RESEARCH ARTICLE

Laundry washing increases dispersal efficiency of cloth-dispersed propagules

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Abstract

Due to increased human mobility, cloth-dispersed propagules can be transported over long distances, which would not have been bridged otherwise. We studied a potentially important component of human-mediated seed dispersal by assessing the effects of laundry washing on the dispersed propagules. We studied the germination of 18 species, which have morphological adaptations for epizoochory and are commonly dispersed by people. We tested six treatments (washing with water, soap nut or detergent, at 30 °C or 60 °C) compared to an untreated control. Washing intensity was the most significant factor affecting germination. Washing at 30 °C was neutral for 14 species, suppressed one species and supported three species. Washing at 60 °C decreased seedling numbers of half of the studied species. The intensive washing treatments at 60 °C significantly decreased the synchrony of germination. We showed that people are not purely transporting propagules from one location to another, but via the laundry cycle, we can also influence the fate of the transported propagules by affecting germination potential, seedling fitness and germination dynamics. These results have new implications for understanding the early stages of biological invasions and call for improved biosecurity measures in nature reserves subjected to a growing pressure of tourism.

Introduction

Increasing human population, mobility and globalisation make humans a highly effective dispersal vector of plant propagules (Bullock et al. 2019). Human-mediated seed dispersal is amongst the most important ways of long-distance plant dispersal in modern times (Nathan 2006; Ansong and Pickering 2014). People play an increasingly important role as dispersal vectors by unintentionally transporting propagules on vehicles (Pickering and Mount 2010; Ansong and Pickering 2013a) and clothes (Ansong and Pickering 2014). Propagules can travel extremely long distances, up to hundreds of kilometres while attached to cars (Taylor et al. 2012). The potential dispersal distances are supposed to be shorter in case of clothing-dispersal (couple of kilometres; Auffret and Cousins 2013; Ansong et al. 2015). However, if clothing-dispersal is combined with transport by vehicles, propagules can travel considerably longer distances. Clothing-dispersal has been documented for approximately 450 plant species so far and, presumably with future studies, this number is certainly going to increase strikingly (Ansong and Pickering 2014).

Morphological adaptations for epizoochory, such as hooks, awns, hairs or glabrous surface (Römermann et al. 2005; Hintze et al. 2013) make propagules especially capable for clothing-dispersal, a modern analogue of the classical epizoochory on mammals' fur. The most striking ecological consequence of clothing-dispersal compared to epizoochory, is that it can connect habitats with completely different species pools, such as isolated mountain ranges, islands with the mainland or biogeographical regions which otherwise would not have any biological connections. This implies that some of the propagules arrive at an environment which is unsuitable for their establishment, but others can establish in novel habitats which can be the first step of biological invasions. Suitability of novel habitats depends on a range of factors. For instance, climatic changes and the heat island effect in urban habitats (Shochat et al. 2006) make cities in the temperate region especially suitable for the establishment of thermophilous species (Rysiak and Czarnecka 2018). This process is further aggravated by the increasing global mobility of people, especially for those living in cities (Glaesser et al. 2017). The vast majority of clothing-dispersed propagules belong to species considered as weeds and it is plausible that clothing-dispersal played an important role in the transport of 43% of the invasive species in the United States (Ansong and Pickering 2014). Clothing-dispersal is of an increasing concern in nature reserves which are receiving growing pressures from tourism (Pickering et al. 2011), as tourists can be very effective dispersal vectors of propagules of alien species (Ansong and Pickering 2013b).

There are many open questions regarding the fate of human-dispersed propagules, especially regarding their establishment prospects. It is still a question how the mechanical and chemical effects to which propagules are exposed during human-mediated dispersal, affect their germination potential and establishment. One of the most drastic events that can happen to a clothing-dispersed propagule is laundry washing. Everyday observations of field biologists, hikers and people participating in outdoor sports show that propagules attached to clothing often end up in washing machine. In a questionnaire survey, Ansong and Pickering (2013) found that approximately 15% of people visiting an Australian nature reserve put their clothes in the laundry without removing the propagules. Even though many people are willing to remove seeds and fruits from their clothes, there are some small propagules, especially in safe microsites, such as pockets, shirt-sleeves or inside socks which are not noticed and hence not removed before washing. Huiskes et al. (2014) studied propagules on the clothes of people visiting Antarctica. They found a considerable amount of propagules on the clothes and the interviewed people were using their clothes in other ecosystems before visiting Antarctica. This is an indirect evidence for the possibility of washed propagules to be introduced into new locations.

Lefcort and Lefcort (2014) reported on the effect of laundry washing on cheatgrass (*Bromus tectorum*). They hypothesised that laundry washing affects the water potential of the propagules which might result in altered germination and establishment rates. They observed no effect of washing on the seedling number and seedling height of the washed seeds; however, they found that addition of bleach significantly decreased seedling heights.

To study the effect of laundry washing on a large set of species, here we tested the germination potential (seedling number), seedling fitness (approximated by seedling biomass) and dynamics (germination time, start of germination, synchrony) of the propagules washed in laundry compared to unwashed seeds. We applied two washing intensities and three types of washing medium to test whether these circumstances have an effect of the germination rates. Washing intensity can have different mechanical and heat effects on the propagules and the presence/absence of toxic compounds (surfactants, brighteners) in detergents can affect their survival (see also Lefcort and Lefcort 2014). Previous studies have shown the potential of bleaching for breaking the dormancy of seeds of grass (Hsiao 1979) and legume species (Okonkwo and Nwoke 1975). Besides studying seedling numbers, we also used seedling biomass as a proxy for seedling fitness (Sonkoly et al. 2020). We used three variables, i.e. germination time, start of germination and germination synchrony to describe germination dynamics, since all of them can be relevant in the establishment of plants in a novel environment; therefore, they can be important factors in an invasion process. Rapid and synchronised germination might be a good strategy to mitigate the effects of interspecific competition (Fenesi et al. 2014), but can be risky in a novel and unpredictable environment (Gioria and Pyšek 2016). The review of Gioria and Pyšek (2016) showed that early germination is more widespread in invasive plants compared to their non-invasive congeners and they assume that the strategy of early occupation of empty niches can

be highly effective in a novel environment. Early germination is a major advantage as it increases seedling growth and fecundity (Verdú and Traveset 2005).

Methods

Studied species

We selected 18 species for the experiments, all species having the ability for epizoochorous and clothing-dispersal and are widespread in Central-Europe (Table 1). The native and non-native ranges of the species are indicated in Table 1. Fourteen of the studied species have already been introduced to continents outside their native range. The propagules were collected in Hungary in 2017 from at least 30 plant individuals per species. The propagules of the tested species were different types of fruits; we call them for convenience 'propagules' hereafter. In Table 1, the morphological units used for the germination experiments and experiments on retention potential are given for each species.

