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Authors: Schweizer, Daniella, and Brancalion, Pedro H. S.

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Research Article

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Daniella Schweizer[1] and Pedro H. S. Brancalion[2]

Abstract

Enrichment planting is a strategy to increase tree diversity and reintroduce desirable species in restored forests, mainly in fragmented landscapes. However, the conditions that improve the performance of enrichment planted seedlings are not yet fully known. Here, we evaluate the role that overstory taxonomic diversity and mean overstory to seedling phylogenetic distance have as predictors of early performance of native tree seedlings planted beneath mixed-species restoration plantations in the Brazilian Atlantic Forest. By applying a phylogenetic approach, our study responds to recent calls for testing the application of such tools in restoration. We planted 12 mid- to late-successional species beneath a mixed-species restoration plantation with three nested tree diversity levels of 19, 58, and 107 species and estimated the mean phylogenetic distance between each seedling species and the overstory community. Seedling performance was not significantly affected by overstory diversity or mean phylogenetic distance. Overall good performance of the seedlings shows that enrichment planting beneath a mixed-species overstory can be successful even under variations in overstory species number and phylogenetic distance. However, significant species-specific differences in performance highlight the importance of an informed selection of which species to enrich plant.

Keywords

enrichment planting, forest restoration, seedling performance, phylogenetic ecology, mixed-species plantings

Introduction

Forest restoration projects have been mostly established in human-modified landscapes, where historical conversion and degradation of natural ecosystems have compromised biodiversity conservation and ecosystem services provisioning (Chazdon et al., 2017; Holl, 2017; Suding et al., 2015). As a consequence of reduced and fragmented forest cover and an intense soil use, natural regeneration potential tends to be limited in agricultural lands (Arroyo-Rodríguez et al., 2017; Crouzeilles et al., 2016; Zermeno-Hernandez, Mendez-Toribio, Siebe, Benitez-Malvido, & Martinez-Ramos, 2015). Under such conditions, mixed species restoration plantations have been promoted to conserve biodiversity and enhance ecosystem functionality (Hulvey et al., 2013; Lamb, 2018; Sapijanskas, Paquette, Potvin, Kunert, & Loreau, 2014).

High-diversity plantations have been particularly recommended for the restoration of certain areas of the Brazilian Atlantic Forest (Brancalion et al., 2010; Rodrigues et al., 2011), where long-term, continuous deforestation left 12% of its original extent as isolated fragments embedded within agricultural landscapes (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Evidence shows that planting a high number of species leads to self-sustainable forests (Rodrigues, Lima, Gandolfi, & Nave, 209), partially due to the mixing of early and late-successional guilds. When

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[1] Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zurich, Switzerland
[2] Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Piracicaba, Brazil

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Corresponding Author:
Daniella Schweizer, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland.
Email: daniellaschweizer@gmail.com

only pioneer species are planted, their early mortality of pioneers can arrest forest succession by allowing invasion of aggressive grasses (Maluf de Souza & Ferreira Batista, 2004).

Despite the planting of a diverse overstory, in some areas, prevailing fragmentation and loss of seed dispersers limits the colonization of restored forests by late successional tree species (Silva & Tabarelli, 2000; Tabarelli, Aguiar, Ribeiro, & Metzger, 2012). In those cases, the understory remains scarcely populated by native tree seedlings (Maluf de Souza & Ferreira Batista, 2004; Rodrigues et al., 2009), showing lower biological complexity, resilience and biomass than native forest remnants (Costa, Melo, Santos, & Tabarelli, 2012; Solar et al., 2015). Poor recruitment in the understory of restoration areas can be overcome by enrichment planting (Bertacchi et al., 2016; Cole, Holl, Keene, & Zahawi, 2011; Lamb, Erskine, & Parrotta, 2005). Enrichment planting consists of the active reintroduction of tree species in the understory of a regenerated or planted forest in a shaded environment created by overstory species (Paquette, Hawryshyn, Senikas, & Potvin, 2009). This technique is useful to introduce species of ecological or economic importance that are not recruiting at the site (Bertacchi et al., 2016; Griscom & Ashton, 2011). But the ecological factors driving the success of enrichment plantings are not yet fully understood.

