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Current Opinion in Environmental Sustainability

World forests, global change, and emerging pests and pathogens

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Global changes play today an important role in altering patterns of human, animal, and plant host–pathogen interactions and invasive pest species. With rapid development in sequencing technology, there is also an increase in pathogen and pest studies adopting a macroscale, biogeographical perspective, and we present the most recent elements on existing ecological and biogeographical trends. We also compare the results on the one hand on emerging infectious diseases of animals and humans, and on the other hand on plant pathogens and pests. International exchanges of people, animals, and plant products currently contribute to their geographical extension but with notable differences across disease and pest systems, and regions. This review highlights that the subject of pathogens and plant pests, traditionally rooted in agronomic approaches, lacks work on macroecology and biogeography. We discuss the research orientations to better anticipate their ecological and economic impacts in order to better achieve environmental sustainability.

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Abbreviations: Forests, Global changes; Emerging infectious diseases, Pests; Plant pathogens, Deforestation; Emerging threats, Emerging risks

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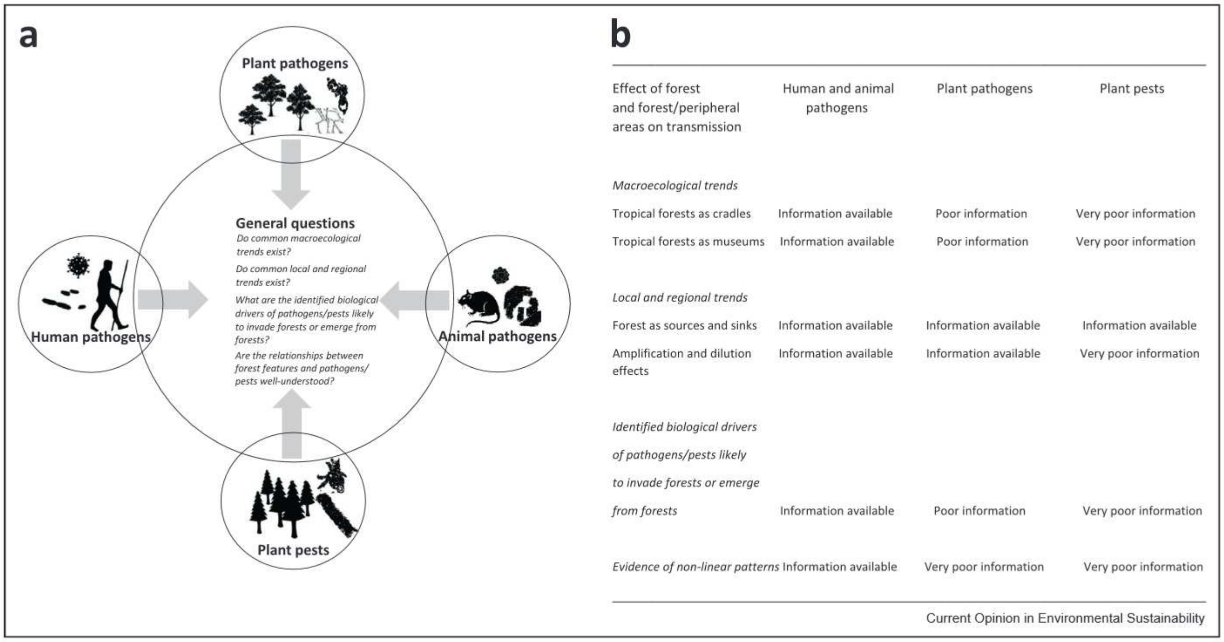
Introduction

According to FAO and UNEP [1], the total cover of the world's forests is 31% (4.06 billion hectares), half still being relatively intact from human disturbances, and more than one-third being primary forest. Forest cover is not equally distributed and five countries, that is, the Russian Federation, Brazil, Canada, United States, and China, harbor more than half of the world's forests. However, worldwide forests are facing increasing anthropogenic disturbances jeopardizing Earth system processes and ecosystem services (e.g. climate regulation through carbon sequestration, habitats for wildlife, water cycle regulation, vital resources for native peoples, and resources for use and trade), and therefore their sustainability as natural heritage [2]. Among disturbances are biological invasions by non-native pests and pathogens, which can have serious impacts on forest ecosystem resilience, productivity, and biodiversity [3]. Forests also shelter a large biodiversity of microbial

