Common pathways by which non-native forest insects move internationally and domestically

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Abstract

International trade and movement of people are largely responsible for increasing numbers of non-native insect introductions to new environments. For forest insects, trade in live plants and transport of wood packaging material (WPM) are considered the most important pathways facilitating long-distance invasions. These two pathways as well as trade in firewood, logs, and processed wood are commonly associated with insect infestations, while "hitchhiking" insects can be moved on cargo, in the conveyances used for transport (e.g., containers, ships), or associated with international movement of passengers and mail. Once established in a new country, insects can spread domestically through all of the above pathways. Considerable national and international efforts have been made in recent years to reduce the risk of international movement of plant pests. International Standards for Phytosanitary Measures (ISPMs) No. 15 (WPM), 36 (plants for planting), and 39 (wood) are examples of phytosanitary standards that have been adopted by the International Plant Protection Convention to reduce risks of invasions of forest pests. The implementation of ISPMs by exporting countries is expected to reduce the arrival rate and establishments of new forest pests. However, many challenges remain to reduce pest transportation through international trade, given the ever-increasing volume of traded goods, variations in quarantine procedures between countries, and rapid changes in distribution networks. It is therefore likely that many more human-assisted invasions of forest insects will take place. New geographic expansions by natural modes are also made possible due to changes in host distribution and/or climate.

Keywords

Biological invasions
Global change
Globalization
Invasion pathways
ISPM
Phytosanitary policy

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Key message

- Rapid increases in globalization and international trade have inadvertently led to higher arrival rates of non-native forest insects in countries worldwide. Forest insects can be transported to new countries via several pathways including trade in live plants, wood-based items, hitchhiking on non-wood items and in international mail, or movement by natural dispersal.
- We review several important pathways that contribute to pest introductions to new areas, focusing on forest insects and their associated phytosanitary policies.

Introduction

Increasing international trade and globalization have led to increasing risk of non-native organism introductions via sea, air, and land pathways (Levine and D’Antonio 2003; Brasier 2008; Westphal et al. 2008; Hulme 2009; Seebens et al. 2017). The vast majority of international trade is carried by ships (IMO 2012). Since 1980, world maritime freight trade volumes have grown about threefold, to reach about 10 billion tonnes in 2015 (UNCTAD 2017). Air transport volumes are much lower, with about 50 million tonnes of air cargo transported annually (ICAO 2016). Passenger flights have also witnessed a very strong increase, approximately 400-fold between 1945 and 2015 (IATA 2017). Each year, about 35 million flights transport 3.5 billion passengers over a network of about 51,000 routes, which are predicted to double again by 2035 (IATA 2017).

In this context, historical accumulation curves of non-native species introductions show no sign of saturation (Brockerhoff and Liebhold 2017; Seebens et al. 2017), highlighting that improved phytosanitary practices struggle to stem the increase in pathway volumes (Saccaggi et al. 2016). This situation is also worsened by the concurrent increasing domestic movement of goods and people which can contribute to range expansion of both native and introduced species (Rassati et al. 2018). Transport data from the Organisation for Economic Co-operation and Development (OECD) show that road and rail are predominant modes for both freight and passenger transportation in most countries (ITF 2017).

Insects are particularly prominent invaders of new environments worldwide (Liebhold et al. 2016), with most being easily transported unintentionally by international movement of goods and people. Compared to other modes of transportation, shorter travel times over long distances lead to increased risk of moving live organisms between continents. Thousands of forest insect species have invaded new areas (Aukema et al. 2010; Liebhold et al. 2017) with some causing massive ecological and economic impacts. For instance, emerald ash borer (*Agrilus planipennis*; Buprestidae) introduced to North America from Asia in the 1990s has killed millions of ash trees (*Fraxinus*) with economic impacts in the billions of dollars (Kovacs et al. 2011; Haack et al. 2015). In comparison, few beneficial insects are introduced to new areas (Brockerhoff and Liebhold 2017). These are generally pollinators and biocontrol agents established intentionally (Donovan 1980; Kenis et al. 2017).

International movement of live plants and wood packaging material (WPM) are considered the most important pathways for forest insect invasions (Brasier 2008; Liebhold et al. 2012; Eschen et al. 2015a). Many other insects travel as hitchhikers without infesting commodities or packaging directly, but rather being transported on the cargo or within the "vessels" used for conveyance, such as packaging, shipping containers, ships, aircraft, vehicles, and machinery (Toy and Newfield 2010). In this paper, we discuss these and other pathways that facilitate entry or spread of insects both internationally and domestically, including trade in logs, firewood, processed wood, passenger baggage, and international mail. We also consider natural modes of geographic expansion by active dispersal or passive transportation.

Live plants, cuttings and seeds

Importation of live plants is an important pathway for the introduction of non-native insects (Smith et al. 2007; Brasier 2008; Hulme et al. 2008; Roques 2010; Liebhold et al. 2012). Live plants are often referred to as "plants for planting" (FAO 2011), imported in many forms including rooted and unrooted plants for retail and propagation, bonsai, bulbs, and budwood, which are dormant cuttings for propagation (Liebhold et al. 2012). Cut flowers, ornamental foliage, and seeds, which are also transported in large volumes, are additional potential pathways for forest insects but will not be addressed in detail here (Areal et al. 2008; Auger-Rozenberg and Boivin 2016; Lee et al. 2017).

The most common forest insects moving on "plants for planting" are Homoptera and Thysanoptera (Roques and Auger-Rozenberg 2006; Liebhold et al. 2012; Tables 1–2; Fig. 1). Pests in many other orders move on live plants, including Coleoptera [e.g., *Anoplophora chinensis* (Cerambycidae, citrus longhorned beetle; Haack et al. 2010a), *Callidiellum rufipenne* (Cerambycidae, Japanese cedar longhorned beetle; Cocquempot 2007), *Xylosandrus morigerus* (Scolytinae, brown twig beetle; Kirkendall and Faccoli 2010], and Lepidoptera [*Epiphyas postvittana* (Tortricidae, light brown apple moth; Venette et al. 2003)].

