

Coextinction is magnifying the current extinction crisis, as illustrated by the eriophyoid mites and their host plants

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Review

ABSTRACT

Coextinction is a major and growing threat to global biodiversity. One of the affected groups is the eriophyoid mites (Prostigmata: Eriophyoidea) which are highly host plant specific. They have been described from an enormous range of annual and perennial plants from grasses to giant forest trees. It is highly likely that there are huge numbers of undescribed eriophyoid species in the subtropical and tropical regions which harbor an extraordinary wealth of plant diversity. The global total of eriophyoid species is estimated to be at least 250,000 but it could be much higher. However, the continuing destruction and degradation of natural habitat, especially tropical forests, and climate change, together pose extreme, on-going threats to the eriophyoid mites because of their vulnerability to co-extinction with their host plants. It has been reported that one third of all the Earth's plant species are now at risk of extinction. Together with enormous numbers of other invertebrate species, it is highly likely that many thousands of eriophyoid species are disappearing in the current mass extinction event. Population decline and co-extinction, especially of the invertebrates, are greatly accelerating total biodiversity losses. The termination of habitat destruction and degradation; establishment of large, representative protected areas; restoration of degraded areas; and rapid reduction of fossil fuel use, are urgent tasks. However, the long term conservation of biodiversity can only be achieved through comprehensive social, economic and political reforms across the world that prioritize environmental protection, peaceful coexistence, social justice and the sustainable use of resources.

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Introduction

There is considerable evidence of a major, continuing global biodiversity crisis seen as population declines, extinctions and coextinctions (Dunn *et al.* 2009; Cowie *et al.* 2022). Moreover, the Earth is currently in the grip of the Sixth Mass Extinction (Ceballos *et al.* 2017; Bradshaw *et al.* 2021; Raven and Wagner 2021; Cowie *et al.* 2022). Bradshaw *et al.* (2021) went further in stating that the magnitude of the threats to the biosphere and all its life forms, including humanity, are so great that even experts find it difficult to comprehend.

Coextinction can be defined as the loss of a species, the affiliate, with another species, the host (Koh *et al.* 2004). Nearly 30 years ago, Stork and Lyl (1993) asserted that more importance should be attached to the phenomenon of coextinction of small species dependent on a single host species. Coextinction rates generally depend on two factors, the rate of host

extinctions and the degree of host specificity of the species affiliated with each host species (Koh *et al.* 2004). Coextinction may actually be the most insidious threat to global biodiversity (Dunn *et al.* 2009). Brodie *et al.* (2014) asserted that the numbers of past and on-going secondary extinctions of species are difficult to quantify; many extinctions may have gone unrecognized and others might be inevitable but have not occurred yet. Koh *et al.* (2004) stated that extinction estimates need to include coextinctions to present a realistic picture.

The mites (Arachnida: Acari), which constitute ~ 20% of all the arthropods (Stork 2018), are an extremely large and particularly diverse group. Conservative estimates of the total number of mite species include: 500,000 to 1,000,000 (Walter and Proctor 2013); ~ 1,000,000 (Seeman 2020); ~ 1,250,000 (Sullivan and Ozman-Sullivan 2021) and < 1,500,000 (Stork 2018). Extant mite species reflect the evolutionary plasticity of this extremely diverse group (Krantz 2009a). Most species are much less than 1 mm in length (Walter and Proctor 2013). These two characteristics have enabled the mites to occupy an enormous range of terrestrial and aquatic ecosystems, habitats and microhabitats from the equator to the polar regions, and from the ocean depths to high altitudes (Krantz 2009 a,b; Walter and Proctor 2013; Sullivan and Ozman-Sullivan 2021). Most species are understood to inhabit tropical regions (Walter *et al.* 1998; Basset *et al.* 2012, 2015; Stork 2018). Mites, which are fundamental contributors to global ecological functioning through their participation in energy, matter and information flows (Gwiazdowicz 2021), can be phytophagous, parasitic and predatory, and also consume algae, decaying organic material, detritus, fungi, lichens, microbes, mosses, nectar and pollen (Krantz 2009b).

