

Article



Similar Impacts of Alien and Native Tree Species on Understory Light Availability in a Temperate Forest

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Received: 18 September 2019; Accepted: 24 October 2019; Published: 25 October 2019



Abstract: Research Highlights: We evaluated influence of alien and native trees and shrubs on stand leaf area index to basal area ratio, indicating that both groups provide similar amounts of foliage. Background and Objectives: Foliage traits determine tree species effect on understory light availability. Direct comparisons of understory light availability due to different foliage traits of tree species are conducted less often at the stand level. We hypothesized that light availability is driven by canopy leaf area, and alien species contribution to canopy foliage will be similar to native species due to analogous patterns of biomass allocation in tree species. Materials and Methods: We studied forests dominated by alien and native tree species in Wielkopolski National Park (Western Poland). We measured light availability using the LAI-2200 canopy analyzer (Li-Cor Inc., Lincoln, NE, USA) and we calculated leaf area index (LAI) in 170 stands using published models of foliage biomass and data on specific leaf area. Results: Our study confirmed an impact of LAI on light availability in the understory layer. Analyzing the proportion of contribution to stand LAI and basal area (BA) we found that most alien species did not differ in LAI to BA ratio from native species. The exception was Prunus serotina Ehrh., with a LAI to BA ratio higher than all native and alien trees. However, the highest LAI to BA ratios we found were for the alien shrub Cotoneaster lucidus Schltdl. and native shrubs of fertile broadleaved forests. Conclusions: Our study showed that alien species contribution to shading the understory is comparable to native species, with the exception of *P. serotina* due to its dominance in the higher shrub canopy strata where it exhibits different patterns of biomass allocation than native trees. Our study explained that invasive tree species impact on light availability in forest ecosystems is mainly mediated by the increased quantity of foliage, not by more effective LAI to BA ratio.

Keywords: *Prunus serotina* Ehrh.; *Quercus rubra* L.; *Robinia pseudoacacia* L.; foliage biomass; exotic tree; basal area; diffuse non-interceptance

1. Introduction

The main concerns connected with the spread of invasive species result from their negative effects on native ecosystems [1–3]. Such impacts cover both direct growth suppression by competition [4–6] or indirect effects connected with habitat modification [7–9]. For that reason some invasive species are called 'transformers' *sensu* Richardson et al. [10]. Alien trees and shrubs have high environmental impacts on native ecosystems due to their longevity and biomass dominance [11–13]. Impacts of invasive tree species cover include nutrient cycling [14–16], fire regimes [17–19], dependent biota assemblages [20–22], and light availability [23–25].

Light interception by canopy is one of the most important drivers of understory functioning. High light availability determines understory productivity [26–28]. It is also one of the most important drivers of plant species composition [24,29,30], as well as soil biota [21]. It is also crucial for regeneration of canopy species [31–33]. Usually minimum light availability for sapling survival is higher for pioneer tree species than mid- and late-successional tree species [25,34,35]. This value varies light availability under open sky by around 5%–10% [32,36,37].

Despite numerous studies confirming light availability limitation by alien species, few studies compare their influence with functionally analogous native competitors. Most studies on invasive plants focused rather on conditions favoring their establishment than their impacts [33,38,39]. For that reason we aimed to assess how much leaf area index (LAI, m² of leaves m⁻² stand area) determines light availability on the forest floor and whether alien, invasive trees contribute more to canopy foliage area (expressed by LAI) than native species, assuming similar contributions to stem quantity (expressed as basal area, BA, m² ha⁻¹). We hypothesized that (1) light availability is driven by canopy leaf area and (2) alien species contribution to canopy foliage (LAI to BA ratio) will be similar to native species due to analogous patterns of biomass allocation in tree species.