Table 1

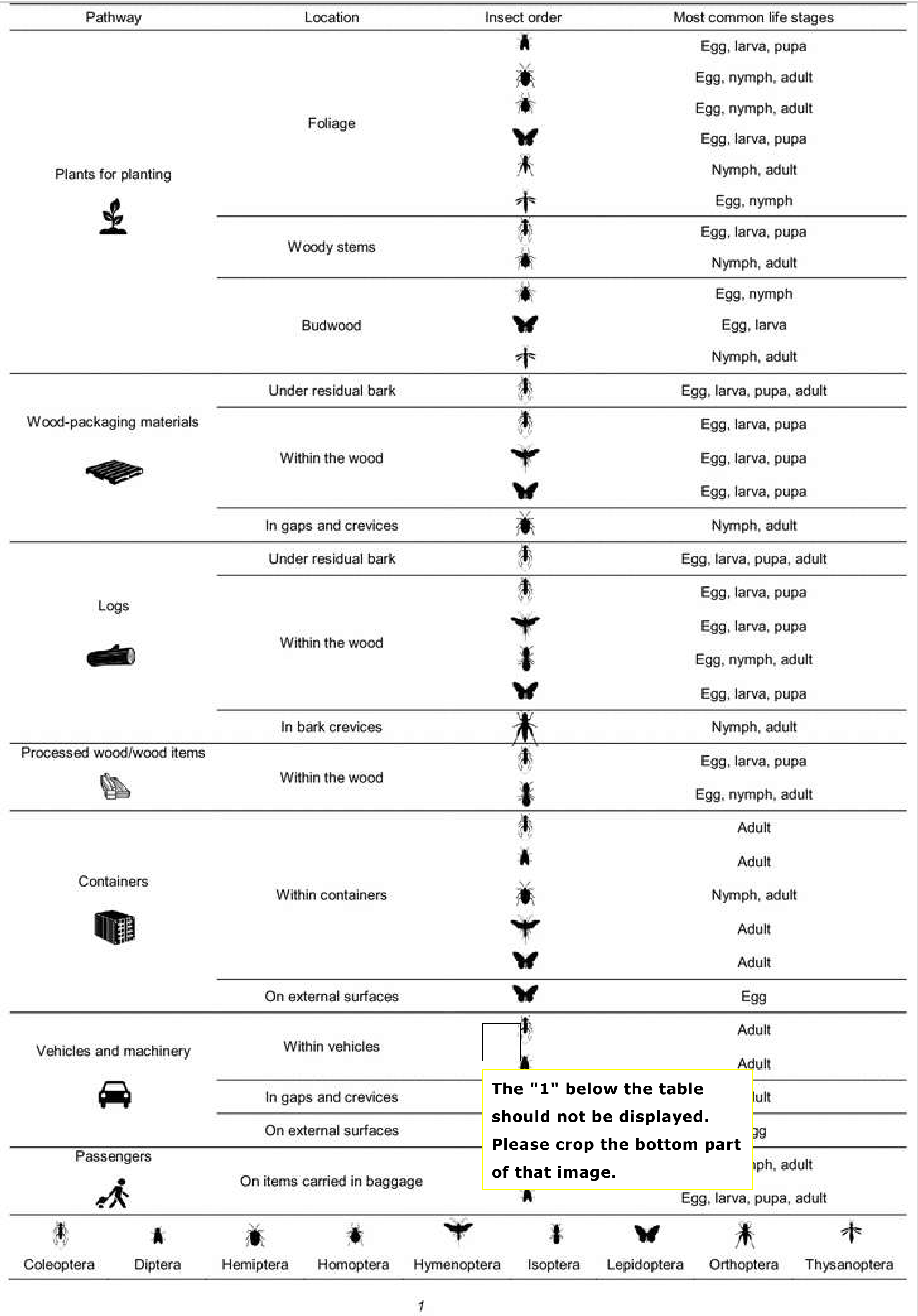
Percent of insect interceptions made at ports-of-entry in various countries by insect order and pathway

Insect order[a]	Importing country and commodities inspected							
	USA				Australia	Chile	EPPO (29 coun	
	All[b]	Live plants	Wood	Airline baggage	Empty containers	WPM	All[c]	Bonsai
Coleoptera	12.8	4.9	91.7	11.9	46.2	84.6	17.8	2.5
Collembola	0.03	1.5	0.01	0.01	0.05			
Dermaptera					1.0	0.4		
Diptera	20.4	1.2	0.3	21.6	30.3	1.6	30.7	
Embioptera					0.04			
Ephemeroptera					0.03			
Heteroptera	3.9	3.8	3.1	1.3	2.6	0.9	0.3	
Homoptera	36.5	53.3	0.3	49.5		0	30.0	84.7
Hymenoptera	0.4	0.8	1.6	0.2	7.0	8.5	0.6	6.1
Isoptera	0.1	0.06	1.3	0.04	1.2	1.6		
Lepidoptera	20.7	7.5	1.4	15.5	5.8	1.1	9.3	0.4
Neuroptera					0.2	0.2		
Odonata					0.01			
Orthoptera	0.9	7.5	0.3	0.09	4.9	0.9	0.2	
Psocoptera					0.5	0.3	0.07	
Siphonaptera					0.01			
Thysanoptera	4.4	19.27	0.08		0.03		11.1	6.4
Thysanura					0.2			
Total number of interceptions	577,343	17,758	7896	289,890	7426	1053	6734	281
Years	1985–2001	2003–2010	1985–2001	1984–2000	1996	1995–99	1995–2004	
Reference	Haack (2001)	Liebhold et al. (2012)	Haack (2001)	Liebhold et al. (2006)	Stanaway et al. (2001)	Beéche-Cisternas (2000)	Roques and Aug Rozenberg (200	

[a] Orders reflect older taxonomy used by many countries in past decades. Some data were reassigned to make all r equivalent. Heteroptera refers to the "true bugs" formerly classified as the order Hemiptera. Homoptera refers to three current suborders Auchenorrhyncha, Sternorrhyncha, and Coleorrhyncha. The order Orthoptera includes Ph and Blattodea (but not termites)

[b] The term "all" means the complete dataset of insect interceptions made at US ports-of-entry and border crossing including baggage, cargo, and conveyances

[c] These data include all interceptions listed in the "EPPO Reporting Service" for non-native species and the assoc pathway (e.g., bonsai, plants for planting, seeds, vegetables, wood packaging, etc.)