Overstory composition affects the light environment, the soil nutrients, water availability and determine biotic interactions in the understory, thus playing a major role in determining seedlings' performance in enrichment plantings (Bertacchi et al., 2016; Parrotta, 1995; Schweizer, Machado, Durigan, & Brancalion, 2015). The effects of the overstory on the planted seedlings may be explained not only by its taxonomic composition but also by its phylogenetic relations to the seedling species. Close relatives have been shown to share diseases and herbivores and compete for similar resources due to the conservatism of traits regarding resource use and defense (Gilbert & Webb, 2007; Novotny, Basset, Miller, Drozd, & Cizek, 2002; Parker et al., 2015; Wiens et al., 2010), whereas facilitation among far relatives can aid in their coexistence (Verdu, Gomez-Aparicio, & Valiente-Banuet, 2012). Therefore, seedlings performance is expected to be negatively affected by the presence of close relatives in the canopy (Schweizer, Gilbert, & Holl, 2013).

When aiming to draw practical application guidelines regarding the use of seedlings for enrichment plantings, taxonomic identity becomes a limited variable to employ (Faith, 1992). Understanding the influence of the canopy species on the performance of enrichment planted seedlings using a phylogenetic ecology approach can provide easily applicable, general rules for forest restoration that are especially important in high-diversity tropical forests, where species-specific planting performance information is generally lacking for most species (Brancalion & Holl, 2016). Phylogeny integrates the evolutionary history of traits that drive the ecological dynamics of communities (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009) and can be a useful predictor of restoration success that has not yet been fully embraced in restoration ecology (Hipp et al., 2015; Verdu et al., 2012).

In this study, we evaluated the early performance (i.e., survival and growth) of nursery-grown seedlings of mid to late-successional tree species planted beneath the canopy of restoration plantations with three levels of species diversity. We tested the hypothesis that seedling performance will increase with overstory diversity and mean phylogenetic distance (MPD) of the planted seedlings to the overstory trees. Our premise is that a higher overstory taxonomic and phylogenetic distance reduces the ecological pressure of negative biotic interactions and competition for resources on the seedlings.

Methods

Site Description

The study was conducted in the Anhembi Experimental Station of Forestry, University of São Paulo, located in Anhembi-SP, southeastern Brazil (22°40′ S and 48°10′ W, 455 masl). The climate of the region is mesothermal Cwa (Köeppen) with wet, hot summers and dry, cool winters (Alvares, Stape, Sentelhas, Moraes Goncalves, & Sparovek, 2013). The mean temperature is 19°C and the annual precipitation is 1,170 mm. The soils are sandy (5% silt, 13% clay, and 82% sand) with low nutrient content, characterized as Yellow Dystrophic Latossols (Embrapa, 2006). The study region was originally covered by seasonal semideciduous Atlantic Forest.

Enrichment Planting

The experiment made use of a previously established restoration plantation conducted in 2008 on a former pasture area covered by the exotic grass *Urochloa decumbens* (Stapf) R.D.Webster (Poaceae). Trees were planted in lines on 45-m × 48-m plots with a spacing of 3.0 m × 1.5 m between individual trees (480 individuals per plot). Selected tree species were planted as seedlings in three, nested, species richness levels: 19, 58, and 107 species per plot, four replicates per treatment (Table 1S), hereafter referred as low-, medium-, and high-diversity treatments. Each diversity treatment contained a subset of the species from the previous level, keeping the same proportion between fast- and slow-growing species. All treatments had the same number of individuals; therefore, as the number of species decreased, the number of individuals per species increased. These species were randomly planted along the planting lines.

We selected 12 mid- to late-successional native tree species from a list of available species at two local nurseries to do the enrichment planting. The species selected represent a sample of species commonly employed in restoration plantations in the study region (Table 1). Of the 12 species selected, 5 also occurred as overstory trees. Seedlings were planted in February 2014, when they were between 120 and 180 days old. We randomly placed four 6 m × 13 m subplots beneath three replicate plots in each of the three diversity levels. The subplots were placed 2 m inward from the plot border to avoid immediate edge effects and were separated by 10 m from each other.