Germination after laundry washing

During the experiments, we applied combinations of washing intensity (30 °C or 60 °C) and washing medium (water, soap nuts or detergent) as follows: (i) unwashed control and washing with (ii) water at 30 °C, (iii) soap nuts at 30 °C, (iv) detergent at 30 °C, (v) water at 60 °C, (vi) soap nuts at 60 °C, (vii) detergent at 60 °C. Washing intensity had two levels: the 'extensive washing' treatment was at 30 °C and lasted for 40 minutes; the 'intensive washing' temperature was 60 °C and the treatment lasted for 185 minutes. Washing medium had three levels: water, soap nuts (four nuts of *Sapindus mukorossi*, representing an eco-friendly alternative) and detergent (66 ml of Ariel Colour fluid detergent).

We tested germination of five replicates of 25 propagules per treatment for 17 species and three replicates of 25 propagules for *Hordeum murinum*. We put the sets of 25 propagules in small fabric sacks (Suppl. material 1: Fig. S1), sewed each sack and appended them with a string to prevent propagules escaping. In total, we had 528 sacks. Each treatment (88 sacks) was washed in a separate laundry cycle in September 2017.

After washing, propagules were germinated in an unheated greenhouse under natural light conditions. We put the propagules from each sack (25 seeds), as well as the unwashed control propagules in pots (8 cm × 8 cm × 12 cm) filled with potting soil. We watered the pots daily with 5 ml tap water. We counted all the emerged seedlings on every fourth day (monitoring days). We terminated the germination for each species when more than 95% of the propagules germinated in at least one treatment or when we did not detect new seedlings for more than 5 monitoring days. When terminating the germination, we removed all individuals and measured the total dry aboveground biomass (referred to as 'seedling biomass') and recorded the total number of germinated individuals per pot.

Table 1. Characteristics of the studied 18 species. Native and non-native ranges are given based on the CABI Invasive Species Compendium (https://www.cabi.org/isc/) and the EPPO Global Database (https://www.gd.eppo.in).

Species	Life form	Morphological adaptation for epizoochory	Morphological unit tested		Native range	Non-native range
			germination experiment	experiments on retention rate		
Agrimonia eupatoria	perennial forb	fruit surface hairy with hooks	fruit	fruit	Eurasia	N-America, Oceania
Arctium lappa	perennial forb	involucrum with many hooks	fruit	flower head at fruiting stage	Eurasia	N-America, Oceania
Bromus sterilis	annual grass	awned lemma with backward hairs as part of the dispersal unit	fruit	fruit	Eurasia	N-Africa, N-America, Oceania
Bromus tectorum	annual grass	awned lemma with backward hairs as part of the dispersal unit	fruit	fruit	Eurasia	N-America, S-America, Oceania
Cenchrus spinifex	annual grass	spiny bracts of infructescences	fruit	fruit	N-America, S-America	Europe, Oceania
Chaerophyllum temulum	biennial forb	fruit surface with smooth hairs	fruit	fruit	Eurasia, N-Africa	
Cruciata pedemontana	annual forb	hooked hairs on the stem, hooked pedicels	seed	–	Eurasia, N-Africa	N-America
Cynoglossum officinale	biennial forb	prickly-surfaced fruit	fruit	fruit	Eurasia	N-America
Daucus carota	biennial forb	hooked bristles on fruit	fruit	fruit	Eurasia	N-America, Oceania
Geum urbanum	perennial forb	fruit with one long hooky attachment	fruit	fruit	Eurasia	N-America, Oceania
Hordeum hystrix	annual grass	awned lemma	fruit	fruit	Eurasia	N-America, S-America, Oceania
Hordeum murinum	annual grass	awned lemma	fruit	fruit	Eurasia	N-America, S-America, Oceania
Melica transsilvanica	perennial grass	hairy diaspore	fruit	fruit	Eurasia	
Physocaulis nodosus	annual forb	fruit surface covered with very low hooks	fruit	fruit	Eurasia	
Secale sylvestris	annual grass	awned lemma	fruit	fruit	Eurasia	
Setaria verticillata	annual grass	bristles with backward barbs on panicle	fruit	fruit	Eurasia	N-America, S-America, Oceania
Torilis arvensis	annual forb	fruit surface covered with fine short hooks	fruit	fruit	Eurasia	Africa, N-America, S-America
Tragus racemosus	annual grass	upper glume with hooked spiny bristles	fruit	fruit	Eurasia, Africa	N-America, S-America

The fate of propagules before and after washing

We tested the likelihood of (i) human-dispersed propagules entering the laundry cycle and (ii) that washed propagules are detached during clothes drying. For these experiments, we used three cloth/fabric types typically worn during outdoor activities: polar fleece sweater (fleece), jeans (denim) and cotton socks (cotton).

For estimating the likelihood of human-dispersed propagules entering the laundry cycle, five people put sets of dry propagules of 17 of the studied species (except for *Cruciata pedemontana*) on their clothing (sweater, jeans, socks) at 09:00 h. All persons put 25 prop-

agules per species on each cloth type; each species was tested on a separate day in the autumn 2017. All persons continued their normal daily activities at the university including mainly indoor, but also several outdoor activities (short walks between buildings). We counted the number of propagules on the three fabric types in every hour until 17:00 h.

We tested the fate of the propagules after washing at 30 °C and 60 °C. We used five replicates of 25 propagules per species and fabric type (fleece, denim, cotton). We cut 6 cm × 6 cm pieces from the three fabrics and attached 25 propagules of one species on one piece (90 pieces per fabric type and washing temperature, in total 540 pieces). In total, we had six separate laundry cycles (three fabric types at 30 °C and 60 °C). Directly after washing, propagules were counted on each fabric piece. We determined the proportion of propagules that (i) remained attached to the original fabric piece, (ii) became attached to another fabric piece and (iii) lost during the laundry washing (remained in the washing machine or passed to the sewerage system; Suppl. material 1: Table S1). After counting the propagules that remained attached on the fabrics after washing (i+ii), fabrics were hung on an indoor washing line (Suppl. material 1: Fig. S1). Fabrics were left for drying for 8 hours. We modelled outdoor drying conditions (e.g. wind) by using a fan. Finally, we counted the propagules that remained attached on the fabrics after drying. In the analyses, we used the ratio of propagules that have been retained on the fabric pieces after drying to the propagules that have been retained on the fabrics after washing.

Statistical analyses

In the analyses, we used dependent variables related to the fitness (seedling number and biomass) and phenology (mean germination time, start of germination, synchrony) of the germinated seedlings. Seedling number was the number of germinated seedlings per pot. Biomass referred to the dry biomass of the germinated seedlings per pot and was used as a proxy of seedling fitness (Sonkoly et al. 2020). Mean germination time (days) was calculated for the seedlings of each pot. Start of germination referred to the first day when a seed germinated in a pot. Germination synchrony was expressed by the Shannon diversity of germination dates of seeds per pot. Zero refers to completely synchronised germination (all seeds germinated at the same date); higher values refer to less synchronised germination.