Pathway	Location	Insect order	Most common life stages
Plants for planting	Foliage	Diptera	Egg, larva, pupa
		Hemiptera	Egg, nymph, adult
		Homoptera	Egg, nymph, adult
		Lepidoptera	Egg, larva, pupa
		Orthoptera	Nymph, adult
		Thysanoptera	Egg, nymph
	Woody stems	Coleoptera	Egg, larva, pupa
		Homoptera	Nymph, adult
	Budwood	Homoptera	Egg, nymph
		Lepidoptera	Egg, larva
		Thysanoptera	Nymph, adult
Wood-packaging materials	Under residual bark	Coleoptera	Egg, larva, pupa, adult
	Within the wood	Coleoptera	Egg, larva, pupa
		Hymenoptera	Egg, larva, pupa
		Lepidoptera	Egg, larva, pupa
	In gaps and crevices	Hemiptera	Nymph, adult
Logs	Under residual bark	Coleoptera	Egg, larva, pupa, adult
	Within the wood	Coleoptera	Egg, larva, pupa
		Hymenoptera	Egg, larva, pupa
		Isoptera	Egg, nymph, adult
		Lepidoptera	Egg, larva, pupa
	In bark crevices	Orthoptera	Nymph, adult
Processed wood/wood items	Within the wood	Coleoptera	Egg, larva, pupa
		Isoptera	Egg, nymph, adult
Containers	Within containers	Coleoptera	Adult
		Diptera	Adult
		Hemiptera	Nymph, adult
		Hymenoptera	Adult
		Lepidoptera	Adult
	On external surfaces	Lepidoptera	Egg
Vehicles and machinery	Within vehicles	Coleoptera	Adult
		Diptera	Adult
	In gaps and crevices		lult
	On external surfaces		gg
Passengers	On items carried in baggage		ph, adult
		Diptera	Egg, larva, pupa, adult

Coleoptera	Diptera	Hemiptera	Homoptera	Hymenoptera	Isoptera	Lepidoptera	Orthoptera	Thysanoptera

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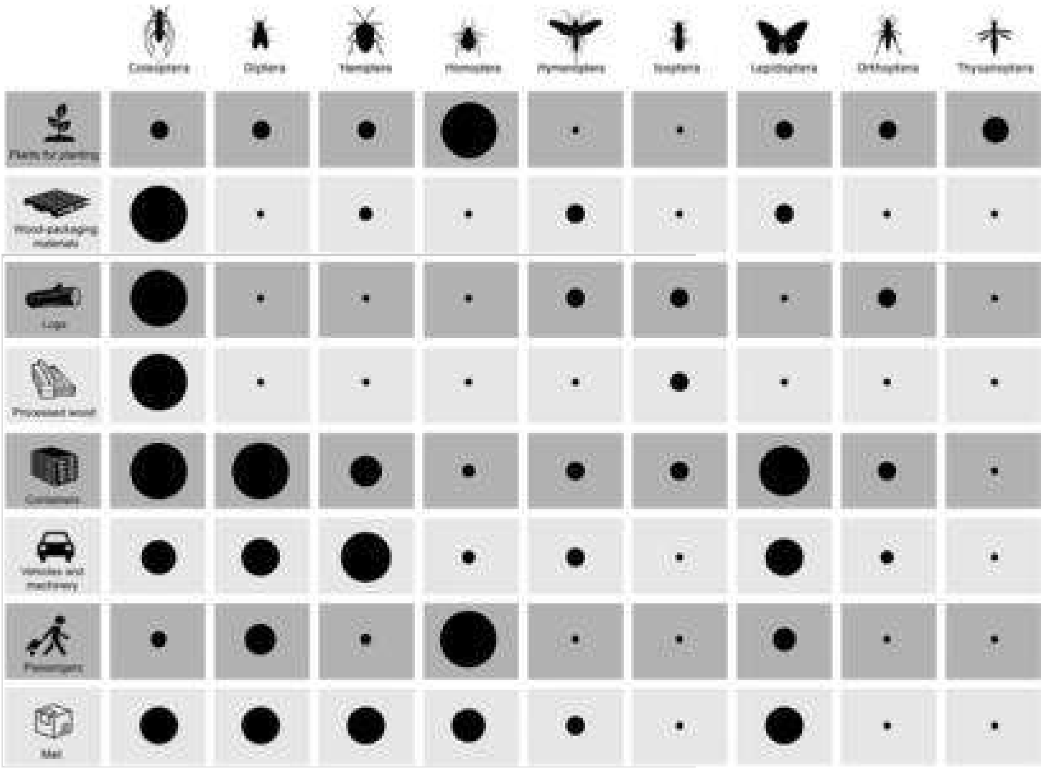
Table 2

Summary details for the most common insects (by order and life stage) to be intercepted at ports by pathway and substrate or plant part

Figure 1. Relative frequency of insect orders unintentionally transported on common pathways. The size of the circle denotes the relative importance of each insect order within each pathway, based on interceptions at ports-of-entry (MAF 2003; Caton et al. 2006; Liebhold et al. 2006; Table 1) and informed estimates. Large circle = common; medium circle = occasional; small circle = rare. Heteroptera refers to the “true bugs” formerly classified as the order Hemiptera. Homoptera refers to the three current suborders Auchenorrhyncha, Sternorrhyncha, and Coleorrhyncha. The order Orthoptera includes Phasmida and Blattodea (but not termites). Live plants = live plants, cuttings, and seeds; Logs = wood traded as logs and which can be used for various purposes such lumber, pulp, or fuel; Wood packaging = blocks, dunnage, crating, pallets, skids, cases, and drums; Processed wood = sawn timber and other processed bulk wooden and flooring; Containers = containers, cargo, sea and air vessels, and land modes of transport. Vehicles = trade, vehicles, and machinery; Passengers = passengers themselves, their luggage, and personal effects