2. Materials and Methods

2.1. Study Design

The study was conducted in Wielkopolski National Park (WNP; Western Poland; 52°16' N, 16°48' E; 7584 ha, mean annual temperature 8.4 °C, mean annual precipitation 521 mm for the years 1951–2010). The WNP covers mainly luvisols (47%) and brunic and haplic soils (30%), while podzols constitute only 7% [40]. We chose the WNP for our study as this is the national park with the highest number of alien trees and shrubs in Poland (158 species; [41,42]). In the WNP we arranged a set of 170 study plots with an area of $150-2000 \text{ m}^2$, with an average of $660 \pm 30 \text{ m}^2$. The area of study plots varied as we aimed to investigate as large an area as possible, but plot area was limited by stand homogeneity. Study plots were arranged in 21 blocks to describe tree stands for natural regeneration studies of three invasive tree species [39,43]. There were nine blocks for Quercus rubra L. and six for Prunus serotina Ehrh. and Robinia pseudoacacia L., with the central part of each block located in a monoculture stand of invasive species. In the center of each block we established a single study plot and then we established additional plots along each of the four sides (north, south, east, and west) at the border of central stand canopies and 30 m from the invasive species stand border. When a stand was homogenous we described the stand covering the border and 30 m from the border zone using one study plot, otherwise we used two study plots (Figure 1). We excluded plots located in non-forest vegetation due to systematic design. Our plots covered wide gradients of resource availability: litter pH ranging from 3.83 to 6.44 and light availability ranging from 0.7% to 25.1% of the open sky [43]. Although our system of study plots was not designed to study effects of invasive trees on ecosystems, we assume that this is an advantage, because systematic design greatly decreases subjectivity of study plot establishment.

In our study we included all tree and shrub species occurring in shrub and canopy layers. In total, we recorded 59 species (Table S1), including 19 alien and four invasive species, according to classification of alien species [44]. These species covered most of the temperate forests of Central Europe, excluding wetland and riparian forests [45]. The study design was developed to cover the most frequent alien species in European woodlands [46], i.e., *P. serotina*, *Q. rubra*, and *R. pseudoacacia*.



Figure 1. Study design: Scheme for a block of experimental plots in the field (each of the 21 blocks is a set of 18 square plots, measuring 100 m² each [43]). Tree stand structure plots (marked by capital letters) are used to describe homogenous tree stands. Vegetation plots (numbers 1–18) were used for light availability measurements.

2.2. Data Collection

Within each stand structure plot (Figure 1) we recorded all trees and shrubs with heights above 1.3 m during August 2014 (9 blocks) and 2015 (12 blocks). We measured all living individuals with diameter at breast height (DBH) \geq 5 cm including bark, whereas we recorded the number of individuals with DBH < 5 cm. To express tree quantities in each plot we calculated basal area (BA, m² ha⁻¹)—a sum of trunk cross-sectional area per plot—for each species over the whole study plot. All individuals were identified at the species level in the field (Table S1). Species nomenclature follows the Global Biodiversity Information Facility taxonomic backbone [47]. For calculation of stand BA and biomass (see details below) we assumed the DBH of trees not measured to be 2.5 cm, as this is the middle point of the non-measured interval (0–4.9 cm). Although this assumption decreases calculation accuracy in comparison with overstory trees reaching large diameters, we considered such bias to have low significance for the total results. For that reason we reported results for two variants, one accounting for all specimens recorded, and one with only specimens with DBH \geq 5 cm (only measured individuals).

To quantify light availability, we measured the canopy openness index (diffuse non-interceptance (DIFN), dimensionless). We measured DIFN in August 2016 within vegetation plots (100 m² each) by using a LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). Within each plot we recorded four series of 10 measurements at the height of 0.5 m above ground, following Machado and Reich [48]. We sampled light availability in August, as our previous studies showed the lowest canopy openness and highest canopy foliage development during this month [24]. Although light availability varies across the growing season [26,28,32], its minimal value has the highest significance for understory vegetation and natural regeneration. Moreover, biomass models are based on samples harvested during full foliage development. For that reason we assumed that both LAI calculation and DIFN will refer to maximum foliage development. We decided to use calculated LAI, as LAI measured by LAI-2200 better reflects light availability than LAI, because it measures amount of diffused radiation

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reaching the lens. Therefore these measurements also cover silhouettes of stems and branches, and do not account for leaves obscured by higher strata of the canopy.