We tested the effect of 'Species identity', 'Washing intensity', 'Washing medium' and their interactions (fixed factors) on the Relative Response Index (RRI, Armas et al. 2004), calculated for each of the above-listed dependent variables with generalised linear models (GLMs) in SPSS 22.0. RRI shows the effects of the washing treatments compared to the unwashed control and was calculated as follows:

$$RRI = (DV_W - DV_C) / (DV_W + DV_C),$$

where DV_W and DV_C are the scores of a dependent variable (DV) in a particular washing treatment (DV_W) and in the control (DV_C), respectively. RRI ranges between –1 and +1, zero means that the control and the treatment are not different. In the GLM

models, we accounted for normal distribution. The values of the dependent variables, i.e. RRIs, calculated for seedling number, seedling biomass, germination time, germination synchrony and start of germination, were log-transformed to approximate them to normal distribution.

We used GLMs for testing which factors influence the retention rate of dry and washed propagules. We tested the effect of 'Species identity', 'Cloth type' and their interaction (fixed factors) on the retention rate of dry propagules after 8 hours (dependent variables). In the analysis of the retention rate of the washed propagules, fixed factors were 'Species identity', 'Cloth type', 'Washing intensity' and their interactions.

Results

Gentle washing at 30 °C did not affect the germination potential of fourteen species, suppressed one and was beneficial for three species (Table 2, Fig. 1, Suppl. material 1: Fig. S2). Intense washing at 60 °C decreased the seedling number of nine and the biomass of ten species (Table 2, Fig. 1, Suppl. material 1: Fig. S2). Washing medium had no effect on germination potential (Table 2).

When exploring the temporal dynamics, we found that the start of germination, mean germination time (MGT) and synchrony were all affected by washing intensity

Table 2. The results of generalised linear models (GLM) fitted on (A) the relative response index (RRI) calculated for the germination characteristics after washing, (B) the attachment rates of propagules on dry clothes and (C) the attachment rate of washed propagules on washed and dried clothes. Significant effects are marked with boldface.

(A) Seed germination characteristics after washing											
	Species		W. intensity		W. medium		Species × W. intensity		Species × W. medium		W. intensity × W. medium	
	F	p	F	p	F	p	F	p	F	p	F	p
Seedling number	**3.63**	**0.000**	**32.66**	**0.000**	0.38	0.682	**8.35**	**0.000**	0.82	0.000	0.53	0.592
Seedling biomass	**3.39**	**0.000**	**60.31**	**0.000**	0.27	0.765	**8.47**	**0.000**	0.90	0.610	0.62	0.541
Mean germination time	**2.66**	**0.002**	**3.64**	**0.057**	0.13	0.880	**5.30**	**0.000**	0.33	0.999	0.18	0.839
Germination synchrony	**1.99**	**0.024**	2.31	0.129	0.14	0.869	**3.14**	**0.000**	0.65	0.900	0.01	0.997
Start of germination	**13.60**	**0.000**	**8.84**	**0.003**	0.29	0.747	**4.53**	**0.000**	1.22	0.189	0.01	0.994
(B) Attachment rate on dry clothes – Possibility for entering the laundry cycle											
	Species		Cloth type		Species × Cloth type							
	F	p	F	p	F	p						
Seed attachment rate	**17.79**	**0.000**	**10.97**	**0.000**	1.21	0.223						
(C) Attachment rates on washed and dried clothes – Possibility for dispersal after washing											
	Species		Cloth type		W. intensity		Species × Cloth type		Species × W. intensity		W. intensity × Cloth type	
	F	p	F	p	F	p	F	p	F	p	F	p
Seed attachment rate	**41.20**	**0.000**	**50.58**	**0.000**	0.02	0.882	**3.39**	**0.000**	0.97	0.476	0.12	0.890

In part A, fixed factors were 'Species' (DF_1 = 12; DF_2 = 336), 'Washing intensity' (DF_1 = 1; DF_2 = 336), 'Washing medium' (DF_1 = 2; DF_2 = 336), the interaction of 'Species × Washing intensity'(DF_1 = 12; DF_2 = 336), the interaction of 'Species × Washing medium'(DF_1 = 24; DF_2 = 336) and the interaction of 'Washing intensity× Washing medium'(DF_1 = 2; DF_2 = 336). In part B, fixed factors were 'Species' (DF_1 = 12; DF_2 = 336), 'Cloth type' (DF_1 = 2; DF_2 = 144) and the interaction of 'Species× Cloth type' (DF_1 = 22; DF_2 =144). In part C, fixed factors were 'Species' (DF_1 = 12; DF_2 = 620),'Cloth type' (DF_1 = 2; DF_2 = 620),'Washing intensity' (DF_1 = 1; DF_2 = 620), the interaction of 'Species × Cloth type'(DF_1 = 24; DF_2 = 620), the interaction of 'Species × Washing intensity'(DF_1 = 12; DF_2 = 620) and the interaction of 'Washing intensity× Cloth type'(DF_1 = 12; DF_2 = 336).
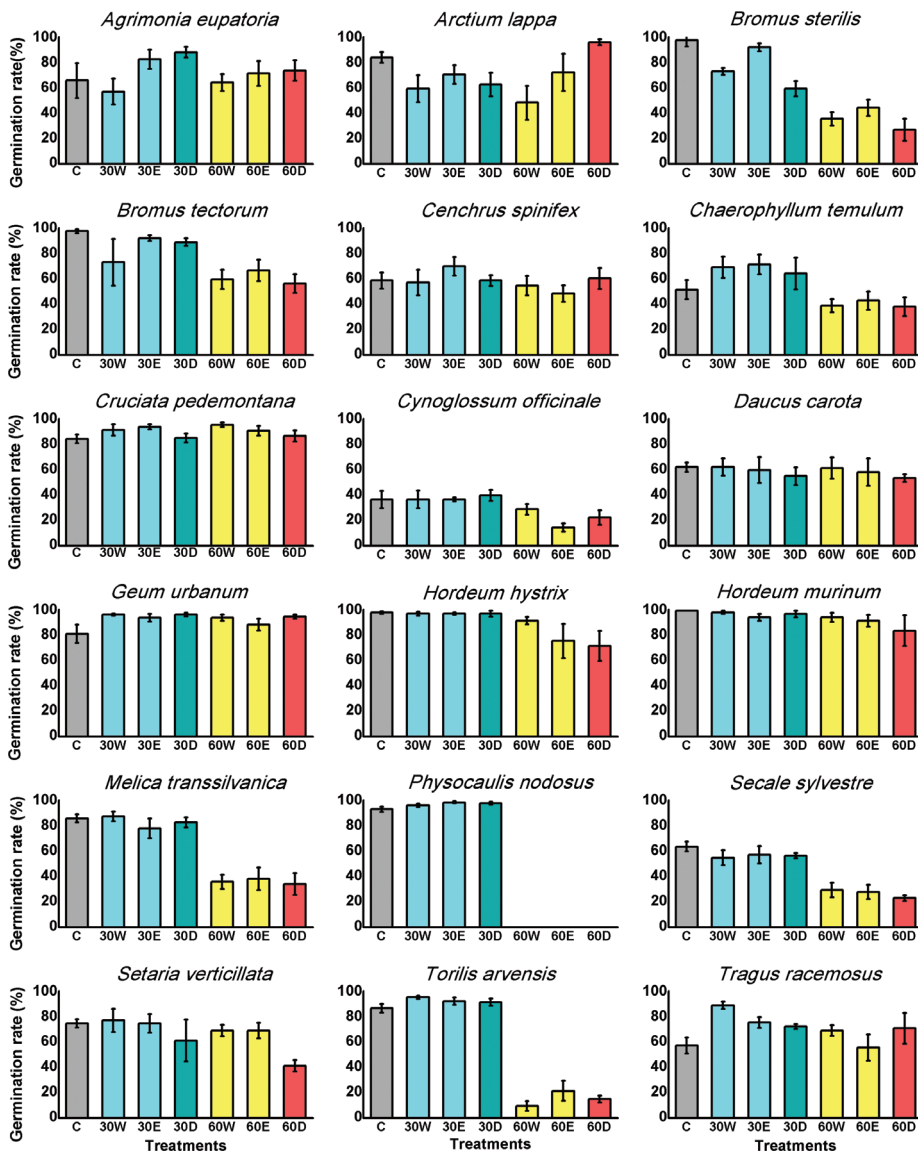
Figure 1. Germination rate (%, mean ± SE) in the control and the six washing treatments. Notations: grey column, C – control; blue columns: gentle washing at 30 °C (30W – washing with water at 30 °C, 30E – washing with eco-friendly soap nut at 30 °C and 30D – washing with detergent at 30 °C); yellow and orange columns – intense washing at 60 °C (60W – washing with water at 60 °C, 60E – washing with eco-friendly soap nut at 60 °C and 60D – washing with detergent at 60 °C). Germination rate is expressed as the percentage of sown propagules that germinated in a treatment (25 propagules were sown in five replicates per treatment except for *H. murinum*, where 25 propagules were sown in three replicates per treatment).