Figure 1



Effect of forest and forest/peripheral areas on transmission	Human and animal pathogens	Plant pathogens	Plant pests
Macroecological trends			
Tropical forests as cradles	Information available	Poor information	Very poor information
Tropical forests as museums	Information available	Poor information	Very poor information
Local and regional trends			
Forest as sources and sinks	Information available	Information available	Information available
Amplification and dilution effects	Information available	Information available	Very poor information
Identified biological drivers of pathogens/pests likely to invade forests or emerge from forests	Information available	Poor information	Very poor information
Evidence of non-linear patterns	Information available	Very poor information	Very poor information

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Cross-cutting research questions. **(a)** Illustration of the questions posed in this review that compares the forest-pathogen/pest relationships, and discusses current research findings. **(b)** Comparison of ecological and biogeographical factors for forest ecosystems affecting the emergence and transmission of human and animal pathogens, plant pathogens, and pests. To go further, we recommend reading the following references (e.g. [5] for microbial biogeography, [4,6] for animal and human pathogen macroepidemiology, and [7] for different pathogen systems).

forms and potential insect pests [4]. Therefore, growing forest fragmentation and loss represent a huge risk for global health security, and increasing exposure of forests to human activity might increase the risk of new emerging diseases in plants, animals, and humans in peripheral human-dominated areas [4].

Despite the existence of impact assessments of biological invasions on the world's forests on the one hand, and on the risks of emerging forest-associated diseases on the other hand, attempts to analyze in a comparative approach their both respective and joint impacts are lacking. Here, we explore how disease ecology and biogeography may explain invasion/pathogen-forest trends to identify potential mechanisms that drive biological invasions and disease emergence (Figure 1). Notably, pathogen and pest taxa may vary in their ability to conform to macroecological patterns due to differences in habitats, in taxonomic groups, or to the importance of international trade of their associated hosts. Despite potential comparable drivers and trends, a very distinct tradition and training between disease ecologists, plant pathologists and plant entomologists lead to distinct approaches and perspectives to study environmental sustainability. Because of a lack of macroscale studies for pests and plant pathogens, we conclude by outlining several outstanding questions and recommendations for future studies.

World forests in the tempest: recent evolution and threats

Three major trends characterize the current dynamics of forests. First, primary forests are still being heavily deforested with a loss of 7.3 million ha/year and 5 million ha/year in tropical countries since 2010 [8]. The main reasons are legal and illegal logging to meet the growing demand for wood products, new transport infrastructures, expansion of agricultural land and industrial plantations, and cattle ranching [9]. Accelerated deforestation of the Amazon rainforest has been observed at an unprecedented scale for the first six months of 2022.

The second trend is the increase in natural disturbances as a result of global warming, causing tree dieback and mortality, and new emerging or re-emerging diseases. Drought, storms, fires, and temperature rise can trigger large-scale mortality events and large pest and pathogen outbreaks (mainly bark beetles) that lead to massive tree death. In Europe, disturbance-induced forest mortality amounted to 56 million m3/year in 2000–2010, and an estimated 33 billion tons of woody biomass could be further lost [10].

The third trend is an increase in plantation forests, at a rate of 3–4 million ha/year since the beginning of the century; they are primarily monocultures that are more vulnerable to natural disturbances, biological invasions,

and pest damage [11]. In the tropics and southern hemisphere, planted forests consist mainly of a few exotic tree genera (e.g. eucalyptus) contributing to global spread of exotic pests and pathogens, especially via bridgehead processes.

Forest loss and fragmentation increase pest and pathogen exchanges with human-dominated landscapes

A greater species diversity occurs in tropical regions compared with temperate zones, producing latitudinal gradients for diverse organism groups. For human and animal infections, depending on host and parasite taxa, these large-scale patterns can also be observed [4]. Many of these pathogens are present only in the tropics, mostly embedded into natural rainforest, that is, the endemics or neglected tropical diseases [4]. Others with a currently widespread distribution may also support a tropical origin: zoonotic infections such as HIV-1 and HIV-2 are originating from SIV*cpz* in Central African chimpanzee and plain gorilla, and SIV*stm* in Western African monkey, respectively; the African swine fever virus that remained endemic in Africa affects both domestic and feral swine in Eurasia today. However, global changes have seriously scrambled these patterns by mixing tropical with temperate infectious diseases [4].