Different forms of live plants can host pests; for example, budwood for propagation was found to host scale insects, Lepidoptera larvae, and thrips in South Africa (Saccaggi and Pieterse 2013), and similarly budwood was the likely pathway through which the Oriental chestnut gall wasp, *Dryocosmus kuriphilus* (Cynipidae), entered the USA (Rieske 2007). A large majority of interceptions on bonsai plants traded from Asia to European countries are Homoptera (Table 1). Bonsai plants have also been shown to be a source of *Anoplophora* longhorned beetles in both Europe and USA (Haack et al. 2010a; Eyre and Haack 2017). Trade in live plants is also considered one of the main pathways for introduction of gall-forming insects of forest trees (Csóka et al. 2017).

Ornamental plants are usually considered the most high-risk form of live plants for moving insects because (1) they are transported swiftly, promoting high insect survival even when large distances are involved (Smith et al. 2007; Colunga-Garcia et al. 2013); (2) the trade volume of ornamentals is increasing worldwide (Eschen et al. 2015a); (3) they tend to be planted outdoors (Liebhold et al. 2012), promoting establishment (van der Gaag et al. 2017); (4) they are often transported with soil or growing media, facilitating transfer of soil-borne insects and pathogens (Migliorini et al. 2015); and (5) fashion trends in garden plants change rapidly (Smith et al. 2007) along with related markets (Liebhold et al. 2012), leading to high turnover in the plant species imported (Eschen et al. 2017). In the EU, for example, the pool of non-native plants in gardens and parks is over 16,000 species, representing over 200 plant families from nearly every continent (Niinemets and Peñuelas 2008).

Wood packaging material (WPM)

WPM is an ideal medium for transporting bark- and wood-boring insects, given that it is normally made from recently cut trees and often has some residual bark (Allen and Humble 2002, Eyre et al. 2018). Thousands of insect species occur worldwide that develop in tree bark and wood, infesting living, dying, and dead trees, as well as moist, dry, and decaying wood (Haack and Slansky 1987; Haack 2017). Larval development times also vary widely among borers, lasting a few weeks or months in most species but multiple years in others (Haack and Slansky 1987; Haack et al. 2017). WPM items such as pallets can be repaired and reused and thereby consist of wood from multiple countries that can differ in their phytosanitary treatments (Clarke et al. 2001; Gu et al. 2006). Furthermore, WPM is used with both agricultural and non-agricultural products and can be fabricated as blocks, dunnage, crating, pallets, skids, cases, and drums (Meissner et al. 2009). WPM was the likely pathway for the introduction of several bark- and wood-infesting insects such as *Agrilus planipennis* (Haack et al. 2015), *Anoplophora glabripennis* (Cerambycidae, Asian longhorned beetle; Haack et al. 2010a), *Ips grandicollis* (Scolytinae, eastern five-spined engraver; Morgan 1967), and *Sirex noctilio* (Siricidae, sirex woodwasp; Hoebeke et al. 2005).

WPM is more commonly associated with maritime than air shipments. For example, about 75% of maritime shipments entering the USA contained WPM compared with 33% of air shipments (Meissner et al. 2009). Similarly, in New Zealand, 40% of maritime shipping containers arrived with WPM, of those 13.4% contained bark (MAF 2006). Military transports also commonly involve the use of WPM, and a case of such WPM being implicated in the invasion of a pine pathogen from the USA to Italy was described by Garbelotto and Gonthier (2013). Given the volume of WPM shipped, it is not surprising that insects are commonly intercepted in WPM at ports-of-entry worldwide. Most insects intercepted on WPM were beetles (Coleoptera; Tables 1–2; Fig. 1), for example, about 92% in the USA (Haack 2001), and nearly 85% in Chile (Beéche-Cisternas 2000). At the family level, most intercepted beetles on WPM were Cerambycidae and Scolytidae (now Scolytinae) (Table S1 in Supplementary Material; Brockerhoff et al. 2006). Other insect orders reported on WPM with important families of wood-boring species include Hymenoptera (Siricidae) and Lepidoptera (Cossidae and Sesiidae) (Tables 1–2; Fig. 1). Besides borers, many other insect species are found in WPM, including predators and parasitoids (Beéche-Cisternas 2000). For example, more than 2500 adult insects were reared from spruce (*Picea*) logs used to brace shipments of granite blocks from Norway to Canada, representing over 40 species, including bark beetles (6 spp.), wood borers (10), and associated parasitoids (> 12), predators (4), and scavengers (> 12) (Humble and Allen 1999).

Logs (roundwood)

Large volumes of logs are transported worldwide and used for lumber, veneer, pulp, and fuel (FAO 2011). Worldwide log exports in 2014 were 133.5 million m^3 for industrial roundwood and 9.3 million m^3 for fuelwood (Allen et al. 2017). During 1996-2009, the USA imported fuelwood from 34 countries that was delivered to 27 US states (Haack et al. 2010b). Logs are generally considered a high-risk pathway (Tkacz 2002; Kliejunas et al. 2006). However, the level of risk associated with log imports depends on multiple factors including the area of origin, the tree species, or the application of specific phytosanitary treatments such as debarking, in-transit fumigations, or seasonal restrictions to transport (USDA APHIS 2010; FAO 2011).

In some countries, such as Canada and the USA, firewood can be transported over long distances by people when driving to recreational sites such as campgrounds (Haack et al. 2010b; USDA APHIS 2010; Jacobi et al. 2011). As with logs, firewood is often untreated, has residual bark, and is stored for long periods before used, and therefore also considered a high-risk pathway for pests (USDA APHIS 2010; FAO 2011).