and species identity (Table 2). Washing at 60 °C significantly increased MGT of eight species (Suppl. material 1: Fig. S3) and desynchronised the germination of eight species (Fig. 2). The intensive washing treatments induced earlier germination for three species and later germination for four species (Suppl. material 1: Fig. S4).
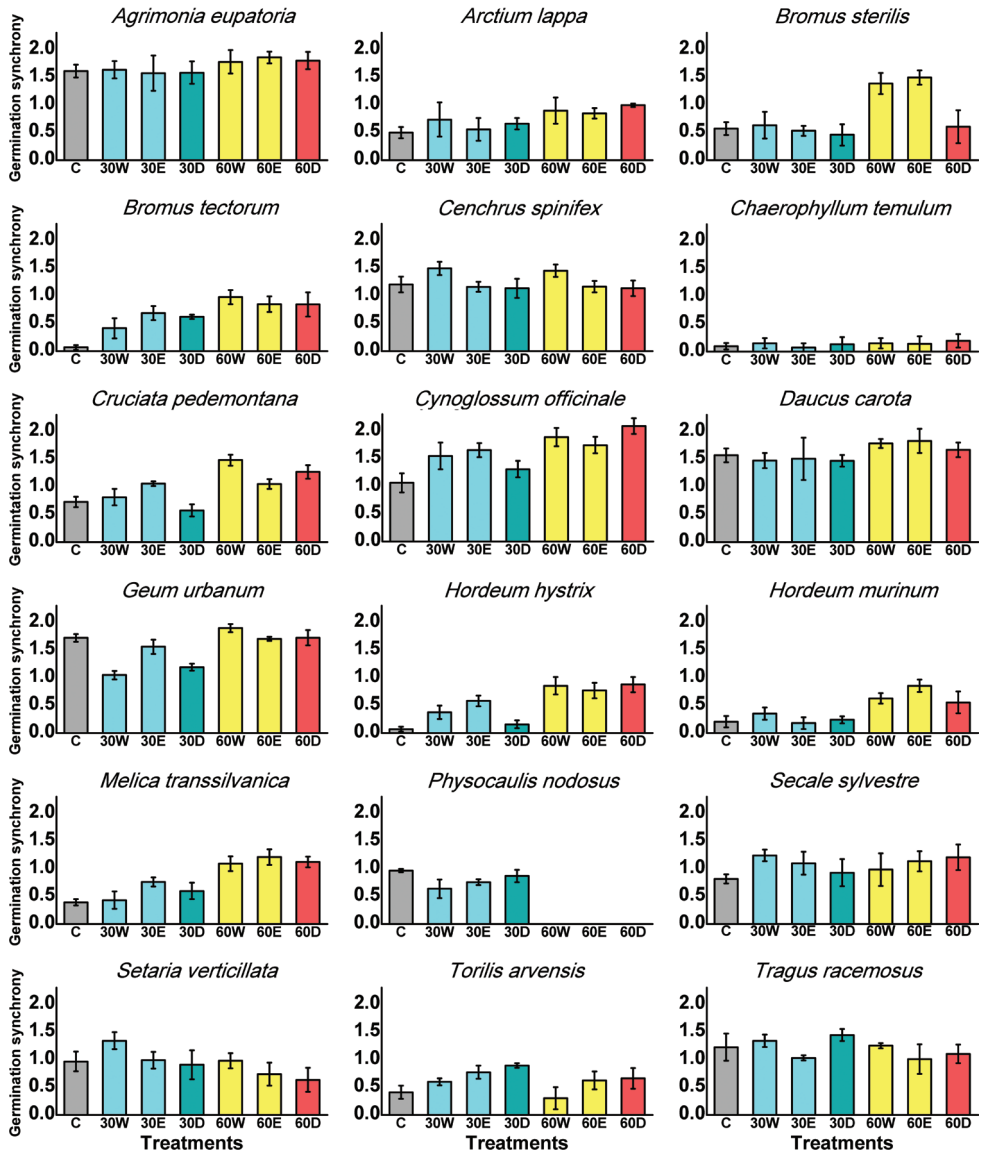
Figure 2. Germination synchrony, expressed as the Shannon diversity of the number of seedlings germinated in certain observation dates (mean ± SE) in the control and in the six washing treatments (5 replicates of 25 seeds were sown per species and treatment). Notations: grey column, C – control; blue columns: gentle washing at 30 °C (30W – washing with water at 30 °C, 30E – washing with eco-friendly soap nut at 30 °C and 30D – washing with detergent at 30 °C); yellow and orange columns – intense washing at 60 °C (60W – washing with water at 60 °C, 60E – washing with eco-friendly soap nut at 60 °C and 60D – washing with detergent at 60 °C).