Concerning forest pathogens and pests, those trends are less supported by current literature (Figure 1). Although insect species richness follows a latitudinal gradient, biogeographic patterns of herbivorous insects are less clear [12], and invasion by forest pests first depends on the biogeography of their respective host trees. Some aggressive plant pathogens, such as *Phytophthora ramorum* and *P. cinnamomi*, with a putative origin in tropical areas, cause important damages in the temperate ecosystems where they have been introduced. Interestingly, a higher diversity of soil fungi, recognized as plant pathogens, has been reported closer to the equator [13], but controversy exists [14]. The most frequent patterns are movements of exotic insects sharing the same tree genera, notably between North America and Europe, or different regions of Eurasia [15]. There are a few examples of species from tropical regions invading temperate forests. With the increased trade with southern countries and global warming in northern countries, these cases could increase. Macroscale patterns of forest pest and pathogen invasions can also be confounded by the international movement of host trees, such as eucalyptus plantations that have been established on many continents other than native-range Australia.

At local scale, forested landscapes have long been known to be reservoirs and occasional sinks for pathogens and pests. There is evidence of human and animal pathogens moving from the main forest to human populations. Edge habitats surrounding forest patches are known for their increased abundance in arthropods and vertebrate hosts due to ideal breeding or feeding habitat conditions [16]. This creates new opportunities for these organisms to act as bridge hosts, *en route* for mobilizing pathogens present into fragmented habitats to domestic animals and human occupying surrounding habitats [17]. Human activity generally leads to landscape homogenization with biodiversity loss and forest fragmentation. This may affect the dynamics of wildlife disease agents and pests and produce new infections or invasions [18]. Disease ecology studies have shown that biodiversity loss would increase infectious disease burden and risk to humans, that is, dilution effect, but other studies support alternative explanations such as no or an opposite amplification effect [18].

Imported trees for planting are the main pathway of accidental pathogen introduction into new geographical areas [19]. The damaging fungus, *P. ramorum*, native to the East Asian Laurosilva forests [20], was introduced through the ornamental plant industry in restoration projects in California, and to wider forested areas in the United Kingdom [21]. The urban-forest interface is also a hotspot for spillovers; in Europe, nearly 90% of exotic forest insect species were first established in urban and peri-urban areas, and then spread to the surrounding forests [22]. *P. ramorum* shows multiple new pathogen–host associations across its non-native distribution with several reservoir plant hosts that contribute to the ongoing epidemics [23]. The agriculture-forest interface also contributes to plant disease epidemics through spillover from wild to domesticated plants, and/or by providing potential new host–pathogen associations and opportunities for rapid evolutionary responses [24]. Asian soybean rust depends on the alternation of crop and unmanaged vegetation allowing overwintering pathogen survival [25]. Land use change, urbanization, and forest fragmentation can then amplify the role of forested areas as sources of plant diseases. At the same time, increasingly fragmented forests can lead to the exposure of these new areas to plant pathogens.

Insect pest invasions follow the global trend of biological invasions, with an exponential increase [26]. The current rate of new exotic insect species detected per year in forests since 2000 is approximately 6 in Europe, 2 in China [27], and 3 in the United States [14]. Their intentional introduction into forests, mainly through the release of biological control agents, has declined sharply, while unintentional introductions through imported goods and products represent today the main pathway [14]. Particularly, live plants trade and wood materials transport are the main pathways for long-distance introductions [28]. The main functional groups of invasive forest insects are sap and foliar feeders (associated with plants for planting) and wood-boring insects (with wood pieces) [14]. This explains why they are increasingly

coming from Southeast Asia where the majority of goods imported into Europe and America come from [29], a trend similar to that observed for recent human pandemics [30]. The use of budwood for propagation has been also identified as a pathway of introduction for forest pests, and was responsible for the invasion by the Asian chestnut gall wasp *Dryocosmus kuriphilus* in the United States [28].