Many species of forest insects and other invertebrates have been intercepted on imported roundwood logs (Bain 1977; Haack 2006; Eyre and Haack 2017). In Finland, Siitonen (1990) recovered several borer species from coniferous logs imported from Russia, including 23 scolytine species. Similarly, log exports from the USA to China introduced two species of *Dendroctonus* (Scolytinae), one of which (*D. valens*, red turpentine beetle) has become a major pest on pines (*Pinus*) in China (Ciesla 1992; Yan et al. 2005). The cerambycids *Phoracantha semipunctata* and *P. recurva* have colonized several *Eucalyptus*-growing regions worldwide, likely being introduced in pulpwood logs (Rassati et al. 2016). In addition, domestic movement of *Larix* logs for home construction in the USA was the likely pathway for movement of the western scolytine *Dendroctonus pseudotsugae* (Douglas-fir beetle) to the eastern USA (Dodds et al. 2010). It is also important to consider illegal trade of logs and other wood products, given that such items could enter a country without treatment or inspection and thus pose a phytosanitary risk (Bisschop 2012).

As with logs, many insects and other invertebrates can be moved in firewood. For example, in Tasmania, Todd and Horwitz (1990) reported that *Eucalyptus* firewood contained worms, spiders, crustaceans, millipedes, centipedes, and insects (eight orders; mostly Coleoptera and Hymenoptera). In the western USA, a survey of untreated firewood obtained from several retail outlets found live insects in 47% of individual firewood bundles, primarily Scolytinae and other insects representing nine orders (Jacobi et al. 2012). In Michigan, Haack et al. (2010b) reported that 23% of individual pieces of firewood transported by the public contained live wood borers (representing at least seven families in three orders~~;~~, mostly Cerambycidae and Scolytinae), and an additional 41% of the firewood pieces had evidence of previous borer infestation. Firewood has been implicated as the likely pathway by which several important bark- and wood-feeding insects have been moved within the USA, such as *Agrilus planipennis* (Cappaert et al. 2005; Haack et al. 2015), *Anoplophora glabripennis* (Haack et al. 2010a), and *Xyleborus glabratus* (Scolytinae, redbay ambrosia beetle; Cameron et al. 2008; Haack et al. 2010b). Species that would normally associate with live plants, but have a propensity to shelter in dark gaps and crevices, can also be transported long distances on logs or firewood. In Canada, the beech leaf-mining weevil *Orchestes fagi* (Curculionidae) overwinters under bark of beech and other non-host trees, facilitating long-distance movement if infested logs or firewood are transported during this period (Morrison et al. 2017).

Wood chips

International movement of wood chips, defined as wood reduced to small pieces that can be used for pulping, fiberboard production, and fuel, represents a potential pathway for bark- and wood-infesting insects (Kopinga et al. 2010; Allen et al. 2017). Global trade in wood chips is growing quickly, with East Asia (China, Japan, and Korea) and Europe being major importers, and Southeast Asia, South America, and Oceania major exporters (Jiang et al. 2017).

Although no established populations of non-native bark- and wood-infesting insects have been traced to wood chips, there is concern for this possibility, especially in Europe where large volumes of wood chips are imported for renewable energy production (Flø et al. 2014). The chipping process usually results in high mortality of borers, but some individuals can survive, especially when the insects are small (e.g., scolytines) relative to chip size (McCullough et al. 2007; Eatough Jones and Paine 2015).

Processed wood and other wood items and cones

Many other types of wood items can serve as pathways for insects, especially borers. The phytosanitary risk of some of these wood items is well recognized, such as lumber with residual bark, while for others the risk is less obvious, for example, decorative items such as Christmas items comprising wooden parts or cones. The bark- and wood-infesting insects intercepted in lumber are basically the same as those reported above for wood packaging, firewood, and logs (Bain 1977; Haack 2006). Even when lumber is treated properly, some borers can successfully infest post-treatment, especially when residual bark is present (Evans 2007; Haack and Petrice 2009). In New Zealand, about 11% of bark and wood borer interceptions were from sawn timber, 7% from logs and other bulk wooden material, and about 2% from wooden cargo (e.g., wooden sport items, furniture, and handicrafts; Ridley et al. 2000). However, as the majority of raw wood imported into the country is sawn timber, these numbers reflect the traded volumes rather than actual infestation rates.

Infested wood can be used inadvertently in the construction of buildings, furniture, and flooring, with some adult borers emerging years after manufacture (Cocquempot and Lindelöw 2010; Haack 2017). Low-quality wood, occasionally infested with borers, can be placed inside upholstered furniture and therefore difficult to detect (Eyre and Haack 2017). At times the paperwork associated with imported products falsely indicates that no wood is present. This was the case with imported “artificial Christmas trees” from China to the USA when it was discovered that the trunk portion was real wood with bark from *Cryptomeria* trees, which were often infested with *Callidiellum* cerambycid species (Maier 2017). Another example involves pine cones from India imported to the USA for use in handicrafts and potpourri mixtures that were infested with the cerambycid *Chlorophorus strobilicola* and tortricid seed-feeding moths in the genus *Cydia* (Kiesz 2003).

Contaminated non-wood items transported as cargo

Cargo items contaminated with hitchhiking forest insects could include anything from forestry machinery and equipment to camping equipment (Ridley et al. 2000; Withers 2001). Although monitoring of this pathway is less common, its importance should not be underestimated.

Cargo transported on airplanes has the shortest travel times relative to distance travelled; hence, this is considered to be a particularly effective pathway leading to introductions by hitchhiking species (McCullough et al. 2006). For instance, 158 insect pest species across 33 families and five orders were intercepted on cargo aircraft from 730 flights at Miami International Airport (Caton et al. 2006), and Lepidoptera and Coleoptera were the dominant orders. Air cargo contamination was most prevalent during the wet seasons (when pests are generally more abundant) and night-time loading operations (when airport lighting attracts insects) (Caton et al. 2006).