After attaching dry propagules on clothes, we found that the lowest proportion of propagules (32.4%) remained attached on jeans (Suppl. material 1: Fig. S5). Average retention rates were 42.6% on the fleece sweater and 47.5% on cotton socks (Suppl. material 1: Fig. S5). We found that approximately one third of the propagules

remained attached on clothes after washing and the others were lost in the washing machine and might have entered the sewerage system (Suppl. material 1: Table S1). After drying, out of the fraction of propagules that remained attached on fabrics after washing, on average 95.2% remained attached on fleece, 54.2% on denim and 72.4% on cotton (Suppl. material 1: Fig. S6).

Discussion

We showed that laundry washing, by affecting seedling fitness, germination dynamics and potential dispersal distances, can enhance the dispersal of species outside their native range. We revealed that gentle washing at 30 °C was neutral or even favourable for the germination of the majority of the studied species. Intense washing at 60 °C was detrimental for half of the species. The most important factors mediating germination are probably related to the intensity of washing, i.e. the duration of water-logging, mechanical effects and heat effects. For separating the effects of the components of washing intensity (water-logging, mechanical effects and heat effects), further experiments, focussing on particular parameters of washing cycles would be needed. Our results suggest that, in general, the new trend for using lower washing temperatures to reduce energy consumption (Morgan et al. 2018) probably increases the ratio of viable propagules that leave the laundry cycle. We found that the washing medium had no effect on germination potential. In future studies, it would be interesting to test detergents with different enzymatic activities, which might affect the germination of washed propagules differentially.

We showed that intensive washing desynchronises the germination. Compared to the classical case of epizoochory on mammal's fur, here the dispersal process itself has direct effects on germination dynamics. These effects of laundry washing on germination dynamics have important consequences for establishment: elongated and desynchronised germination is especially advantageous in unstable environments characterised by frequent and unpredictable disturbances (Sales et al. 2013), although it is disadvantageous for establishment in stable or harsh environments (Giménez-Benavides and Milla 2013). If germination is desynchronised, there is a higher chance that at least some seeds will germinate under the most suitable conditions in a new environment (Verdú and Traveset 2005).

In our experiments, we tested the most typical scenario, when propagules are attached on clothes at the time the seeds are ripened (typically early autumn) and the clothes are washed right after that. To model the fate of propagules, we monitored the germination from early autumn until late spring, which includes the main germination period for Central-European plants. For twelve species already germinated in the autumn, washing did not have an effect on the start of the germination (see Suppl. material 1: Fig. S4). There were six species whose control seeds germinated only or mostly in spring. For *Daucus carota* and *Tragus racemosus*, we found that the washed propagules germinated significantly earlier than the control, which implies probably that the mechanical and chemical effects during washing could break the dormancy of these seeds (Hsiao 1979; Okonkwo and Nwoke 1975). However, understanding the physiological background behind the effect of washing treatments on dormancy needs further experimental testing.

We found that a considerable amount of propagules has the potential to enter the laundry cycle, especially in the case of cotton and fleece clothing. We found that washed propagules had even higher retention rates compared to dry ones; thus, laundry washing increases potential dispersal distances for a fraction of the propagules that remain attached even after washing. The retention rates of dry and washed propagules were influenced by species identity, being the longest for species with the most developed appendages. Species with the highest potential for zoochory are amongst the most successful invasives (Moravcová et al. 2015). Additionally, these are the ones that enter the laundry cycle with the highest chance and have the longest potential dispersal distances.

Our results suggest that there are two main directions of post-washing dispersal. (i) Propagules that are detached during drying of the clothes probably get into rural or urban environments or some of them do not get outside of the houses. As urban habitats often provide suitable conditions for the establishment of alien species, it is possible that some of the seeds will germinate and establish in urban habitats and it is also possible that some might become urban invaders (Richardson et al. 2000; Wichmann et al. 2009; Arredondo et al. 2018). Altered germination dynamics after washing can support the establishment of clothing-dispersed propagules in urban areas, which are often starting points of invasions to the peri-urban natural habitats (Chytrý et al. 2008). (ii) Those propagules that remain attached on clothes after drying have the potential for post-laundry long-distance dispersal. We showed that, after laundry washing and drying, there is a fraction of the washed propagules that attach better to the clothes than the dry ones (Suppl. material 1: Figs S5, S6). The transport of washed propagules on the clothes to natural ecosystems is a realistic threat if we consider that people wear their outdoor clothes primarily during their outdoor activities and therefore propagules have a high chance to be dispersed outdoors.

Globally, the largest mass invasion events are connected with transport by vehicles, construction of roads and buildings, international trade and agriculture (Liu et al. 2019); all these processes move a considerable amount of soil, plants and animals over large distances and contain a large number of viable propagules. Clothing-dispersal can also transport a large number of propagules from native ranges to new areas, if we consider the increasing size and mobility of the human population. However, the most important feature of clothing-dispersal is that it can also affect the relatively undisturbed nature reserves which are not exposed to the above-mentioned mass invasions caused by vehicles, construction works, trade or agriculture. Long-distance dispersal after laundry washing might be a major source of plant invasions in such reserves, hiking areas and other remote locations having a unique flora (see also Pickering and Hill 2007; Pickering and Mount 2010; Pickering et al. 2011). Mountains and islands harbour a considerable amount of the protected areas worldwide, but they are also under an increasing pressure by tourism (Pauchard et al. 2009). Geographical isolation and the harsh environmental conditions were able to prevent the spread of invasive species in these areas in the past, but due to the increased human pressure and climatic changes, these areas have recently become increasingly threatened by plant invasions (Pauchard et al. 2009). The dispersal mode described in our study can further aggravate this process and increase the vulnerability of these ecosystems to invasions.

We found that washing of clothing-dispersed propagules might increase the dispersal distances and also affect germination dynamics. In this way, laundry washing can support alien species in a new environment to overcome both propagule and establishment limitations, those factors that controlled their establishment in the past.

Visitors to nature reserves can be the most important dispersal vectors of propagules of non-native species which would otherwise have little chance for being transported there (Pickering et al. 2011). We draw attention to the fact that not only the plants growing along the visitors' actual routes represent a potential source of invasion, but also the whole 'trekking history' of visitors should be considered. This process is already demonstrated for footwear: Ware et al. (2012) estimated that tourists coming from arctic and alpine regions introduce approximately 270,000 propagules yearly into Svalbard on their shoes and the majority of the propagules belong to non-native species. In another study, they found that golf players can carry propagules of non-native species on their shoes to alpine environments in New-Zealand (McNeill et al. 2011). These all emphasise the importance of trekking history in human-mediated seed dispersal and our results suggest that biosecurity protocols should target not only footwear, but also tourists' clothing items. In island countries that face a huge risk of unintended introduction of plants and animals by passengers, such as in Australia (https://www.agriculture.gov.au/biosecurity/avm/military/adf/adf-cleaning-instructions) and New Zealand (https://www.mpi.govt.nz/travel-and-recreation/arriving-in-new-zealand/items-to-declare/#types), regulations on entering the country include the clearance from seeds of the worn clothes. However, these regulations usually do not apply to the clothes carried in the luggage and, in many countries, such biosecurity regulations have not yet been established. Additionally, these rules apply only to the crossing of national borders or other administrative boundaries, such as the Schengen zone of the European Union, implying that, within large countries or within the EU, seeds might be dispersed on passengers' clothes between distant biogeographical regions. For protecting the flora of nature reserves, the establishment of biosecurity regulations would also be necessary at the site level. Our study highlights the importance of personal responsibility for introducing exotic species to areas with high conservation value. Wearing clothes made of fabrics with low seed retention potential (e.g. linen or denim, Ansong and Pickering 2016) in nature reserves can effectively decrease retention rates and can be a good mitigation measure. It is also crucial not picking and leaving the attached propagules on natural sites.

