in N-limited forest/ no change in P-limited forest	P addition increases microbial biomass in TDF more than N	Water availability, plant-microbe competition	Galicia and Garcia-Oliva, 2004; Montano et al., 2007; Waring et al., 2013; Li et al., 2015a
Microbial enzymes	Increase hydrolytic enzymes and decrease oxidative	Supported in wet tropical forests; no data for TDF	Nutrient limitation of microbial biomass	Cusack et al., 2010, 2011
Mycorrhizae	Biomass decreases in N-limited forests/increases in P limited systems	Supported in temperate and wet tropical forests /no data for TDF	Mycorrhizal type, underlying nutrient limitation	Johnson et al., 2003; Treseeder, 2004; Camenzind et al., 2014; Wurzburger and Wright, 2015
Plant diversity	Decrease	Insufficient long-term data from TDF/seedling growth and survival vary with N and/or P addition	Light availability, species traits	Huante et al., 1995a,b; Ceccon et al., 2003, 2004; Khurana and Singh, 2004; Bobbink et al., 2010; Siddique et al., 2010; Tripathi and Raghubanshi, 2014
ANPP	Increase on N-limited soils/no change on P-limited soils	Data are equivocal; results often suggest P and N co-limitation and species-specific responses	Soil age, successional stage	Torres and Franco, 1994; Campo and Vázquez-Yanes, 2004; Campo et al., 2012
BNPP	Decrease	No data for TDF /in savanna, N addition did not change BNPP but PK increased it	Soil age, successional stage	Barger et al., 2002; Li et al., 2015b
Litter decomposition	Decrease	Supported in TDF/P addition increases decomposition and N decreases it	Rainfall regime, plant species	Campo et al., 2007; Powers and Salute, 2011; Anaya et al., 2012; Lv et al., 2014
Soil C stocks	Slow pools increase/fast pools decrease	No N effects but P addition decreased soil C in young TDF, increased soil C in old TDF/ no TDF data on soil C fractions	Mineralogy, ANPP responses, rainfall regime	Gamboa et al., 2010; Bejarano et al., 2014b
Soil N transformations and N ₂ fixation	Decrease N fixation, but accelerate N	Soil N pools and mineralization rates increased with N/ no TDF data for N₂ fixation	Water availability, season, successional status	Erickson et al., 2002; Solís and Campo, 2004; Verma et al., 2013

No empirical data from tropical dry forests is indicated in bold.

pasture with N and P in a highly seasonal region in Amazonia favored the growth of a few nutrient-responsive early-successional tree species, decreasing tree assemblage evenness (Siddique et al., 2010). We hypothesize that higher nutrient availability could impact species composition through similar mechanisms in regenerating TDFs (Figure 1), though there is a dearth of long-term experimental data that can clarify community-wide impacts (Table 1).

Ecosystem Processes: Net Primary Production

Responses of NPP to added N or P indicate whether primary productivity is limited by N, P, or both (Figure 1). Fertilization experiments can also offer mechanistic insight by demonstrating how tree stem diameter growth, litterfall, and fine root

production each respond to increases in nutrient availability. Fertilization experiments that measured ANPP in TDFs after nutrient addition have yielded varied results. A fertilization study in a plantation forest in Venezuela showed no effect of P on wood production (Torres and Franco, 1994), while other studies have demonstrated strong co-limitation of ANPP by N and P (Campo and Vázquez-Yanes, 2004). In the latter study, responses of litterfall to nutrient addition depended upon soil type, underscoring that leaf and wood production may respond differently to element availability. Complicating matters further, the experiment in Mexico also showed that diameter growth responses to added nutrients depended on species identity (Campo et al., 2012).

Belowground NPP results are similarly heterogeneous. A meta-analysis of fine root production across temperate and wet tropical ecosystems showed decreases in fine root production

with increases in N deposition, coupled with an increase in coarse root stocks (Li et al., 2015b). By contrast, a savannah fertilization experiment showed increased fine root production only in plots fertilized with P, and not with N (Barger et al., 2002). While these studies have done much to elucidate how N and P influence NPP, more detailed fertilization experiments in TDF are needed that address interactions between nutrient addition and factors that modify forest responses including succession, edaphic gradients, management, and water availability.

Ecosystem Processes: Decomposition

In general, decomposition rates are mediated by interactions among climate, litter quality, and decomposer communities (Meentemeyer, 1978; Kwabiah et al., 1999). Nutrient addition could affect decomposition via changes in litter chemistry or alterations to microbial community composition or function (Hobbie and Vitousek, 2000; Campo et al., 2012). However, within TDFs litterfall and soil nutrient availability are regulated by intra-annual precipitation events (Anaya et al., 2012), and as a result, decomposition may be primarily limited by water availability (Lambert et al., 1980; Read and Lawrence, 2006).

Plot-scale fertilization with N and/or P changed both litter nutrient concentrations and quantities in a TDF in Mexico, although the magnitude of change depended on forest successional age (Campo et al., 2007) and soil N availability (Campo et al., 2012). This is consistent with evidence that N addition effects depend on the form of added N (Lv et al., 2013), litter chemistry or quality (Kwabiah et al., 1999), and site-specific characteristics such as annual rainfall and soil nutrient availability (Bejarano et al., 2014a). In another fertilization experiment in a seasonal tropical forest in China, added P increased decomposition rates while the addition of N inhibited decomposition (Chen et al., 2013). Lab experiments also find that P and micronutrients accelerate leaf litter decay in TDF, while added N retards it (Powers and Salute, 2011). The mechanisms for why added N decreases decomposition, even in N-limited systems include both biotic and abiotic explanations, and this pattern appears robust across ecosystems (Treseder, 2008).