We planted a total of 2,160 seedlings along six 13-m long planting lines separated at 1 m from each other in each subplot. We did not add fertilizer or irrigate the seedlings to simulate natural regenerating conditions. We controlled leaf-cutter ants in all sites once after planting by distributing insecticide, sulflurami baits. We assumed that ants would not affect the responses of the experiment because the species controlled (*Atta* spp.) is generalist thus with a wide spatial foraging (Leal, Wirth, & Tabarelli, 2014). We monitored seedling apical growth and survival at 1, 5, 12, 16, and 31 months after planting.

Mean Phylogenetic Distance

We constructed the tree of phylogenetic relations among all the species planted, both in the overstory and as enrichment planted seedlings using the angiosperm phylogeny: R20120829 (available at: github.com/camwebb/). We employed the Bladj algorithm from Phylocom (Webb, Ackerly, & Kembel, 2008) and evolutionary ages published by Wikstrom, Savolainen, and Chase (2001) to estimate the ages of interior nodes and evenly space the nodes between them. Before aging the file, we checked for internal node inconsistencies as recommended by Gastauer and Meira-Neto (2013). An internal node represents a hypothetical common ancestral population and is a point of species diversification (Faith, 1992). We built the phylogenetic distance matrix, which gives the million years that separate each pair of species, among all species pairs using the Phylomatic software implemented in Phylocom. The phylogenetic distances ranged from 26.8 million years (my) for congeners up to 324 my for extra-ordinal species.

Table 1. Seedling Species Planted in the Understory of the Restoration Plantations.

Family	Species	Species code
Anacardiaceae	*Astronium graveolens* Jacq.*	*Astrgr*
Lecythidaceae	*Cariniana estrellensis* (Raddi) Kuntze*	*Caries*
Meliaceae	*Cedrela odorata* L.*	*Cedrod*
Boraginaceae	*Cordia glabrata* (Mart.) A. DC.	*Cordgl*
Lauraceae	*Cryptocarya aschersoniana* Mez	*Crypas*
Fabaceae	*Erythrina verna* Vell.	*Erytve*
Rutaceae	*Esenbeckia febrifuga* (A.St.-Hil.) A. Juss. ex Mart.	*Esenfe*
Bignoniaceae	*Handroanthus chrysotrichus* (Mart. ex DC.) Mattos*	*Handch*
Bignoniaceae	*Jacaranda puberula* Cham.	*Jacapu*
Lythraceae	*Lafoensia pacari* A. St.-Hil.*	*Lafopa*
Rubiaceae	*Simira sampaioana* (Standl.) Steyerm	*Simisa*
Lamiaceae	*Vitex montevidensis* Cham.	*Vitemo*

Note. Asterisk next to the species name denotes their presence also as overstory trees in the restoration plantations (Table S1).

Using the distance matrices, we estimated the MPD of each enrichment planting seedling species to the overstory trees at the plot and subplot scales. However, as results did not differ between the two scales, we report results at the plot scale only. MPD evaluates the average branch length that separates each enrichment planted seedling species to all trees planted in the overstory (Webb, 2000). Branch length is the distance between two nodes in a cladogram in millions of years. The higher the MPD, the further related the overstory species are to that specific seedling species.

There are different phylogenetic metrics that can be employed when linking phylogenetics and community ecology. We chose MPD as it is less susceptible to problems of tree resolution at the tips of the tree than the Mean Nearest Taxon Distance (MNTD) and correlates less with taxonomic diversity than phylogenetic diversity (PD) (Tucker et al., 2017). MPD was significantly different among overstory diversity treatments (Kruskal–Wallis test $X^2 = 84.894$, $p < .0001$) but did not correlate with taxonomic diversity (Figure 1S), thus adding valuable information of the potential effect of evolutionary relatedness between seedlings and overstory species on seedlings performance.

Light Interception by the Canopy

To control for differences in resources availability mediated by overstory diversity differences, we employed data on intercepted photosynthetic active radiation (iPAR) from the work of Melo Duarte (2018). iPAR is the difference between the PAR that reaches the canopy and the amount that passes through the canopy (Nouvellon et al., 2000), thus encompassing the portion of radiation intercepted by the canopy leaves. The higher the intercepting radiation, the less light reaches the seedlings planted in the understory, which could affect their performance.