Acknowledgements

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Supplementary material 1

Figs S1–S6 and Table S1

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Explanation note: **Fig. S1.** Photos about the experiments. **Fig. S2.** Seedling dry mass (g, mean ± SE) in the control and the six washing treatments (5 replicates of 25 propagules were sown per species and treatment, except for *H. murinum*, where 3 replicates of 25 propagules were used). Notations: grey column, C – control; blue columns: gentle washing at 30 °C (30W – washing with water at 30 °C, 30E – washing with eco-friendly soap nut at 30 °C and 30D – washing with detergent at 30 °C); yellow and orange columns – intense washing at 60 °C (60W – washing with water at 60 °C, 60E – washing with eco-friendly soap nut at 60 °C and 60D – washing with detergent at 60 °C). **Fig. S3.** Mean germination time (day, mean ± SE) in the control and the six washing treatments (5 replicates of 25 propagules were sown per species and treatment, except for *H. murinum*, where 3 replicates of 25 propagules were used). Notations: grey column, C – control; blue columns: gentle washing at 30 °C (30W – washing with water at 30 °C, 30E – washing with eco-friendly soap nut at 30 °C and 30D – washing with detergent at 30 °C); yel-

low and orange columns – intense washing at 60 °C (60W – washing with water at 60 °C, 60E – washing with eco-friendly soap nut at 60 °C and 60D – washing with detergent at 60 °C). **Fig. S4.** Start of germination (days after sowing, mean ± SE) in the control and the six washing treatments (5 replicates of 25 propagules were sown per species and treatment, except for _H. murinum_, where 3 replicates of 25 propagules were used). Notations: grey column, C – control; blue columns: gentle washing at 30 °C (30W – washing with water at 30 °C, 30E – washing with eco-friendly soap nut at 30 °C and 30D – washing with detergent at 30 °C); yellow and orange columns – intense washing at 60 °C (60W – washing with water at 60 °C, 60E – washing with eco-friendly soap nut at 60 °C and 60D – washing with detergent at 60 °C). **Fig. S5.** Retention rate (%, mean ± SE) of dry propagules of the studied species on three types of fabrics (blue jeans, cotton socks and fleece sweater) during a period of 8 hours. Notations: blue symbols – blue jeans, grey symbols – cotton socks, orange symbols – fleece sweater. **Fig. S6.** Retention rate (%, mean ± SE) of propagules of the studied species washed at 30 °C and 60 °C on washed and dried fabrics of three types (denim, cotton and fleece). Species are listed in a decreasing order of mean retention rate. Notations: blue symbols – denim, grey symbols – cotton, orange symbols – fleece. Species names are abbreviated using the first letters of their genus and species names. Retention rate is calculated as the percentage of the propagules that remained attached on the fabrics after drying in relation to the propagules that remained attached after washing. **Table S1.** Fate of the propagules right after washing at 30 °C, on three fabric types, given as the proportion of propagules (%) remaining on the same fabric where it was originally attached ('same fabric'), moved to other fabric piece ('other fabric') and lost in the washing machine or into the sewerage system ('lost').

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RESEARCH ARTICLE

NeoBiota

Eat and be eaten: trophic interactions of the introduced frog *Scinax quinquefasciatus* in anthropogenic environments in Galápagos

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Abstract

While the Galápagos Archipelago is known for its endemic flora and fauna, many introduced species have also become naturalised there, especially on the human-inhabited islands. The only amphibian species known to have established on the islands, the Fowler's snouted treefrog (*Scinax quinquefasciatus*), is thought to have arrived about two decades ago. Since then, this treefrog has substantially extended its range to the islands of Santa Cruz and Isabela. Our study explores the potential influence of this introduced amphibian on native trophic systems on Santa Cruz and identifies potential antagonists likely to control larval frog populations. To understand the impact of *S. quinquefasciatus* as a predator of local invertebrate fauna, we performed a stomach-content analysis of 228 preserved adult specimens from seven different localities on Santa Cruz. Of the 11 macroinvertebrate orders recorded, Lepidoptera constituted more than 60% of the contents. We also identified active predators of *S. quinquefasciatus* tadpoles: larvae of the endemic diving

beetle (*Thermonectus basillarus galapagoensis*). To determine the efficiency of this predator, we conducted predator-prey experiments in ex situ conditions. Tadpole predation was highest after first exposure to the predator and significantly decreased over time. Our experimental results demonstrate that although *T. b. galapagoensis* larvae are effective tadpole predators, their feeding saturation rates are likely inadequate for frog population control. Our findings provide the first baseline data necessary to make informed ecological impact assessments and monitoring schemes on Santa Cruz for this introduced treefrog.

Introduction

Introduced species, which often transition to invasive species, are considered to be a major threat to global biodiversity (Early et al. 2016). The negative impacts of invasive species on native biota are particularly severe in insular ecosystems with high influxes of human trade and travel (Courchamp et al. 2003), such as the Hawaiian Archipelago (Beard and Pitt 2006), Guam (Christy et al. 2007) and Taiwan (Jang-Liaw and Chou 2015). The Galápagos Archipelago is no exception, with over 1500 established introduced species, many of which are invasive (Toral-Granda et al. 2017). Worldwide, frogs represent the highest proportion of the 322 herpetological reported invasions (Kraus 2009). However, apart from a few well-known examples, such as the cane toad (*Rhinella marina*) or the American bullfrog (*Lithobates catesbeianus*) (e.g. Laufer et al. 2008; Measey et al. 2016; Kosmala et al. 2017), amphibian invasions and their impacts on native biota are not well studied. Fowler's snouted treefrog, *Scinax quinquefasciatus* (Fowler 1913), represents one of these cases. Basic data on this species are still lacking, despite its comparatively long introduction history (Cisneros-Heredia 2018): *S. quinquefasciatus* is assumed to have been introduced to Galápagos in the late 1990s (Snell et al. 1999).

Of the four human-inhabited islands of the Archipelago, *S. quinquefasciatus* is only known to occur on Santa Cruz and Isabela. It was formerly also present on San Cristóbal (Cisneros-Heredia 2018), but this could not be confirmed in a recent assessment (Ernst et al. unpubl. data) and breeding populations have never been reported on the island.