How are population declines, extinctions and coextinctions related to mites? Cardoso *et al.* (2011) asserted that the full extent of the existing extinction problem is hidden as the vast majority of direct extinctions and coextinctions go unnoticed because they occur within groups of small, neglected organisms as their hosts or partners decline and go extinct. The coextinction of insects with their hosts has been widely reported (Diamond 1989; Stork and Lyal 1993; Koh *et al.* 2004; Dunn 2005; Dunn *et al.* 2009; Fonseca 2009; Colwell *et al.* 2012; Brodie *et al.* 2014; Plein *et al.* 2017; Sanchez-Bayo and Wyckhuys 2019; Cardoso *et al.* 2020; Raven and Wagner 2021). However, the population decline, extinction and coextinction of mite and tick species were first raised as global issues more recently (Koh *et al.* 2004; Mihalca *et al.* 2011; Carlson *et al.* 2017; Napierala *et al.* 2018; Esser *et al.* 2019; Sullivan and Ozman-Sullivan 2021).

Eriophyoid mites (Eriophyoidea) in essentially their current form were reported from amber inclusions associated with fossilized gymnosperms from ~ 230 mya (Schmidt *et al.* 2012). The extant eriophyoid species, which belong to three families, Phytoptidae, Eriophyidae and Diptilomiopidae (Amrine *et al.* 2003), have distinctive morphological, biological and behavioral specializations. They are extremely small, with most species between 0.1 mm and 0.3 mm in length, and are morphologically simplified, including having only four legs (Lindquist *et al.* 1996; Krantz 2009c; Michalska *et al.* 2010; Walter and Proctor 2013; de Lillo *et al.* 2018).

The eriophyoid mites are highly host plant specific; 80%, 95% and 99% of species have been reported from only one plant species, genus or family, respectively (Skoracka *et al.* 2010). Declining populations and extinctions of plant species across the world (Pimm and Joppa 2015; Anonymous 2021; Weisse and Goldman 2021) are fundamental to the problems of global extinction and coextinction, including eriophyoid species; Pimm and Joppa (2015) asserted that one-third of an estimated 450,000 plant species on Earth are threatened with extinction, with extinctions occurring at 1,000 to 10,000 times the natural rate.

In this paper, the subject of the population decline and co-extinction of the highly host specific eriophyoid mites with their host plant species is explored. More specifically, through some direct evidence, a large body of indirect evidence, and also estimations and inferences, the serious, continuing loss of eriophyoid mite biodiversity, especially in tropical environments, through habitat destruction, fragmentation and degradation, and climate change, is detailed.

In addition, measures and actions that can counter these destructive phenomena and thereby dramatically slow the loss of all biodiversity, including the eriophyoid mites, are discussed.

Discussion

Eriophyoid mites – an overview

The eriophyoid mites, which have an extremely wide distribution, have a large range of morphological, biological and behavioural specializations. They are strictly phytophagous and have been reported from a wide range of annual and perennial host plants in numerous families (Jeppson *et al.* 1975; Amrine and Stasny 1994; Lindquist *et al.* 1996; Jovic and Petanovic 2012; Denizhan *et al.* 2015; de Lillo *et al.* 2018; Navia *et al.* 2021; Sullivan and Ozman-Sullivan 2021). Around 80% of the known eriophyoid species are dependent on a single host plant species (Skoracka *et al.* 2010). Eriophyoids are vagrant, gall inducing or refuge inhabiting (de Lillo *et al.* 2018). Vagrant species, which move about freely and mostly feed on leaf surfaces, constitute the majority of the known species (Amrine and Stasny 1994; Oldfield 1996; Denizhan *et al.* 2015; Navia *et al.* 2021, Ozman-Sullivan and Sullivan 2021a). Their short generation time, ability to quickly increase population size and high mobility via aerial dispersal suggest that the eriophyoids evolve at a more rapid rate than other arthropods (Smith *et al.* 2010).

There have been numerous reports of two or more eriophyoid mite species being associated with a single host plant species, and a staggering 20 or more species on some well-studied host species (Amrine and Stasny 1994; Knihinicki and Boczek 2003; Xue *et al.* 2009; Jovic and Petanovic 2012; Elhalawany *et al.* 2021; Navia *et al.* 2021; Sullivan and Ozman-Sullivan 2021; J. Amrine, pers. comm., 16 May 2022). There are at least 4531 valid eriophyoid species in 410 valid genera (J. Amrine, pers. comm., 27 September 2021). Plant diversity is extremely high in tropical environments (Pimm and Joppa 2015; Christenhusz and Byng 2016) so a huge number of undescribed eriophyoid species can be expected to be associated with them (Fenton 2002; Navia *et al.* 2021; Ozman-Sullivan and Sullivan 2021a; Sullivan and Ozman-Sullivan 2021).