The iPAR was estimated in each one of the treatment replicate plots in 98 different points established by a 3 m × 6 m grid. In the center of each point the iPAR was measured using a leveled Decagon AccuPAR LP-80 ceptometer held 1-m high. In addition, an identical ceptometer was placed outside the plantations to estimate the PAR that reached the canopy. We employed an average of those points that were closer to the enrichment planted seedlings for an estimate of the light environment directly affecting the planted seedlings. Measurements were taken at the peak of the dry season (August 2015), when iPAR should be lowest due to the deciduousness of many of the overstory tree species, and again at the end of the rainy season (March 2016), when iPAR should be highest. Measurements were taken under clear sky conditions.

Data Analysis

We modeled seedlings performance through time as a function of overstory taxonomic diversity and MPD but checked for the effect of two additional explanatory variables: enrich-planted seedlings identity and light. We modeled survival using the Cox proportional hazards model that allows relating survival of the seedlings through time as a function one of more predictor variables. The Cox model is semiparametric as it does not require a specific distribution of the survival function but does assume that the effect of the predictor variable is constant over time and that they are additive in one scale (Cox, 1972).

We modeled growth through time using linear mixed effect models. We employed the natural logarithm of growth to reduce variance heterogeneity. Plot by treatment, subplot within each treatment, and individual seedling number were used as random factors. We ran models using seedling taxonomic identity as a random factor to extract the effect of taxonomic diversity and MPD. We checked model assumptions by visual inspection of residual plots. *p* values were obtained by likelihood ratio tests comparing the model derived from each fixed factor, and its interaction with time, against the model without the factor. Analyses were performed in R 3.1.1 packages (R Core Team, 2013): “lme4” (Bates, Maechler, Bolker, & Walker, 2014) and “survival” (Therneau & Lumley, 2009).

Results

Over 40% of the individuals planted survived through time. However, there were differences among the species. The species *Astronium graveolens* Jacq. had close to 100% survival probability, while the species *Erythrina verna* Vell. had less than 25% survival (Figure 2S). Neither overstory diversity (Cox coefficient $= 0.075$, $p > .05$, Figure 1(a)) nor MPD (Cox coefficient $= -0.02$, $p > .05$, Figure 1(b)) affected seedling survival. The potential significance of MPD on survival was affected by the very low survival (<25%) of two species at opposite extremes of phylogenetic distance: *E. verna* Vell. had an MPD of up to 205 million years to the surrounding overstory and *Cryptocaria aschersoniana* Mez. had an average MPD of 324 million years (Figure 3S). Species survival was best explained by species identity (Table 2S).

Seedlings grew on average 2.27 cm more with every unit of increase in in phylogenetic distance ($t_{379} = 3.09$, $p = .002$). However, overstory diversity or MPD were not significant predictors of seedlings growth in the model (Table 2). There was a significant, positive, effect of time on seedlings growth, and this effect was different across treatments and along MPD. Increased light in the dry season positively affected seedling growth