Which categories of pest species and pathogens/hosts and vectors are likely to invade forest ecosystems and emerge from forests?

Animal and human-emerging diseases share with biological invasions and plant pathogens the same dependence on human activities [31]. Crossing geographic barriers, leading to disease emergence in new areas, results from human or animal dispersal of pathogens [32] and of their hosts, mainly synanthropic species such as rodents and mosquitoes. Pathogen evolution may lead to increased capability to infect new hosts and habitats, even if the impacts of host genetic background on the pathogen post-emergence evolution are still unclear [33]. Human and animal viruses share some characteristics with a high potential for emergence: single-stranded RNA viruses are highly adaptable due to high mutation and evolution rate, and, being shared by multiple vertebrate hosts, the ability to switch to a wide species range [34]. In plant pathogens, interspecific hybridization can generate increased pathogenicity and variability of pathogen responses, such as the hybrid fungus *Phytophthora* x *alni*, an agent of the severe alder decline in Europe [35]. For forest pests, there are no clear data on the intrinsic causes for the emergence of more virulent species, the sudden increase in damage being rather attributable to environmental changes.

A recent meta-analysis recognized other abiotic and biotic drivers of zoonotic disease emergence. Areas with low biodiversity were long thought to favor emergence, but changes of the respective abundances of species in pristine versus human-dominated ecosystems, rather than host richness modifications, need to be better scrutinized [17]. Most zoonotic diseases rely on host species that are dominant in anthropized ecosystems having experienced a strong biodiversity decline, but not in naturally low-diversity habitats [36]. Urban and synanthropic animals harbor less potential human pathogens than previously expected [37], and some animal and zoonotic pathogens have been found to be favored by land use transitions [38]. Rather than clear-cut interfaces between forested areas and human-dominated ecosystems, a continuum of changing ecological conditions seems to favor increasing disease risk and emergence.

Concerning pest biological invasions, at the point of arrival, the likelihood of exotic forest pest establishment increases with forest species diversity at regional scale, because it increases the probability of finding a suitable host tree species [39]. However, consistent with the invasion paradox, the level of damage decreases with increasing forest diversity at the local scale, due to associational resistance [40].