2.3. Data Analysis

We calculated LAI of each species using specific leaf area (SLA, $m^2 kg^{-1}$) and leaf biomass, assuming LAI = leaf area/plot area. We calculated leaf area as a sum of multiplications of tree foliage biomass and SLA. We compiled data about specific leaf area (Table S2) using three main data sources: values from the LEDA database [49], the Botanical Information and Ecology Network (BIEN) database [50], and values provided by Forrester et al. [51]. BIEN and LEDA are databases collecting functional trait measurements, including SLA, while Forrester et al. [47] compiled SLA values for European tree species. These three sources were chosen to provide the most accurate SLA values of species occurring in the study plots. As BIEN included data from LEDA we excluded such observations to avoid redundancy. From the dataset provided by Forrester et al. [51] we excluded trees younger than five years old, as traits of young trees differ from those in the shrub and canopy layers [38,43]. Mean values from the LEDA database were replicated according to the replication number provided in the database, to weight values averaged for species analyzed in our study. We excluded values provided in LEDA for Ulmus laevis Pall., as leaves of this species are morphologically similar to other congeneric species, for which LEDA and BIEN values were around half as high (44.01 m² kg⁻¹ for *U. laevis* versus 19.10 m² kg⁻¹ for *U. glabra* and 24.71 m² kg⁻¹ for *U. minor*). Therefore, for *U. laevis* we used only data from the BIEN database (19.12 m² kg). There were no SLA values for *Crataegus rhipidophylla* Gand. in the searched datasets; therefore we assumed averaged SLA for congeneric species from our database. For Cotoneaster lucidus Schltdl. we assumed SLA of C. acutifolius Lindl, as C. lucidus was assumed to be a subspecies of C. acutifolius [47]. For Populus × canadensis Moench we used the average SLA for the two parental species: P. nigra L. and P. deltoides W. Bartram ex Marshall. Although SLA shows intraspecific variability, especially connected with light availability and canopy position [52,53], interspecific effects are more important in shaping SLA than intraspecific variability [54]. For that reason we assumed that lower levels of intra- than interspecific variability justified usage of SLA values from databases. We also provided SE for averaged values for species, to acknowledge intraspecific variability (Table S2). To calculate foliage biomass we used available allometric models, trying to use those developed in the most similar conditions, due to impact of climate on allometric trajectories [55,56].

We used allometric models to calculate leaf biomass in the tree stands studied (Table S3). When tree dimensions exceeded maximum diameter of sample trees from the dataset used for a particular allometric model by >20%, or no data for a particular species were available, we used the general model for broadleaved trees, provided by Forrester et al. [51]. This problem was noted in single tree species, usually in the top 5% of diameters. In cases when available models only allowed calculation of biomass for younger trees we used two types of models or we used the general model for broadleaved trees, provided by Forrester et al. [51]. For Prunus spp. we used unpublished data from an earlier survey (Jagodziński unpbl., see details in Table S3), even when extrapolating over the range of sample trees, as models provided by Forrester et al. (2017) for Prunus spp. were based on agroforestry systems and North America, where *P. serotina* exhibits lower productivity [57]. Values obtained using unpublished models seemed to be more reliable for understory shrubs than generalized models for *Prunus* spp. based on *P. serotina* [51], which in its native range is usually a tree rather than a shrub [58]. We did not use models provided by Annighöfer et al. [57] as they provided models for foliage biomass for young *P. serotina* only. For some species not reaching DBH > 5 cm we chose to use species-specific models based on root collar diameter [59,60], despite the lack of these measurements. We assumed root collar diameter to be 2.5 cm.

All analyses were performed using R software [61]. We assessed the relationship between DIFN and LAI using generalized additive models (GAMs), implemented in the mgcv package [62]. We decided to use GAMs due to non-normal distributions of independent variables and its non-linear

character, easier to parametrize using splines than curves, which could lead to models breaking the logical assumption of positive values of DIFN. In the model we assumed block of study plots as a random effect to account for dependence of plots connected by study design, assuming plots from the same block might share some variance connected with the locality. To assess the impact of particular species on LAI we divided LAI by BA to obtain information about leaf area per BA unit. We also divided woody species into trees and shrubs, according to their most frequent position in stand vertical structure.