Containers, used vehicles, and machinery

Hitchhiking insects are regularly found in shipping containers. Most are agricultural pests, but some significant forest pests are occasionally found (Table 1; Fig. 1). Given the large volumes of containers transported worldwide, even relatively low contamination rates represent a significant risk. In Australia, a survey of 3001 empty containers showed 39% were internally contaminated with live and dead insects; 176 containers (5.9%) had live individuals, including one scolytine (Stanaway et al. 2001; Table 1). In New Zealand, a survey of 11,265 containers arriving at ports found live insects in 4.1% of loaded containers and 3.6% of empty containers (MAF 2003). Of 173 live insects identified in the above survey, there were 15 Coleoptera species, two Hemiptera, three Hymenoptera (all ants), and four Psocoptera. Forest insects included one live bostrichid powderpost beetle (*Sinoxylon* sp.) (MAF 2003). In a similar survey at the port of Auckland, New Zealand, contamination rates by live insects were 7.4% internally and 0.4% externally in loaded containers, compared with 3% internally and no record externally in empty containers (MAF 2006). Dead individuals of significant forest pests were also found, including one ambrosia beetle (*Xyleborus* sp.; Scolytinae) and one larval gypsy moth (*Lymantria dispar*; Erebidae). In the above two surveys, little external contamination was reported (~ 0.1% overall), which may reflect the fact that only the four lateral sides of each container were inspected. By contrast, Gadgil et al. (2000) examined the six external sides of 3681 containers imported to New Zealand and found live insects externally on 5% of inspected containers, either as adults or immature stages. Forest pests included four bag moths (Psychidae), and one gypsy moth egg mass. Of the dead individuals, 49 were from insect groups with potential to become tree pests, including termites, cicadas, longhorned beetles, and weevils.

Species that have a propensity to shelter in dark gaps and crevices, or that have pupae or eggs that may be affixed to steel surfaces, are particularly prone to transportation by containers. These include adults of the brown marmorated stink bug, *Halyomorpha halys* (Pentatomidae), which was probably introduced to North America as a hitchhiker with shipping containers from Asia (Hoebeke and Carter 2003), and the painted apple moth, *Teia anartoides* (Erebidae), which was presumably introduced from Australia to New Zealand as eggs attached externally to sea containers (Harris 1988).

Many Lepidoptera have behaviors that allow them to be associated with objects other than host plants, especially during the egg or pupal stages. For example, adult female Asian gypsy moth, *Lymantria dispar,* are attracted to artificial lights in ports, where they may lay egg masses on the surfaces of containers, vehicles, vessels, and other cargo (Schaefer and Strothkamp 2014). Interceptions of gypsy moth egg masses on ships and their containers are frequent in North America and Australasia (Gray 2017). In New Zealand, for example, 22 gypsy moth egg masses were found on containers during 1995–1997, arriving from Russia, Hong Kong, and Japan (Newfield 2008). Because of the difficulties to detect egg masses on containers, likely many more enter undetected.

As for shipping containers, species that have the ability to colonize gaps and crevices on manmade equipment, or affix as eggs or pupae to steel surfaces of vehicles and machinery, are more likely to remain hidden and protected and undetected during transport. Colonization is more likely on used cars, trucks, or farm and forestry machinery, which is typically kept outdoors for long periods. Records in New Zealand showed that most (38.5%) brown marmorated stink bug interceptions were on used and new vehicles, especially at a time of the year when adults are looking for shelter in their area of origin (Brockerhoff et al. 2016; Catherine Duthie, pers. comm.).

Marine and air vessels, and land modes of transport

Hitchhiking insects are increasingly reported associated with various modes of transportation (planes, ships, trucks, vehicles, and trains) and with containers and cargo items (Fig. 1). The Asian gypsy moth has triggered much attention worldwide as a potential hitchhiker due to frequently finding its egg masses on sea vessels (see also section on “Containers”). For instance, the superstructure of 6% of 478 inspected sea vessels arriving in Australia from high-risk Asian ports was carrying gypsy moth egg masses, with a total of 514 egg masses (Nielsen et al. 2013). When ships are close to land, neonate larvae can balloon to shore on spun silken threads and settle on suitable host plants (Zlotina et al. 1999).

Reports of hitchhiking pests on land modes of transports are generally less well documented. Occasional reports are made of insects entering vehicles on people’s clothing or hair, or flying in and out of vehicles and trailers [e.g., for the bronze bug *Thaumastocoris peregrinus* (Thaumastocoridae) in New Zealand (NM, pers. obs.) and South Africa (BPH, pers. obs.)]. Similar observations have been made for *Agrilus planipennis* in North America (Buck and Marshall 2009; RAH, pers. obs.).

Travelers with personal baggage and food items

Travelers can also inadvertently transport forest insects between countries. In New Zealand and Australia, where most international travelers arrive by air, national phytosanitary authorities inform incoming passengers about biosecurity concerns and that systematic baggage inspection will be conducted, often involving X-ray scanning and sniffer dogs. A recent baggage survey of 6816 passengers entering New Zealand at international airports showed 3% of travelers carried fresh or dry plant products (MPI 2013). Travelers often carried food items such as fresh fruits, which can be contaminated with a variety of agricultural insect pests, while only a few articles of baggage contained nursery stock, wood items, or other plant items that are more likely to be associated with forest species. In the same survey (MPI 2013), there were 127 discoveries of improperly cleaned camping and hiking gear, which can introduce non-native species to recreation areas (Anderson et al. 2015). For instance, Gadgil and Flint (1983) found live insects (including forest species), in six out of 45 tents accompanying passengers arriving in New Zealand.

Analysis of US insect interception data with passenger baggage arriving mostly by air during 1984-2000 showed that most insects were associated with fresh plant items, either for consumption, propagation, or other plant parts (McCullough et al. 2006). About 1% of baggage interceptions were not directly associated with any sort of material (i.e., hitchhikers), and less than 0.1% of baggage interceptions were associated with wood material. Most insects intercepted on air baggage entering the USA during this 17-year period were Homoptera in the suborders Sternorrhyncha, Auchenorrhyncha, or Coleorrhyncha, followed by Diptera, Lepidoptera, and Coleoptera (Liebhold et al. 2006; Tables 1–2; Fig. 1).