Pazmiño (2011) reported a close genetic relationship between the population on Isabela and several populations in the lowlands of western Ecuador (north of Guayas, south of the Manabí and Los Rios Provinces). At least two independent colonisation events took place on the islands (Pazmiño 2011); further investigations of these introduction events are currently underway (Ernst et al. in prep).

The ecology and potential impact of *S. quinquefasciatus* on the native ecosystems of Isabela have previously been addressed in Zurita (2004), Vintimilla (2005) and Mieles (2006). No information of this kind currently exists for Santa Cruz, which has recently experienced agricultural intensification and rapid urbanisation of rural areas

(CGREG 2016). These land-use changes have resulted in the expansion of irrigation systems, including water reservoirs that now provide large permanent freshwater habitats. Since these human developments are likely facilitating the successful establishment and spread of *S. quinquefasciatus* on Santa Cruz, there is an urgent need to study the impacts of this species on the resident fauna.

Invasive species often disrupt predator-prey interactions: as a new predator that consumes native prey (Krisp and Maier 2005), as a new prey item for native predators (Petrie and Knapton 1999; Bulté and Blouin-Demers 2008) or both (Holway et al. 2002). Here, we address both sides of this trophic relationship by (1) determining and quantifying the dietary preferences of adult *S. quinquefasciatus* via stomach-content analysis and (2) identifying potential native tadpole predators and quantifying their predation capacity in controlled ex situ experiments.

Methods

Study Area

Our study was conducted in the highlands of Santa Cruz, located at the centre of the Galápagos Archipelago (Fig. 1). The first settlers arrived in the highlands between 1910 and 1938 (Lundh 1995, 1996), subsisting on agriculture and fishing. Over time, the human population grew and spread due to fishing and tourism (Epler 2007). Population growth, combined with the associated plant invasions, led to the degradation of approximately 86% of the highland ecosystems (Trueman et al. 2013).

The highlands of Santa Cruz support greater biodiversity and thus productivity than the lowlands, which are more extensive, but drier (Porter 1984). The annual mean climatic values for the study sites in the highlands of Santa Cruz for the years 1987 to 2019 were: 1380 mm for precipitation, 22.2 °C for temperature and 90.3% for relative humidity (Charles Darwin Foundation, unpubl. data). However, the means for these parameters can vary considerably from year to year, due to the El Niño-Southern Oscillation (ENSO) phenomenon (Snell and Rea 1999).

This study was conducted from April to May 2017–during the rainy season-at one ranch and six agricultural sites in the highlands of Santa Cruz (Fig. 1). Our core site, Rancho El Manzanillo, is located 3 km off the main road that connects the airport ferry port with the town of Puerto Ayora. This traditionally agricultural ranch has recently become a popular ecotourism destination for spotting wild giant tortoises (*Chelonoidis porteri*) in their natural habitat. In the late 1990s, landowners created several artificial ponds to attract tortoises; these water sources now also provide reproductive habitats for *S. quinquefasciatus*. We collected adult frogs and predatory beetle larvae within or near water features at Rancho El Manzanillo (hereafter 'core locality') and six similar agricultural sites (B, C, D, E, F, G; Fig. 1). We conducted the predatory capacity experiments at the core locality.
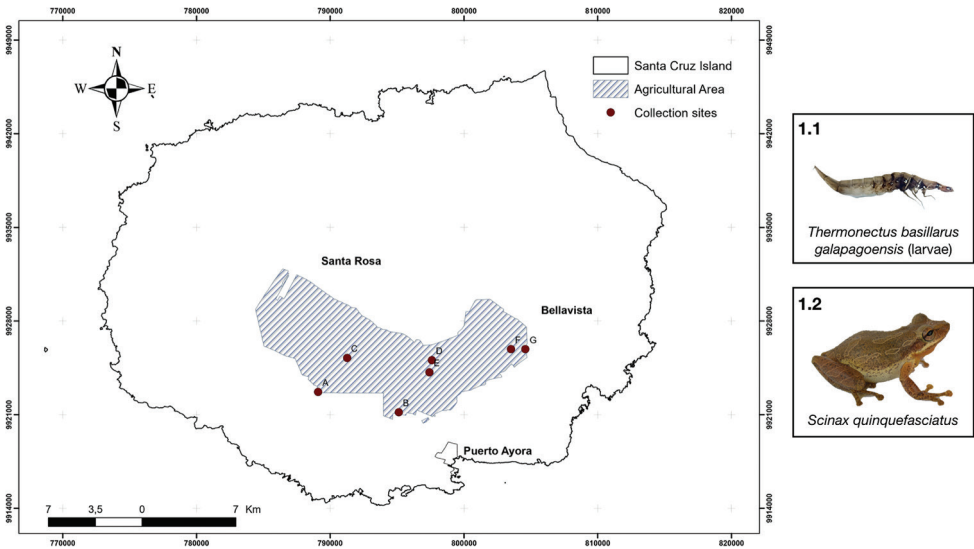
Figure 1. Study area and collection sites (red dots) of *Scinax quinquefasciatus* specimens in the highlands of Santa Cruz, Galápagos, Ecuador. A = Rancho El Manzanillo (core locality). B – G = additional collection sites within the agricultural area (grey shading) of the island. 1.1) Larvae of the endemic diving beetle *Thermonectus basillarus galapagoensis*. 1.2) Adult of the introduced frog *Scinax quinquefasciatus*. Not to scale.

Stomach-content analyses

We captured adult and sub-adult individuals of *S. quinquefasciatus* using Visual (VES) and Acoustic Encounter Surveys (AES), as described by Rödel and Ernst (2004), from 8 pm to 12 am, for 14 consecutive nights. All frogs were euthanised with liquid lidocaine and fixed in 70% ethanol no more than five hours after capture. Samples were then transported to the Charles Darwin Research Station (CDRS), where their digestive tracts were removed following procedures described in Döring et al. (2016). Prey items were examined under an Olympus Stereo Microscope SZ61-RT and identified to order, using reference material from the Terrestrial Invertebrate Collection of the CDRS (ICCDRS 2020). We examined the stomach and intestine content of 228 frogs, 156 from the core locality and 72 from the six other agricultural sites.

Predatory capacity experiments

For five consecutive days, we surveyed potential larval habitats, including seasonal and artificial ponds, for the presence of tadpoles and their potential aquatic predators. While we observed Anisoptera (dragonfly) larvae-known to be effective tadpole predators elsewhere-in some water bodies, they never co-occurred with *S. quinquefasciatus* tadpoles. Since we only observed the endemic diving beetle *Thermonectus basillarus galapagoensis* in the same water bodies, we chose this species as the target organism for the following predation experiments.