3. Results

Accounting for trees with DBH > 5 cm (trees and taller shrubs) we found that DIFN decreased with increasing LAI (Figure 2a; Table 1). However, above LAI of 5 m² m⁻² DIFN stopped decreasing, reaching a mean value of 0.025. Random effects connected with study design (block system) were negligible. Comparing species LAI to BA ratio we found that among all species studied, *P. serotina* had the highest leaf area per unit basal area (Figure 3). Other species from Rosaceae family, invasive *Acer negundo* L., species usually forming the second canopy level or dynamically regenerating (*Acer* spp., *Ulmus minor* Mill.), and species usually occurring in lower strata of the stand canopy (e.g., *Carpinus betulus* L. or *Corylus avellana* L.) had higher leaf area. The lowest values occurred for species usually dominating the canopy, e.g., *Quercus* spp., *Fagus sylvatica* L., and *Pinus sylvestris* L.



Figure 2. Relationship between diffuse non-interceptance (DIFN) and leaf area index (LAI) estimated using generalized additive models (GAMs; for parameters see Table 1) for trees and shrubs with diameter at breast height (DBH) > 5 cm (**a**) and all trees and shrubs recorded (**b**).

Table 1. GAM describing DIFN based on LAI and block (random effect accounting for study design). Akaike's Information Criterion (AIC) of null model refers to a model with an intercept only, to express final model inertia. SE – standard error, edf—estimated degree of freedom, Ref.df—reference degree of freedom, used for *F* test for *p*-value computation.

Trees and Shrubs with DBH > 5 cm				
Parametric Coefficients:	Estimate	SE	t	p
(Intercept)	0.0439	0.0023	18.7100	< 0.0001
Approximate significance of smooth terms:	edf	Ref.df	F	р
LAI	1.9667	1.9990	38.2800	< 0.0001
random effect (block)	0.0004	1.0000	0.0000	0.4760
Model parameters	R^2	Deviance Explained	AIC	AIC of Null Model
	0.307	31.50%	-692.2	-523.8
All Trees and Shrubs				
Parametric coefficients:	Estimate	SE	t	р
(Intercept)	0.0475	0.0022	21.8200	< 0.0001
Approximate significance of smooth terms:	edf	Ref.df	F	р
LAI	7.6457	8.5370	45.3500	< 0.0001
random effect (block)	0.0000	1.0000	0.0000	0.9650
Model parameters	R ²	Deviance Explained	AIC	AIC of Null Model
	0.695	70.90%	-717.4	-523.8



Figure 3. Distributions of LAI to BA ratio (relation of leaf area to basal area; m^2 of foliage per m^2 ha⁻¹ of basal area) for tree species (alien species bolded and with grey boxes) including only specimens with DBH > 5 cm. Only species occurring in at least five plots were presented. Boxplots indicate the first and third quartiles, the line inside box indicates the median, and whiskers indicate the minimum, and maximum without outstanding observations (>1.5 interquartile range).

Accounting for all trees and shrubs recorded (without DBH > 5 cm threshold) we found that DIFN decreased with increasing LAI (Figure 2b; Table 1). Similarly to the case for trees and shrubs with DBH > 5 cm, DIFN decreased with increasing LAI up to 5 m² m⁻² threshold and then it reached a mean value of 0.025. However, the rate of initial decrease was higher. Random effects connected with study design (block system) were negligible. Comparing LAI to BA ratio we found that shrub species had higher values (Figure 4). Among them we found the highest value for *Cotoneaster lucidus* Schltdl, and then native shrubs of fertile broadleaved forests: *Sambucus nigra* L., *Lonicera xylosteum* L., *Corylus avellana* L. and *Cornus sanguinea* L. Among species which can occur both as trees and shrubs *P. serotina* had the highest leaf area compared to basal area (Figure 4). For tree species we found a similar pattern as in the case of DBH threshold of 5 cm, with the lowest values for *P. sylvestris*. However, *R. pseudoacacia* showed higher LAI to BA ratio than a higher number of species, due to presence of individuals < 5 cm DBH in some study plots.



Figure 4. Distributions of LAI to BA ratio (relation of leaf area to basal area, m^2 of foliage per m^2 ha⁻¹ of basal area) for tree species (alien species bolded and with grey boxes), including all specimens (without DBH threshold). Only species occurring in at least five plots were presented. Boxplots indicate the first and third quartiles, the line inside the box indicates the median, and whiskers indicate the minimum and maximum without outstanding observations (>1.5 interquartile range). Note log-transformation of x axis.