The eriophyoid mites include pests of food crops, industrial plant crops and ornamental plants, whereas other species have been investigated for their potential role in the biological control of weeds (Ozman-Sullivan and Sullivan 2021a), with some species having been released for that purpose (Marini *et al.* 2021). However, the vast majority of known species appear to have little obvious effect on their host plants. Parasitic species play critical roles in ecosystems by contributing to biomass flow, the connectivity of food webs and population control, and by driving the evolution of other species (Carlson *et al.* 2020). The eriophyoid mites likely make similar but less obvious contributions to global ecology.

Number of plant species globally

Christenhusz and Byng (2016) reported ~308,000 described vascular plant species worldwide that included ~295,000 angiosperms, ~11,000 ferns and ~1,000 gymnosperms. However, Pimm and Joppa (2015) estimated that there are 450,000 plant species, of which 300,000 are tropical, and 150,000 are at risk of extinction, and that they are going extinct at 1,000 to 10,000 times the natural or background rate.

Estimates of the global total of eriophyoid species

The total number of eriophyoid species worldwide was estimated to be at least 240,000 (Sullivan and Ozman-Sullivan (2021), based on 300,000 potential host plant species (Cowan *et al.* 2006), approximately 80% host specificity (Skoracka *et al.* 2010), and most flowering plant species hosting at least one eriophyoid species (Fenton 2002). More recently, Christenhusz

and Byng (2016) reported ~308,000 described vascular plants worldwide and that ~2,000 new species are being described each year. Using the conservative numbers of 320,000 potential host plant species and a mean number of 0.8 different eriophyoid species / potential host species support an estimate of 256,000 eriophyoid species worldwide. However, that number may be a considerable underestimate because there are tens of thousands of undescribed vascular plant species globally (Pimm and Joppa 2015; Christenhusz and Byng 2016; Corlett 2016; Cazzolla Gatti *et al.* 2022), which would likely add many thousands of undescribed eriophyoid mite species to the total. Based on a high estimate of 450,000 plant species (Pimm and Joppa 2015), the estimated global total of eriophyoid species would be 360,000.

However, numerous reports of two or more eriophyoid species on a single host plant species raise the distinct possibility of a much higher number of eriophyoid species than 360,000. Amrine and Stasny (1994) reported 18, 18 and 15 species of eriophyoids on *Acer campestre* L., *Acer pseudoplatanus* L. and *Juglans regia* L., respectively. The currently known numbers of eriophyoid species on these host plants are: *A. campestre* – 23 species, *A. pseudoplatanus* – 21 species and *J. regia* – 16 species, and another species, *Acer platanoides* L., has 26 species (J. Amrine, pers. comm., 16 May 2022). In addition, Xue *et al.* (2009) reported 189 eriophyoid species from 86 plant species in 71 genera in the family Fagaceae (mean of 2.2 different species / host plant species), including 22 species in 13 genera from *Quercus robur* L., the common oak; 14 species in 10 genera from *Fagus sylvatica* L., the common beech; and seven species from seven genera on *Cyclobalanopsis glauca* (Thunb.). Also, Sullivan and Ozman-Sullivan (2021) listed five cultivated food and beverage plants, namely coffee, longan, mango, sugarcane and tea, which collectively host around 60 species, and Elhalawany *et al.* (2021) reported 21 species from mango trees in nine countries (now 19 valid species, J. Amrine, pers. comm., 16 May 2022). In addition, Navia *et al.* (2021) reported three or more eriophyoid species from each of at least 30 plant species in Brazil. The host plants included a number of species in different genera in the family Arecaceae (palms), including eight species in six genera on the Queen palm, *Syagrus romanzoffiana* (Cham.) Glassman, six species in four genera on the coconut palm, *Cocos nucifera* L., and six species in four genera on *Bactris setosa* Mart. Also from the Southern Hemisphere, Knihinicki and Boczek (2003) reported five species in five genera from *Melaleuca alternifolia* (Maiden & Betch) Cheel (Myrtaceae) in Australia.