Ecosystem Processes: Soil Carbon Dynamics

Soils contain the largest terrestrial carbon stock, thus changes to the inputs, outputs, or turnover times of soil organic carbon (SOC) may affect atmospheric CO₂ concentrations and climate (Schlesinger, 1997). Much research has been devoted to understanding how N deposition affects SOC storage in temperate ecosystems (Liu and Greaver, 2010; Lu et al., 2011), and the mechanisms that mediate such changes (Li et al., 2015b). If increased N deposition stimulates plant productivity, inputs to the soil from leaf or root litter may increase. Furthermore, N deposition may also repress lignolytic enzyme activity, causing decreases in organic matter decay rates and enhancing

SOC storage (Eisenlord et al., 2013). Alternatively, changes in nutrient availability may increase root exudation, “priming” the decomposition of organic matter and decreasing soil C storage (Phillips et al., 2011). Understanding the net effects of these processes is further complicated by the fact that SOC is composed of diverse compounds or fractions that vary in turnover times and mechanisms of stabilization (Sollins et al., 1996), and labile, slow, and stable SOC fractions may respond differently to N or P addition (Cusack et al., 2010; Nottingham et al., 2015).

In an experiment in a wet tropical forest, long-term N addition reduced labile SOC pools, corresponding to increased hydrolytic enzyme activity (Cusack et al., 2010, 2011). However, overall slow SOC pools (and thus total SOC) increased, as a function of reductions in oxidative enzymes (Cusack et al., 2010, 2011). By contrast, in a large-scale experiment in 10 and 60-year old regenerating TDF in Mexico, 3 years of P fertilization decreased total SOC in the young, N-limited forest, but increased it in the P-limited older forest, with no significant effects of N or N+P addition (Gamboa et al., 2010). Together with laboratory incubation experiments (Bejarano et al., 2014b), these studies emphasize that the response of SOC in TDFs to N deposition may be complex, and vary according to the nutrient limitation status of plants and soil microbial biomass.

Ecosystem Processes: Nitrogen Cycling

N₂ fixation, N mineralization, and (de)nitrification are all regulated by the availability of N. Evidence from wet forests suggests that legumes down-regulate symbiotic N₂ fixation as soil N becomes more available through secondary succession (Batterman et al., 2013; Sullivan et al., 2014a). Similarly, rates of free-living N₂ fixation in soils and the forest floor may decrease with increasing N availability, as seen in wet forests of Puerto Rico (Cusack et al., 2009). However, water availability may be a more important control on legume nodulation in TDFs (Gei and Powers, 2015), in which case N₂ fixation rates may change little with nutrient addition. A fertilization study in a TDF in India showed that N pools and mineralization rates increased with added N (Verma et al., 2013); however, both nitrogen cycling (Saynes et al., 2005) and nutrient addition effects on N cycling in another TDF in Mexico depended on season and forest successional status (Solís and Campo, 2004). Last, nitric and nitrous oxide emissions should increase under N deposition, particularly during the wet season (Erickson et al., 2002; Wang et al., 2014), and especially from N-saturated or P-limited forests (Hall and Matson, 1999).

Conclusions and Directions for Future Research

Taken together, the evidence on tropical dry forest responses to nutrient availability suggests several robust generalizations (Table 1). First, tree species respond individually to amendments with different nutrients, which likely reflects differences in life history strategies and functional traits. Second, TDF ecosystem responses to increased N or P are context-dependent and are

mediated by ecosystem state factors such as soil parent material, prior land-use history, species composition, and both intra- and interannual variation in water availability.

Our analysis also revealed large knowledge gaps that represent critical directions for future research (Table 1). A major uncertainty in TDF ecology is understanding the extent to which N, P, or other elements most limit productivity, the consequences of nutrient limitation under altered nutrient deposition regimes, and how belowground communities and processes respond (Table 1). Although many methods have been proposed to accomplish this (Sullivan et al., 2014b), the “gold standard” of ecosystem ecology remains large-scale fertilization experiments. Such experiments provide the opportunity to resolve nutrient addition effects and mechanisms across a hierarchy of scales from microbial to trees. Ideally, such experiments could be established along gradients of ecosystem state factors such as annual rainfall (Bejarano et al., 2014a) or forest age (Campo and Vázquez-Yanes,

2004), and in a greater diversity of dry forests including those in India and Africa, which are poorly represented in the literature. Most of the handful of field-scale fertilization experiments in TDF occurred in Mexico. Although these studies have provided valuable insights, establishing similar studies in a range of dry forests is critical if we are to advance our knowledge of TDF responses to global change (Fahey et al., 2015). Moreover, we need to look beyond N and P to the other elements that affect forest processes (Kaspari et al., 2009; Powers and Salute, 2011). Such knowledge is necessary for both accurately representing TDF dynamics in ecosystem simulation models and managing TDF under anthropogenic nutrient deposition.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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