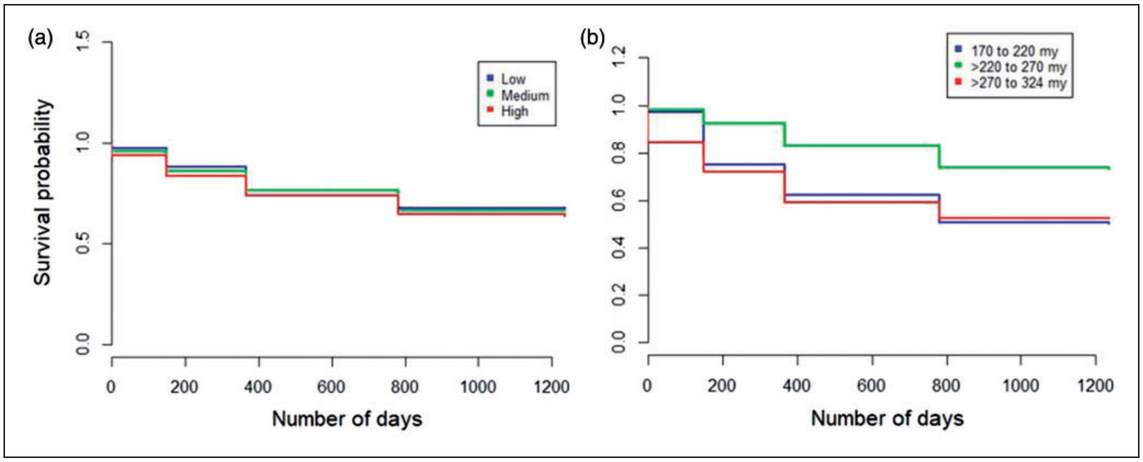

Figure 1. Survival curve of enrichment planted seedlings as a function of (a) overstory taxonomic diversity and (b) MPD.

Table 2. Model Analysis of Variance of Seedling Growth in Response to Overstory Taxonomic Diversity, MPD, Light, and Seedling Species Identity.

	df	*F* value	*p*
Diversity treatment			
Intercept	6798	15,882.5	<.0001
Time	6798	1,788.9	<.0001
Treatment	6	2.4	.17
Time:Treatment	6798	22.6	<.0001
MPD			
Intercept	6799	13,452.00	<.0001
Time	6799	1,802.20	<.0001
MPD	379	0.77	.38
Time:MPD	6799	101.50	<.0001
Light			
Intercept	6798	15,920.50	<.0001
Time	6798	1,790.50	<.0001
Light dry season	1649	4.58	.03
Light rainy season	1649	0.01	.93
Time:Light dry	6798	48.60	<.0001
Time:Light rain	6798	4.40	.03
Species identity			
Intercept	6779	12,918.29	<.0001
Time	6779	2,849.59	<.0001
Species	6779	417.31	<.0001
Time:Species	6779	170.051	<.0001

Note. MPD = mean phylogenetic distance.

(Table 2), but differences in light interception across treatments (Figure 5S) did not make diversity treatment a significant predictor of performance. Seedling growth through time varied depending on the seedling species (Figure 4S). *A. graveolens* and *Esenbeckia febrifuga* (A.St.-Hil.) A.Juss. ex Mart. grew significantly more than the other species, irrespective of overstory diversity or MPD.

Discussion

Overall, the enrichment planted seedlings survived well and overcame in 2014, the driest period of the last 80 years in the region. The seedlings did not suffer from the transplant shock reported for semideciduous tropical forest seedlings planted in unusually dry years (Barajas-Guzman, Campo, & Barradas, 2006). We expect, therefore, that a large portion of these seedlings will be able to recruit to larger size classes and play a relevant role in the future functioning of the restored ecosystem.

Seedling performance was not predicted by overstory taxonomic diversity or phylogenetic distance. We observed a weak positive relationship between MPD and seedling growth that indicates that, as expected, seedlings grew better when the overstory canopy was composed of further relatives. However, this result may be taken with caution as our large dataset inflates the likelihood of a significant response. Relationships between taxonomic and phylogenetic distance and seedling performance is complex. A positive effect of MPD on performance agrees with studies that found that due to competition with close relatives, and the effect of shared enemies, plant species perform best when surrounded by further relatives (Burns & Strauss, 2012; Gilbert & Webb, 2007; Wilson & Stubbs, 2012). In contrast, competition irrespective of canopy species diversity or phylogenetic relatedness may be a stronger factor. A study conducted in a wet tropical forest found a stronger negative effect of overstory trees size than that of phylogenetic relatedness on seedlings first-year survival (Lebrija-Trejos, Wright, Hernandez, & Reich, 2014).

The use of a high number of tree species may have diluted the effect of each overstory species on the performance of the enrichment planted seedlings, thus reducing the importance of enrichment plantings' planning and design based on overstory species diversity or phylogenetic relations for mixed-species restoration plantings. In a previous study conducted in monoculture plantings, we found that enrichment planted seedling performance and foliar health significantly improved the further related seedlings were to the canopy species (Schweizer et al., 2013). The dry conditions of our study area may have reduced the effect of negative biotic interactions. A study by Inman-Narahari et al. (2016) found stronger negative density dependence among seedlings in wet, evergreen, forests than in dry forests. This effect mediated strongly by greater light availability in dry forests can reduce the likelihood of diseases.