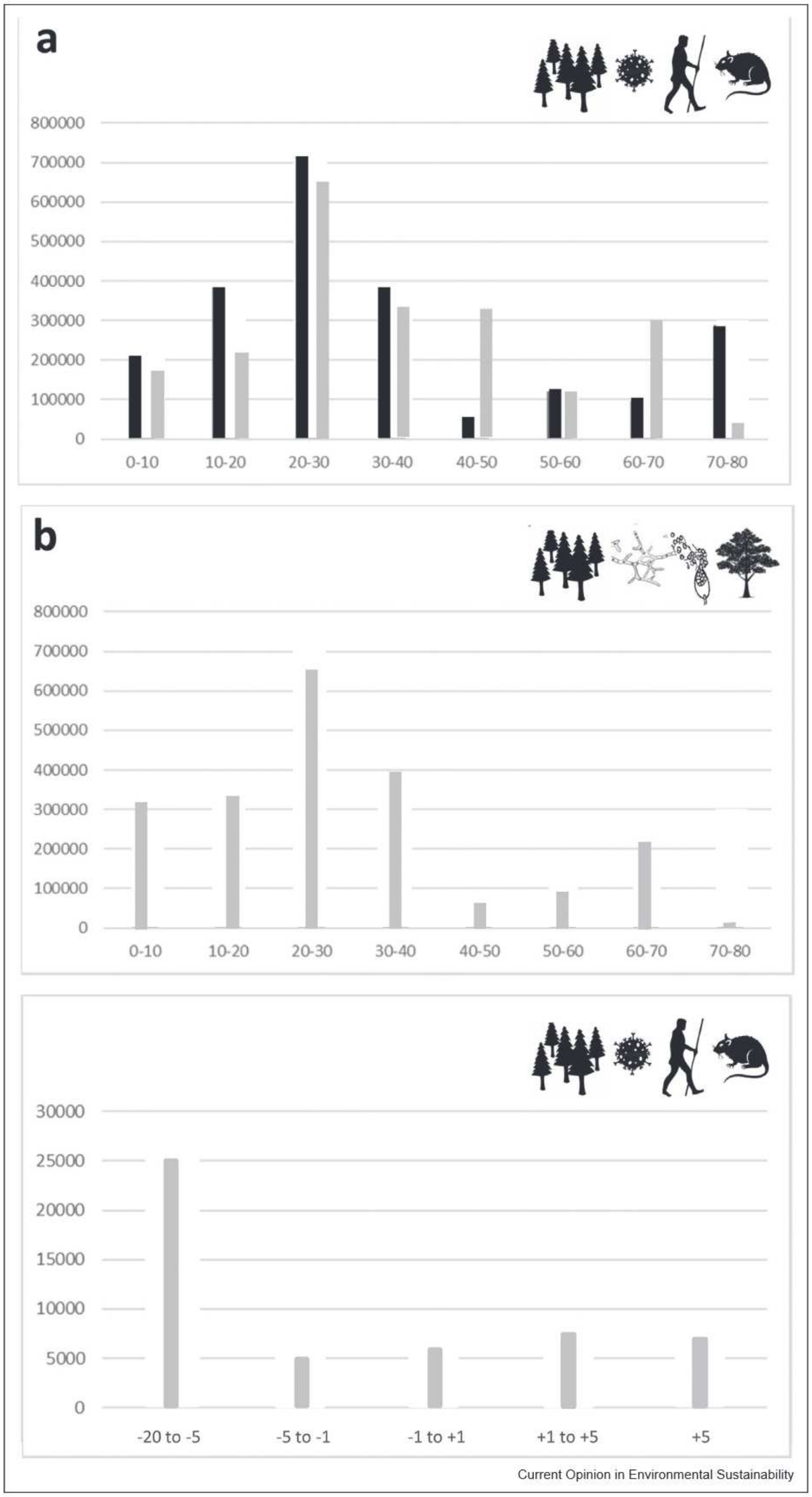
The risk of spillover of alien forest insects depends mainly on the existence of common host plants and the degree of herbivore specialization. The Asian gall wasp has found large host reserves in natural European forests, leading to outbreaks that resulted in a large reduction of production in chestnut orchards. More worryingly, recently several cosmopolitan and highly polyphagous beetle species have been detected worldwide, with exchanges between forest and urban or agricultural environments, such as the Japanese beetle (*Popillia japonica*) or the shot hole borer (*Euwallacea fornicatus*) [41].

The main sources of plant pathogens likely to emerge from forests are poorly explored [42]. Ascomycota fungi are the most frequent group causing emerging forest diseases (70%) followed by Oomycota (21%) in Europe [42]. While ascomycete introduction has continuously increased during the last decades, the rate of introduction of oomycetes has dramatically accelerated since the 1990s in Europe [42]. *Phytophthora* pathogens, presenting high pathogenicity and hybridization rates, typify the pathogen class that will pose the highest biosecurity challenges [43]. Further, root-infecting pathogens are reported in more countries and in more host plant families than foliar-infecting pathogens. Finally, generalist pathogens present higher phytosanitary risk. Two traits have been linked to generalist behavior and might be good predictors of risk: fast growth rates at their optimum temperature and long-term survival for dormant propagules [44].

Forested landscapes — pest and disease relationships are complex and nonlinear

The relationship between changes in forest cover and pest and disease emergence risk is complex, context-specific, and often nonlinear. Landscape configuration may strongly influence pest and disease spillover and spread as demonstrated for human zoonosis (e.g. Ebola virus [45]) and plant pathogens (e.g. Asian soybean rust [25]). Emerging zoonotic and vector-borne diseases do not directly result from deforestation or fragmentation but from a compounded impact of forest loss and spatial distribution of forest remnants. Typically, emerging zoonoses vary with forest cover in a bell-shaped curve

Figure 2



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Disease/pest-forest relationships. **(a)** Number of worldwide epidemic outbreak cases in humans per forest cover percentage per country for years 1990 (black histograms) and 2020 (gray histograms). **(b)** Trend in the number of tree pathogen occurrences. Both outbreak cases in humans and tree pathogen occurrences peak at medium forest cover values. **(c)** Mean number of human disease cases per epidemic outbreak with forest cover evolution between 1990 and 2020. Negative value indicates loss of forest cover, and positive value forest cover gain. Highest mean number of human cases in worldwide outbreaks are present for largest forest cover loss.
(b) Data source from [42]. **(c)** Data for **(a)** and **(c)** from [48] and reinterpreted.