New eriophyoid taxa can be easily collected, especially on endemic, rare and non-economically important host plants (Chetverikov *et al.* 2021). A total of 156 eriophyoid mite species in 36 genera was reported from 130 host plant species (mean of 1.2 different eriophyoid species/host plant species) in 42 plant families in Montenegro in south-eastern Europe (Jocic and Petanovic 2012). Basset *et al.* (2015) asserted that the tropical rainforest arthropods are the most diverse group of eukaryotes on Earth. It is highly likely that a large majority of mite diversity, including eriophyoid diversity, inhabits the tropics (Walter and Proctor 1998; Walter 2001; Tixier and Kreiter, 2009; Basset *et al.* 2012; Navia *et al.* 2021; Sullivan and Ozman-Sullivan 2021). A total of 234 species in 92 genera have been reported from 233 host plants in Brazil (Navia *et al.* 2021). However, Brazil is the world's most plant rich nation, with more than 35,000 described native species (Martins *et al.* 2017). This means the eriophyoid fauna of more than 99% of native Brazilian plant species is unknown, and a similar situation applies to other subtropical and tropical environments.

To better estimate the total number of eriophyoid species, a detailed study of the number of species associated with at least five species in each of five genera of a plant family would be informative. Even more helpful in estimating the total number of eriophyoid species would be a detailed study that involved five plant species in each of five genera in five families with distant relationships and conducted across the full extent of their distributions. This type of study is necessary because studies to date have not systematically determined how many eriophyoid species are actually associated with particular host plants across their full range.

Plant extinctions and the coextinction of their dependent eriophyoid mites

The current strong focus on the extinction of species has led to a common and dangerous misunderstanding that the Earth's biota is not immediately threatened but just slowly entering a period of major biodiversity loss. However, the reality is that continuing population declines and range reductions are causing a massive erosion of biodiversity (Ceballos *et al.* 2017). The actual number of eriophyoid species is unknown, but more importantly, in recent times there has been a flood of warnings in biodiversity, climate, conservation and ecology journals about major biodiversity losses. Pimm and Raven (2000) estimated that the clearing of 50% of the total area of tropical rainforests, mostly in recent times, had eliminated 15% of the species that they had harboured. Many of those species were likely to have been the highly host-specific eriophyoids. The clearing of tropical forests for crops, pasture and fuel wood is occurring at alarming rates in Central Africa, Central America, many parts of South America and Southeast Asia, with its effects on insects and other arthropods essentially unassessed (Raven and Wagner 2021).

The tropics lost 12.2 million hectares of tree cover in 2020, of which 4.2 million hectares (35%), an area the size of the Netherlands, was humid tropical primary forests. Primary forest loss was 12% higher in 2020 than in 2019 and the second year in succession that primary forest loss increased in the tropics (Weisse and Goldman 2021). Martins *et al.* (2017) reported that more than 2000 species are threatened with extinction in Brazil alone where a large proportion of the flora is still poorly known. Given the continuing high rate of destruction of subtropical and tropical forests in South America, Central America, Asia and Africa (Raven and Wagner 2021; Weisse and Goldman 2021), the eriophyoid mites are at particular risk of coextinction with their host plants (Sullivan and Ozman-Sullivan 2021).

Recent regional reports and monitoring suggest that insects are in a multicontinental crisis being seen as reductions in abundance, biomass and diversity (Forister *et al.* 2019). Diamond (1989) suggested four main drivers of extinction, namely habitat loss, invasive species, overkill and cascades of extinction and coextinction. Dunn (2005) suggested that two types of extinction might be common for insects but rare for other taxa, namely the extinction of narrow habitat specialists and the coextinctions of affiliates with the extinctions of their hosts. These phenomena are likely to apply to a greater or lesser degree to mites, including the eriophyoid mites (Sullivan and Ozman-Sullivan 2021).