Due to the deciduousness of the forest studied, light reaching the seedlings increased in the dry season and positively affected seedlings growth. Research has shown that deciduousness positively influences the seedling community of semideciduous forests (Souza, Gandolfi, & Rodrigues, 2014) as light is a highly influential factor of forest seedling dynamics (Dupuy & Chazdon, 2006). A previous study, conducted also in semideciduous Atlantic Forest restoration sites, found that decreased seedling survival in old restoration sites was driven by reductions in light reaching the understory (Bertacchi et al., 2016).

In temperate forests, canopies composed of a higher number of species have been found to be more complex and capture more light (Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011), thus reducing herb growth and diversity (Chamagne et al., 2016). However, significantly less light interception by the canopy species in the low-diversity treatment did not lead to better performance through time.

The lack of a significant response of seedling performance to changes in overstory diversity levels, MPD, or light interception may have been due to the nested setup of the canopy species diversity treatments: The medium- and low-diversity treatments contained a subset of the species from the high-diversity treatment. Studies have found that a few dominant species can have very large impacts on ecosystem processes (Hooper et al., 2005). If a dominant species remained in all diversity treatments, there may not have been a significant change in the abiotic or biotic environment that affected the performance of the seedlings. For example, the species *Acacia polyphylla* was planted in all three overstory diversity treatments and was the single most dominant species naturally regenerating in the understory of the plots. This species is a pioneer dry forest species that dominates early successional logging gaps (Park, Justiniano, & Fredericksen, 2005).

Time significantly affected the response of the seedlings to variations in overstory taxonomic diversity and phylogenetic distance. Therefore, we expect that with time seedlings in the high-diversity plantation may outperform those in the low-diversity planting as dominant pioneer overstory species leave the system, and biotic interactions become more important (Chazdon, 2014; Norden, Letcher, Boukili, Swenson, & Chazdon, 2012). Density-dependence effects and negative ecological interactions have long been described as key drivers of old-growth forest functioning and diversity (Paine et al., 2012; Terborgh, 2012; Wright, 2002) with phylogenetic distance among coexisting species increasing with succession (Letcher, 2010; Letcher et al., 2012).

In our experiment, seedling taxonomic identity better predicted variations in performance, highlighting the importance of field tests of species performance on a site by sites basis in forest restoration (González-Tokman et al., 2018). Some seedling species performed much better than others. The species *A. graveolens*, for example, had almost 100% survival until the last census, compared with others with less than 25% survival. Aspects of the species life history that lack a phylogenetic signal are important determinants of seedlings performance.

Recent research shows that seedling recruitment is greater below diverse forest canopies than below monocultures (Wills, Herbohn, Maranguit Moreno, Avela, & Firn, 2017). However, the effects of differential canopy diversity mixes may require long-term studies to better understand how the balance between environmental filters, competition, and other negative biotic interactions varies with time across different levels of canopy diversity during understory assembly. However, for the time we conducted our study, enrichment planting proved successful when conducted beneath mixed species plantations irrespective from the loss of certain species in the overstory but that it is important to adequately select seedling species when planning the enrichment planting as some grow faster and survive better than others.

Implications for Conservation

The use of mixed species plantings in forest restoration is an important strategy for reintroducing high levels of taxonomic and phylogenetic tree diversity in fragmented landscapes with reduced natural regeneration potential. In addition, enrichment planting of the restored areas with additional taxa that will not disperse to the area can fill in missing species not naturally recruiting. We showed that tree seedlings planted beneath mixed species canopies had good survival overall and that any differences in performance were more due to species-specific traits and could not be predicted by differences in the overstory taxonomic diversity or phylogenetic distance. Therefore, our study highlights the importance of choosing adequate species to guarantee the success of enrichment planting, regardless of canopy diversity.

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Declaration of Conflicting Interests

The author(s) declare no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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