Contaminated mail and packages

Contaminated courier mail and packages is a less obvious and less well-documented pathway for forest insect introductions. Examples of mailed items that could harbor forest insects include wooden ornaments/gifts, wood blocks for carving, fresh or dried plant parts, and seeds (GISTF 2017). In Fig. 1, we considered the types of insects commonly associated with mail to be similar to those intercepted in passenger baggage (Table 1; Liebhold et al. 2006).

Insects can also be transported intentionally by mail. Introductions of beneficial insects such as pollinators or biological control agents are usually strictly regulated and therefore are expected to have little or no adverse effects (Brockerhoff and Liebhold 2017). On the other hand, there are several historical examples of unintended escapes of insects followed by establishment in the natural environments, notably from pet trade or exhibits, or from rearing/production facilities (Kumschick et al. 2016). For example, the Australian *Eucalyptus*-feeding stick insect *Extatosoma tiaratum* (Phasmatidae) is exported as an insect pet to many countries such as South Africa, where *Eucalyptus* is grown commercially (Hurley et al. 2016). Insects purchased as pets are often carelessly discarded in gardens or fields, thus providing an opportunity for their establishment.

Natural dispersal

For non-native insects, geographic expansion usually follows human-assisted movement into a new region. In recent history, however, there are examples where native and non-native forest insects have significantly expanded their geographic ranges naturally (i.e., not human-assisted). These are usually in relation to major changes in host distribution and/or climate. For instance, the progressive southern and western expansion of two European spruce-infesting scolytines (*Dendroctonus micans* and *Ips typographus*) and their natural enemies have followed the expansion, essentially during the nineteenth century, of spruce plantations from southwestern Eurasia (Mayer et al. 2015). Increasing temperatures have also facilitated range expansion in some forest insects, especially at higher latitudes and elevations. In Europe, higher winter temperatures have increased larval survival and nocturnal adult dispersal of the pine processionary moth, *Thaumetopoea pityocampa* (Thaumetopoeidae), allowing northern expansion (Battisti et al., 2006). Similarly, in North America, warmer temperatures have allowed the mountain pine beetle, *Dendroctonus ponderosae* (Scolytinae), to spread northward in Canada and cross the Rocky Mountains, thereby threatening pines in the East (Carroll et al. 2003).

In these examples, the mode of dispersal is either adult active flight or passive transportation, usually supported by wind currents. Although not as common as range expansion over land, there are also reports of natural dispersal of insects across oceans. The aerial movement of insects from Australia to New Zealand by means of the trans-Tasman airstreams is a common occurrence (Close et al. 1978). New Zealand lies approximately 1800 km downwind from Australia, and a number of small insects, such as aphids, but also Lepidoptera, have been introduced to New Zealand by these air currents (Close et al. 1978; Fox 1978; Hoare 2001), although most have not established. Australia is the native range of *Eucalyptus* trees, and their associated herbivorous insects, and thus wind-assisted introductions of eucalypt insect pests are a potential threat to *Eucalyptus* plantations in New Zealand (Withers 2001). Natural rafts can also provide insects, including xylophagous beetles, the means to cross oceans. Logs from the Amazon have been recorded as far as 1600 km from the coast (Holzapfel and Harrell 1968). Another form of natural dispersal is when insects are vectored by another animal species (excluding humans), such as birds and mammals. For example, birds in North America help disperse the hemlock woolly adelgid, *Adelges tsugae* (Adelgidae; McClure 1990).

Policy and management

There have been strong global efforts in recent years to reduce the risk of international movement of plant pests by the pathways discussed here. The International Plant Protection Convention (IPPC) is the main organization that sets global standards for plant health (Allen et al. 2017; Ormsby and Brenton-Rule 2017). As of April 2018 the IPPC had 41 adopted standards known as International Standards for Phytosanitary Measures (ISPMs; IPPC 2017a). The ISPMs that deal most directly with forest pests include ISPM 15 (wood packaging materials, WPM; first adopted in 2002), ISPM-36 (plants for planting; 2012), ISPM 38 (seeds; 2017), ISPM 39 (wood; 2017), ISPM 40 (growing media; 2017), and ISPM 41 (used vehicles, machinery and equipment (VME); 2017) (IPPC 2017a; Table S2 in Supplementary material).

ISPM 15 lists specific guidelines for manufacturing, treating, and marking WPM (including dunnage). Since first adopted in 2002, ISPM 15 was substantially revised in 2006, 2009, and 2013 on topics such as debarking, maximum size of residual bark pieces, and new treatment options (IPPC 2017a). Setting limits on the maximum allowable size for residual bark pieces was based on field research in Europe and North America (Evans 2007; Haack and Petrice 2009). ISPM 15 has reduced the percentage of international shipments with live wood pests (Haack et al. 2014), but not eliminated the threat as evidenced by recent interceptions in WPM that have the ISPM 15 mark (Eyre et al. 2018; Wu et al. 2017). Such interceptions could indicate issues such as ineffective treatment standards, faulty equipment, or fraud (Haack et al. 2014). Interception records of insects associated with WPM also vary among countries, likely reflecting differences in trading partners and inspection protocols (Eyre et al. 2018). For example, the USA historically placed more emphasis on insects that infest living trees rather than dead trees or processed wood, which resulted in inspectors reporting true bark beetles (which often infest live trees) more often than ambrosia beetles, Anobiidae and Bostrichidae (which often infest dead trees or lumber) (Haack 2001, 2006). Nevertheless, even if only partially effective, ISPM 15 still likely provides large economic benefits by reducing the arrival rate of new forest pests (Leung et al. 2014).