4. Discussion

4.1. Drivers of Light Interception by Canopy

Light interception by forest canopies is driven by different features describing foliage: its vertical distribution, biomass quantity, and allocation, as well as leaf traits. Leaf distribution across strata in tree stands is determined by canopy dominant light transmittance. The most frequent tree species in the study area—*P. sylvestris*—has loose crowns, allowing higher light availability beneath its crowns than the other species [24,63,64]. Similarly, a small LAI to BA ratio for *P. sylvestris* in mature tree stands was reported by Bauer [65]. For that reason its stands are usually occupied by dense shrub layers, including invasive species [66]. For species with higher light interception, e.g., *Q. rubra* and *F. sylvatica*, presence of shrub layers is least developed. Different proportions of tree species in the main (highest) canopy layer determine overall light availability at lower forest strata [30]. For that reason forests with dominance of light-transmitting species in the overstory have more developed shrub layers, which also determines lower light availability at the forest floor. However, in stands with well-developed both canopy and shrub layers, increasing LAI does not decrease DIFN, because light availability is vertically stratified—more than one layer of leaves covers open sky.

Quantity of foliage biomass depends on tree dimensions, according to metabolic scaling theory [67,68]. However, the exponent of this relationship is size-dependent, as more biomass is allocated to stems in larger trees [69]. Despite decreasing allocation, foliage biomass increases with stand age [51,55,70]. In older stands, due to self-thinning and years of light competition, more gaps provide more light into the lower strata [71,72]. Lower trees and shrubs have lower total biomass, and therefore higher biomass allocation to foliage [60,69,73]. For that reason we found the highest LAI to BA ratios in shrubs and the lowest in trees.

Leaf area in the canopy layer also depends on leaf architecture and functioning. The wide range of SLA shows that for trees similar leaf mass might differ in area up to one order of magnitude [52,74]. This trait reflects plant strategy of facing limited resources and life span, as well as investment in foliage development [74]. Although SLA varies with climate [75,76], light availability [38,43,77], and growing season [78], interspecific variation is higher than intraspecific [54]. Therefore, each tree species LAI to BA ratio is also dependent on leaf morphology, compromising species-specific evolutionary legacies [79].

4.2. Impacts of Alien Species

We found the highest LAI to BA ratio in *C. lucidus*, a species coming from Central Asia. This species is known as a naturalized, potentially invasive species in Poland [44], a casual neophyte in Czechia [80], and as naturalized in Armenia, Canada, Finland, Latvia, Norway, Russia, Sweden, the United Kingdom, and the United States [81]. This species is known for creating dense stands which decrease the richness and abundance of native species [82,83]. The cited authors suggested that the mechanism of negative impacts might be limiting of light availability, however, they did not provide a quantitative assessment. In the study area *C. lucidus* had limited distribution—we found it only in one of the study blocks, but with high abundances. Due to its ability to be bird-dispersed [83], a risk assessment is highly needed [84] for this species, which might cause more severe impacts than the currently most frequent invasive species.

Our study showed different impacts of four main invasive tree species. *P. serotina* revealed the highest LAI to BA ratio. This species, which in Europe usually has the form of a shrub or small tree [57,58], is able to dominate lower strata of forest ecosystems [85–87]. Similar to our results, a twice higher leaf area index of *P. serotina* than *P. sylvestris* was also reported from forests in Belgium [88]. This influence gives *P. serotina* an impact, especially high in cases of changing species composition of understory vegetation [89,90]. As young regeneration of *P. serotina* requires light to grow [39,86,91], decrease of light availability would stop further invasion of *P. serotina* beneath already invaded canopies. However, due to vegetative regeneration, as well as high number of seedlings able to survive in less-suitable conditions for a few years [39,91,92], it is able to develop a persistent sapling bank [87].

Although impact of *P. serotina* on LAI is lower than impact of native shrubs, this species is able to reach higher BA, making its quantity the most important driver of light availability modification.

Another invasive species with relatively high LAI to BA ratio is *A. negundo*. This species has high SLA, which is helpful in invading pioneer vegetation of riparian forests [93,94]. This species is mid-successional, which allows it to take advantage of release opportunities from forest disturbance in riparian ecosystems [93,95,96]. However, it was not frequent in the ecosystem studied here, as riparian forests were not frequent.