Fonseca (2009) estimated that between 214,000 and 548,000 monophagous insect species are destined for extinction in the global biodiversity hotspots alone because of the reduction of the ranges of their 150,000 endemic host plants. Moreover, Wagner *et al.* (2021) reported that the principal causes of insect declines, which also affect other organisms, are land-use change (especially deforestation), agriculture, nitrification, introduced species, pollution and climate change, and that in local and regional environments, insects are also affected by herbicides, insecticides, light pollution and urbanization. Furthermore, Wagner *et al.* (2021) asserted that multiple causes of decline are occurring simultaneously in areas of high human activity and that is where insect declines are most apparent. The same authors concluded that global insect diversity is currently suffering 'death by a thousand cuts'. There is also growing evidence of the population decline, extinction and coextinction of mites and ticks (Koh *et al.* 2004; Mihalca *et al.* 2011; Carlson *et al.* 2017; Napierala *et al.* 2018; Esser *et al.* 2019; Sullivan and Ozman-Sullivan 2021).

Worsening the threat to all biodiversity posed by the widespread destruction, degradation and fragmentation of habitat in all of its many forms is climate change. Urban (2015) stated that the extinction risk from climate change is accelerating, and Warren *et al.* (2018) modeled the distributions of various taxa under different climate change scenarios and estimated that 6% of invertebrates would lose at least 50% of their ranges with warming of 1.5 °C above pre-industrialization levels.

The ecologies of mites and insects are interconnected in many ways, including phoretic and parasitic relationships, and shared plant and animal hosts, in almost all environments across the

planet (Lindquist 1970; Campbell *et al.* 2013; Baumann 2018; Elo and Sorvari 2019; Seeman 2020; Bartlow and Agosta 2021). This suggests that the wide range of threats to insects outlined earlier in this section are more or less likely to apply to mites, depending on the particular mite group or species in question. Napierala *et al.* (2018) reported that > 40% of the uropodid mite species collected during more than 50 years of sampling across Poland are endangered or critically endangered. Sullivan and Ozman-Sullivan (2021) asserted that it is likely that 15% of all mite species had gone extinct up to the year 2000 and highly likely that at least 150,000 more mite species in host specific relationships with insects and plants in the 36 global biodiversity hotspots will become extinct.

The continuing, direct threat to eriophyoid mite diversity posed by their high level of host specificity is exemplified by a comprehensive recent global study that reported 142 tree species are now recorded as extinct and that ~ 30% (~ 17,500 species) of the planet's tree species are threatened with extinction, including 440 species on the verge of extinction, i.e., with less than 50 individuals remaining (Anonymous 2021). Based on an estimate of 0.8 different eriophyoid species / host plant species, more than 110 eriophyoid species were likely to have been lost with the 142 extinct tree species.

Brazil, which has some of the world's most biodiverse forests, has the highest number of tree species (8,847) and also the most threatened tree species (1,788, ~20%). The other 5 countries richest in tree species in descending order, Colombia, Indonesia, Malaysia, Venezuela and China, collectively have 26,426 tree species, with 5,939 species (~22%) threatened. However, the problem is not restricted to tropical environments; approximately 58% of Europe's native tree species are threatened with extinction in the wild (Anonymous 2021).

Given that tree species constitute less than 25% of all vascular plant species (Christenhusz and Byng 2016; Cazzolla Gatti *et al.* 2022), and the continuing widespread destruction, degradation and fragmentation of habitat and the accelerating impacts of climate change globally, many tens of thousands of eriophyoid mite species are highly likely to be in population decline and committed to extinction, unless a comprehensive set of corrective measures is implemented across the planet. Other groups of host-specific mites are also at a high level of risk, e. g., Beard *et al.* (2014) reported 12 new, apparently host-specific species of phytophagous flat mites (Tenuipalpidae) from she-oak (Casuarinaceae) species in Australia, with up to three species collected from a single host species.

Case studies of eriophyoid mites associated with threatened plant species

The conservation status of the highly host specific eriophyoid mites is extremely difficult to determine directly so is best pursued by inference from the conservation status of their host species. Unfortunately, information on the eriophyoid species associated with threatened plant species is extremely sparse.