The recently approved ISPM 39 addresses most types of wood other than WPM, but its implementation will likely require further legislation. For instance, wood chips are recommended to be less than 3 cm in at least two dimensions, but the ideal size will vary depending on the intended use (IPPC 2017a). Many countries require coniferous wood chips to be treated because they could contain pinewood nematode, *Bursaphelenchus xylophilus* (Parasitaphelenchidae; Allen et al. 2017; Hopf-Biziks et al. 2017), although similar regulations are mostly lacking for hardwood chips (Flø et al. 2014).

The other ISPMs (ISPM 36, 38, 40, and 41; IPPC 2017a) take more of a “systems approach” to pest reduction by integrating several independent phytosanitary measures that are applied throughout the production process of each commodity (Allen et al. 2017). The combination of multiple measures in a “systems approach” cumulatively reduces pest risk, often providing equivalent and more reliable alternatives than a single more expensive or limiting measure (FAO 2011). For example, ISPM 36 (plants for planting) deals with selecting production sites, pest management programs, training, packaging, transportation, internal audits, and record keeping of live plants for export (IPPC 2017a). A separate ISPM addresses seeds (ISPM 38), and another is being drafted for cut flowers and ornamental foliage, which are not classified as live plants and so are not included under ISPM 36 (IPPC 2017a, 2017b). Another example of a systems approach to pest reduction is ISPM 41 (used VME), which deals with topics such as cleaning and treatment of VME, prevention of contamination, facilities and waste disposal requirements, and verification procedures (IPPC 2017a).

Apart from the ISPMs, Regional Standards for Phytosanitary Measures (RSPMs) are also developed by Regional Plant Protection Organizations (RPPOs), such as the European and Mediterranean Plant Protection Organization (EPPO) or the North American Plant Protection Organization (NAPPO) (MacLeod et al. 2010). Most countries also have official agencies in charge of plant protection, which are called National Plant Protection Organizations (NPPOs) in the IPPC context (MacLeod et al. 2010). NPPOs can also set specific regulations to manage imports presenting risks to plant health. For example, New Zealand’s phytosanitary standard for importation of nursery stock prescribes inspection on arrival, the presence of an import permit, labeling and a phytosanitary certificate, treatment with pesticides or hot water, and post-entry quarantine for up to 36 months (MPI 2017). These measures are stringent compared with the measures most other countries prescribe for importation of nursery stock (Eschen et al. 2015b). Similarly, in the case of wood chips imported into Great Britain, requirements vary depending on country of origin, tree species, and the presence of bark and may also require harvesting from pest-free areas (Forestry Commission 2015).

To mitigate the risk of movement of hitchhikers, soil, and other contaminants with shipments of empty sea containers, New Zealand implemented a bilateral sea container hygiene system with several Pacific Island nations. This entails storing containers on hard surfaces, cleaning all container surfaces, pest control and reducing pest habitat in port areas, auditing and other measures (MAF 2009). When fully implemented, the sea container hygiene system was found to be highly effective (MAF 2009). For instance, a 98.5% reduction in ant contamination of imported containers was observed following implementation between 2002 and 2006 (Ashcroft et al. 2008). Despite the additional costs of these measures, the entire systems approach was considered to provide net financial benefits due to reduced inspection and treatment costs on arrival (MAF 2009).

Concluding remarks

International trade of goods and movements of people are largely responsible for introductions of non-native forest insects worldwide. Efforts to reduce these insect introductions have included the development of international standards for phytosanitary measures. For WPM, likely the most important pathway for bark and wood borers, recent global harmonization in phytosanitary treatments provided by ISPM 15 has been at least partially effective (Haack et al. 2014; Leung et al. 2014). In addition, the IPPC has recently approved several other ISPMs related to forest pests and is now finalizing standards for international movement of cut flowers and foliage (IPPC 2017b), which could prove useful to reduce transportation of tree foliage and sap feeders. However, despite increasing phytosanitary regulation to reduce unintentional pest movement (Haack et al. 2014, Eschen et al. 2015b), recent data have shown rates of new establishments still remain high (Boyd et al. 2013; Brockerhoff and Liebhold 2017). Factors that limit risk reduction come from increasing volumes of transported goods, variation in quarantine procedures between countries, and rapid changes in distribution networks (Leung et al. 2014; Eschen et al. 2015b; Ormsby and Brenton-Rule 2017).

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Evaluation of future threats to forests by non-native tree pests is predominantly based on pest risk assessments of well-defined lists of species (e.g., Eschen et al. 2015b). However, the ongoing arrival of pests and the continuous emergence of new invasive pest species (Seebens et al. 2018), of which many were either unknown or harmless in their areas of origin, indicate that reliance on a limited number of species on pest lists is not entirely effective. Furthermore, there is an apparent mismatch between species intercepted during inspections at the border and those that established, which, in part, may be caused by disproportionate attention being given to regulated organisms (Eschen et al. 2015c). This suggests a better strategy is to evaluate risks at the pathway level. Rather than focussing mainly on particular pests that are perceived to be especially invasive and damaging, it is preferable to evaluate (and manage) pathways in a more generic fashion to address risks associated with all the species potentially transported that way (Hulme 2009, Boyd et al. 2013, Brockerhoff and Bulman 2014, Wingfield et al. 2015). Evaluating pathways should focus on (1) broader pest categories (e.g., wood borers or defoliating insects); (2) the most likely modes of transportation involved; and (3) medium-and long-term economic, environmental, or sociocultural impacts of pest establishment. Pathway-based analyses can be used with risk maps of pest introduction to improve deployment of early detection tools and mitigation strategies for non-native forest insects.

Author contribution

NM, DR, BPH, and RAH conceived, organized, and wrote the initial draft. EGB added details to all sections. RAH, NM, and DR prepared figures and tables. All authors reviewed and approved the manuscript.

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Compliance with ethical standards

Conflict of interest NM, DR, BPH, EGB, and RAH declare that they have no conflicts of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Electronic supplementary material

Below is the link to the electronic supplementary material. Supplementary material 1 (DOCX 31 kb)

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