Although we expected higher LAI to BA ratios of two invasive trees—*Q. rubra* and *R. pseudoacacia*—they did not reveal such a pattern. Despite studies from other regions where N-fixing species have high impacts on light availability [97], a similar invasive tree (*R. pseudoacacia*) did not reveal any pattern of increased leaf development. This might be connected with its life form—mainly dominant in the canopy layer, as well as biomass allocation patterns—*R. pseudoacacia* in stands has rather loose crowns. This speculation might be confirmed by increasing LAI to BA ratio when accounting for all specimens. As *R. pseudoacacia* can be abundant in the shrub layer, this might increase leaf area in a forest ecosystem and provide more severe impact on light availability than mature trees, transmitting more light into the understory. The latter is manifested by high understory species richness in *R. pseudoacacia* stands [98–100], both due to nitrogen fixation and allowing a sufficient amount of light to the forest floor. For *Q. rubra* we found higher LAI to BA ratio than for native oak species. However, the difference was very small, and might be connected with higher growth rate of *Q. rubra*. The difference between *Q. rubra* and *Q. petraea* (Matt.) Liebl. (more frequent in the study area than *Q. robur* L.) might be driven by SLA differences (11.52 and 15.46 m² kg⁻¹, for *Q. petraea* and *Q. rubra*, respectively).

4.3. Sources of Uncertainty

Our study was based on leaf area index calculated using models for biomass estimation and the trait reflecting leaf area per mass. Therefore, uncertainty connected with biomass estimation and SLA variability might bias the results. The main source of potential bias is lack of species-specific allometric models for a number of species. Despite wide interest of forest science and developing >1000 models [51,101], some species are not covered by tree-level models, or are covered over a limited range of DBH. Especially in case of shrubs, modeling their biomass is very challenging [73]. This forced us to use generalized models, which did not account for species-specific patterns in biomass allocation and crown architecture, which is crucial for estimation of foliage biomass. Also, we used averaged SLA, which according to data collection guidelines [102] accounts for the sunny part of the tree crown, usually with lower SLA than shaded leaves [53,103]. This might underestimate the total leaf area.

5. Conclusions

Our study demonstrated that different tree species shape light availability on the forest floor via leaf area index. Comparing LAI to BA ratio, we found that the most common tree species in the Central European lowlands (*P. sylvestris*) provides the lowest amount of leaf area per unit basal area. Our study showed that the contribution of alien species (including the very frequent *Q. rubra* and *R. pseudoacacia*) to shading the understory is comparable with native species, with the exception of *P. serotina* due to its dominance in the higher shrub canopy strata where it exhibits a pattern of biomass allocation different than native trees. Accounting also for shrubs and trees with DBH < 5 cm, we found that native shrubs and alien *C. lucidus* have much higher LAI to BA ratio than alien tree species, including *P. serotina*. The latter prefers occurrence in *P. sylvestris* stands, where it can develop beneath loose crowns of *P. sylvestris*, with low LAI. Our study suggests that the impact of invasive tree species on light availability in forest ecosystems is mainly mediated by the increased quantity of foliage, not by a more effective LAI to BA ratio.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/11/951/s1, Table S1: List of species present in study plots, allometric models used for foliage biomass estimation (Table S3), and alien status; Table S2: Mean + SE values of SLA obtained from databases for species present in study plots; Table S3: Allometric equations determining foliage biomass of particular tree species recorded on the study plots.

Author Contributions: Conceptualization, M.K.D. and A.M.J.; methodology, M.K.D. and A.M.J.; data collection and formal analysis, M.K.D.; data curation, M.K.D.; writing—original draft preparation, M.K.D.; writing—review and editing, A.M.J.; supervision, A.M.J.; funding acquisition, M.K.D. and A.M.J.

Funding: The study was financed by National Science Centre, Poland, under the project no. 2015/19/N/NZ8/03822 entitled: 'Ecophysiological and ecological determinants of invasiveness of trees and shrubs with the examples of *Padus serotina, Quercus rubra* and *Robinia pseudoacacia*'. MKD received a doctoral scholarship from National Science Centre, Poland, under the project no. 2018/28/T/NZ8/00290.

Acknowledgments: We are grateful to Lee E. Frelich (Department of Forest Resources, University of Minnesota, USA) for linguistic revision of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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