A checklist of the known eriophyoid species of Brazil (Navia *et al.* 2021) contains at least five species associated with endangered or critically endangered plants. *Acaphyllisa araucariae* Flechtmann, *Araucarioptes scutifera* Flechtmann and *Tecarus curinomus* Flechtmann (Acari: Eriophyidae: Phyllocoptinae) were reported from the coniferous tree, *Araucaria angustifolia* (Bertol.) Kuntze in Brazil (Flechtmann 2000). *Araucaria angustifolia* is listed as critically endangered on the IUCN's Red List of Threatened Species (RLTS) (Thomas 2013). In addition, *Paubrasilia echinata* is an endemic forest tree of the Mata Atlantica biome in Brazil (Gagnon *et al.* 2020) that is listed as endangered on the IUCN RLTS (Varty 1998). Britto *et al.* (2008) reported *Aceria inusitata* Britto and Navia from *Paubrasilia echinata* (Lam.) (= *Caesalpinia echinata* Lam.) (Fabaceae), and Reis *et al.* (2014) reported *Thamnacus paubrasil* Reis and Navia from the same host.

Measures that can reduce biodiversity loss

Bradshaw *et al.* (2021), in a paper titled ‘Underestimating the challenges of avoiding a ghastly future’, stated that without fully appreciating the existing environmental problems and the enormous range of solutions required, society will not achieve even modest sustainability goals. Within that hugely challenging framework, Raven and Wagner (2021) reported that, to limit the extent of the Sixth Mass Extinction event that we have caused and are currently experiencing, the following steps are necessary: a stable (and almost certainly lower) human population, sustainable levels of consumption, and social justice for the disadvantaged majority of the world’s inhabitants. Sullivan and Ozman-Sullivan (2021) proposed urgent additional measures to conserve the biodiversity contained in the 36 global biodiversity hotspots, the expansion of the protected area estate to improve its representativeness, and prioritization of the maintenance of the biodiversity in the vast areas currently without legislative protection.

Forister *et al.* (2019) concluded that society must address the drivers of declines in insect diversity and abundance while basic and applied research proceeds. Harvey *et al.* (2020) formulated a comprehensive ‘roadmap’ for insect conservation and recovery. The eight actions recommended for immediate implementation included the conservation of threatened species, enhanced restoration and conservation programs, education for awareness and citizen science, avoidance/mitigation of alien species introductions, phasing out pesticide use and reducing pollution in all its forms. These proposed actions are also directly applicable to mites, including the eriophyoid mites, especially given that the ecologies of the insects and arachnids are so intimately intertwined.

Groups promoting mite conservation, directly or indirectly

Ozman-Sullivan and Sullivan (2021b) reported that the newly formed Mite Specialist Group of the IUCN’s Species Survival Commission, through its research, education, advocacy and conservation goals, aims to put mites and their fundamental role in global ecology directly on the international conservation agenda. To achieve the group’s goals, more detailed information on both spatial differences in mite assemblages and anthropogenic threats worldwide is crucial because they underpin the total number of species and their vulnerability to extinction, respectively (Sullivan and Ozman-Sullivan, 2021). Ultimately, to be effective in promoting and achieving the conservation of mites, Mite Specialist Group members must be involved in education and advocacy, if research data is to be translated into local, regional, national and transnational conservation and sustainability outcomes. Moreover, there is already enough information available pointing to habitat destruction and degradation and climate change as the major causes of biodiversity loss, including eriophyoid mites, so education and advocacy need to be at the forefront as research continues.

Across the world, the International Union for Conservation of Nature, World Wildlife Fund, Conservation International, The Nature Conservancy, Botanic Gardens Conservation International, Rainforest Action Network, BirdLife International, Flora and Fauna International, Greenpeace, Saving Nature and The Thin Green Line Foundation, are among the many organizations whose activities complement public biodiversity conservation programs. Furthermore, indigenous communities across the world also make substantial contributions to nature conservation at a fundamental level. These efforts are generally focused on trees and vertebrates but the ‘other 99%’, the invertebrates, including the eriophyoid mites, greatly benefit indirectly.

Conclusions

The eriophyoid mites are a highly evolved, species rich, highly host specific and ecologically important group at the base of complex food webs. Their genetic profiles, morphologies and behaviours reflect their physical, ecological and biochemical interactions with their host plants and relationships with other species associated with those plants through ~ 400 million years.

However, many thousands of eriophyoid species and their hosts are disappearing in the massive, on-going, human-induced wave of population declines, extinctions and coextinctions being experienced across all forms of biodiversity. Binding global, intergovernmental action that terminates habitat destruction, restores degraded areas, stops climate change, and achieves social justice and sustainable communities, is urgently required.

Conflicts of Interest Statement

The authors declare that they have no conflicts of interest with respect to the subject matter of this paper.

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