(Figure 2a) because massive deforestation tends to reduce interface zones. Human malaria due to *Plasmodium falciparum* in Brazil, human incidence of zoonotic malaria by *P. knowlesi* in South-East Asia [46], and human cutaneous leishmaniasis in Southern America follow this trend [47]. A similar trend is also observed for tree pathogens (Figure 2b). However, worldwide, human disease risk is the highest for the greatest losses of forest cover between 1990 and 2010 (Figure 2c). Fragmentation of forest landscapes appears to have a negative effect on alien pest richness, suggesting higher establishment in the most forested areas. Nevertheless, an increase in the amount of edges between forests and anthropized environments leads to an apparent increase in exotic species diversity. Once established, the spread rate of invasive forest pests is favored by the connectivity between suitable tree habitat patches but prevented or slowed down by the landscape heterogeneity resulting from unfavorable habitat patches.

By contrast, the recrudescence of human incidence in Lyme disease and other tick-borne diseases in the United States and Europe appears to be related to reforestation and increased wilderness areas. Locally, host biodiversity changes may lead to opposite mechanisms on pathogen cycles, simultaneously diluting and amplifying transmission [36]. Research evidence identifies potential opposite influence of change in forest cover on disease occurrence [46] with a negative effect of the proportion of cleared forest near homes on human outbreaks, but with a positive effect of forest loss at relatively large spatial scales on disease cases [47].

The paradox of the ‘skin of shagreen’ and main recommendations

From the Neolithic period, through the massive deforestation of the 11th century by Cistercian monks in Western Europe and the current deforestation in many tropical regions, world’s forests have slowly shrunk in surface area such as a trickle. Once dominant as ecosystems, they are now threatened.

First, the drivers of pest and pathogen emergence and their spread need to be better understood, and field experiments along forest use gradients will help identify the fine-scale processes behind these threats [49]. Future work should shift from studies on pest or pathogen species to that of functional groups (based on relevant life traits) to provide a more mechanistic understanding of emerging/invasive processes [50]. Ecological traits of human-dominated ecosystems and how social changes can alter ecological networks, transmission modes, and pathways at different spatial and temporal scales should inform the probability to host new pathogens/pests and potential hosts.

Second, sampling effort and bias still remain a major problem. Sample collection, methods, and statistics should be standardized in order to avoid sampled area gaps, under- and overestimation of both taxonomic host groups and microorganisms. Gap trends indicate that effort is less important in tropical regions while they harbor a vast forest domain. In addition, biogeographic studies on forest pests and pathogens on a global scale are needed to verify whether emergence and spread follow the same patterns as animal and human pathogens.

Third, an important question is how forests/human-dominated ecosystem interfaces may favor pathogen diversification and increase pest and pathogen circulation across these landscapes, facilitating spillover into wild and domestic animals, wild and cultivated plants, and humans.

In addition, we should develop long-term longitudinal studies to understand forest and habitat interface pathogen and pest fluctuations due to ecological and evolutionary processes, and the impacts of global changes on these interactions. For example, monitoring selected forest plots, their natural enemies, and also animal and human microbes, in time and space, appears to be of major importance.

Finally, shared international databases of pathogens, pests, and their host species should considerably help decipher which are the host–pathogen and host–pest groups the most sensitive to local and global changes and thus better predict future invasion and spread.

These recommendations provide a roadmap to guide research forecasts of forest-associated human, animal, and plant microbial and pest distributions and spread under global changes.

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CRediT authorship contribution statement

J-FG conceptualized the review paper, and all authors (J-FG, BdT, MGG, and HJ) contributed equally to the writing and editing of the present review.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare having no conflict(s) of interest(s).

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- •• of outstanding interest

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