In order to (1) ensure that tadpole exposure to beetle predators was novel and (2) minimise ontogenetic and interpopulation differences in larval predation response (Narayan et al. 2013), we reared the tadpoles used in our experiments rather than collecting them from available ponds. To do so, we first captured four amplectant *S. quinquefasciatus* couples at the core locality and kept them in plastic containers with 100 ml of mixed water (75% rainwater and 25% pond water). After the females had spawned, eggs were transferred to different plastic containers with 200 ml of mixed water. Hatched tadpoles were used in experiments after they reached Gosner stages 21–25 (Gosner 1960). From two different ponds at the core locality, we captured 28 *T. b. galapagoensis* beetle larvae (mean length: 1.59 ± 0.18 cm) with a strainer. Larvae were transferred to plastic containers with 200 ml of mixed water prior to the experiment. In order to equalise their feeding motivation, we fed beetle larvae with two tadpoles from our hatchery every four hours for 24 hours and then deprived them of food for another 24 hours prior to experimentation. To prevent predation events from external predators, all plastic containers were covered prior and during experimentation.

Our experiments consisted of one treatment (predatory capacity) and two survival control experiments (tadpole survival and beetle larvae survival). For the predatory capacity experiments (N = 14), we introduced one food-deprived beetle larva into a plastic container with 20 tadpoles from our hatchery. For the tadpole survival experiments (N = 14), we transferred 20 tadpoles into one plastic container under the same conditions as the previous treatment, but without beetle larva. Finally, for the beetle survival experiments (N = 14), we added one food-deprived beetle larva to one plastic container under the same conditions, but without any tadpoles. Treatments and control experiments were run at the same time over the course of four days.

We monitored experiments and recorded data every two hours during each 12-hour period. Fourteen experiments were conducted from 12:00 am until 12:00 pm over four consecutive days (day 1 = four replicates, day 2 = three replicates, day 3 = four replicates and day 4 = three replicates), according to the number of tadpoles and beetles ready to be introduced into an experiment. We then measured mortality in tadpole survival experiments and both control treatments. Dead, but physically intact tadpoles with no signs of injury/attack were not included in the predation mortality totals. Individual beetle larvae and tadpoles were only used once.

Statistical analyses

To estimate the overall dietary composition of *S. quinquefasciatus* in the agricultural areas of Santa Cruz, we calculated two indices for each taxon found in the stomach contents: (1) numerical percentage of each prey consumed and (2) frequency of occurrence. Numerical percentage estimates the quantity of ingested prey items by dividing the total stomach contents from a specific order by the total number of prey items (according to the method of Calver and Wooller 1982). Frequency of occurrence estimates the per-taxa breakdown within the diet by dividing the number of digestive

tracks containing a specific taxon by the number of stomachs containing food content. Frogs with empty stomachs were not included in the analysis.

Since we sampled frogs in the breeding season, we also hypothesised that the presence of prey in the stomach (vs. an empty stomach) would differ based on sex. We conducted an analysis of variance (ANOVA) to compare the amount of stomachs with prey items amongst males and females. We previously checked for homogeneity of variances amongst groups by using a Hartley's F_{max} test.

To determine if the predation-related mortality in tadpoles was time-dependent, we used a Generalised Estimating Equation (GEE). The GEE tests for subject (trial number) and within-subject (time-interval) effects in a repeated-measure experimental design, considering these as random factors. In our model, the response variable was cumulative predation-related mortality, while the explanatory variable was time interval. We only counted the experimental units in which the predator remained alive until the end. After running the model, we used a post-hoc Bonferroni test ($\alpha = 0.05$) to determine which time intervals were responsible for significant differences in cumulative predation-related mortality.

We used another GEE test to determine if cumulative non-predation-related mortality was significantly different between tadpole survival (control) and predatory capacity experiments. Since mortality was not normally distributed, we chose a negative binomial distribution with a logarithmic link function for the model. Cumulative non-predation-related mortality was selected as the response variable, while experiment type (predatory capacity vs. tadpole survival) and time intervals were set as explanatory variables. Subject and within-subject effects were the same as in the previous analysis. All statistical analyses were performed with SPSS, version 22 (IBM Corp. 2013).

Results

Stomach-content analyses

Out of the 228 captured individuals (136 males, 79 females and 13 subadults), 54 had stomach content (34 males, 18 females–16 of which were gravid-and 2 subadults). Of those, 36 were collected from the core locality and 18 from the additional agricultural sites (Fig. 1). Five of the seven collection sites had individuals with ingested terrestrial invertebrates (Core location, B, C, D and E). Adult males were more frequently collected than either females or sub-adults. The stomachs of 5.8% of the collected specimens contained food items with a high degree of digestion, forming an amorphous substance for which identification of individual invertebrates was not possible.

The 54 specimens found in *S. quinquefasciatus* stomachs consisted mostly of Lepidopterans (numerical percentage [NP]: 30%, frequency of occurrence [FO]: 61.11%), followed by Acarina (NP: 44.38%, FO: 5.56%). In total, 160 macroinvertebrates from

Table 1. Description of prey items identified in *Scinax quinquefasciatus* individuals, classified by order. Total number of prey items represents the total number of individual invertebrates in each order consumed by collected frogs (multiple individuals could be found in the same stomach). Frequency of consumption represents the number of stomachs in which a specific order was found. Numerical percentage is the number of prey items (per order) divided by the total number of prey items (n = 160). Frequency of occurrence represents the number of stomachs that contained a specific taxon (frequency of consumption) divided by the total number of stomachs with food content (n = 54).

Order	Total number of prey items	Frequency of consumption	Numerical percentage	Frequency of occurrence
Lepidoptera	48	33	30	61.11
Acarina	71	3	44.38	5.56
Araneae	6	5	3.75	9.26
Blattodea	1	1	0.63	1.85
Neuroptera	2	2	1.25	3.70
Hymenoptera	9	6	5.63	11.11
Orthoptera	5	5	3.13	9.26
Hemiptera	2	2	1.25	3.70
Isopoda	9	2	5.63	3.70
Coleoptera	5	4	3.13	7.41
Dyptera	2	1	1.25	1.85

11 orders were identified as prey items (Table 1). The Hartley's F_{max} test verified the assumption that variances were equal across groups. We found no significant differences in the number of stomachs with prey items between males and females (ANOVA: F [1,8] = 0.40, p < 0.05).

Predator-prey experiments

Nine out of the fourteen predator capacity experiments were included in the final model, since we only used the trials in which the beetle predator survived the entire experiment duration (4 days). Cumulative predation-related mortality significantly decreased over time (Wald Chi-Square = 125.92, df = 5, p = 0.001, Fig. 2). The post-hoc Bonferroni test (α = 0.05) showed that during the first two-hour interval, the number of predated tadpoles was the highest, with a mean value of 4.89 tadpoles. This was significantly different from the third-, fourth-, fifth- and sixth-time intervals (Table 2).

There was no significant difference in tadpole mortality between the non-predation deaths that occurred in the predatory capacity experiments versus those that occurred without the presence of a predator (Wald Chi-Square = 1.61, df = 1, p = 0.20, Fig. 2). Tadpole mortality was not significantly different over time (Wald Chi-Square = 5.03, df = 3, p = 0.17, Fig. 2). Only four of the tadpole control trials ended with one or two dead tadpoles; none died in the other ten experiments. Beetle larvae died before the end of the experiment in eight of the larvae control trials.
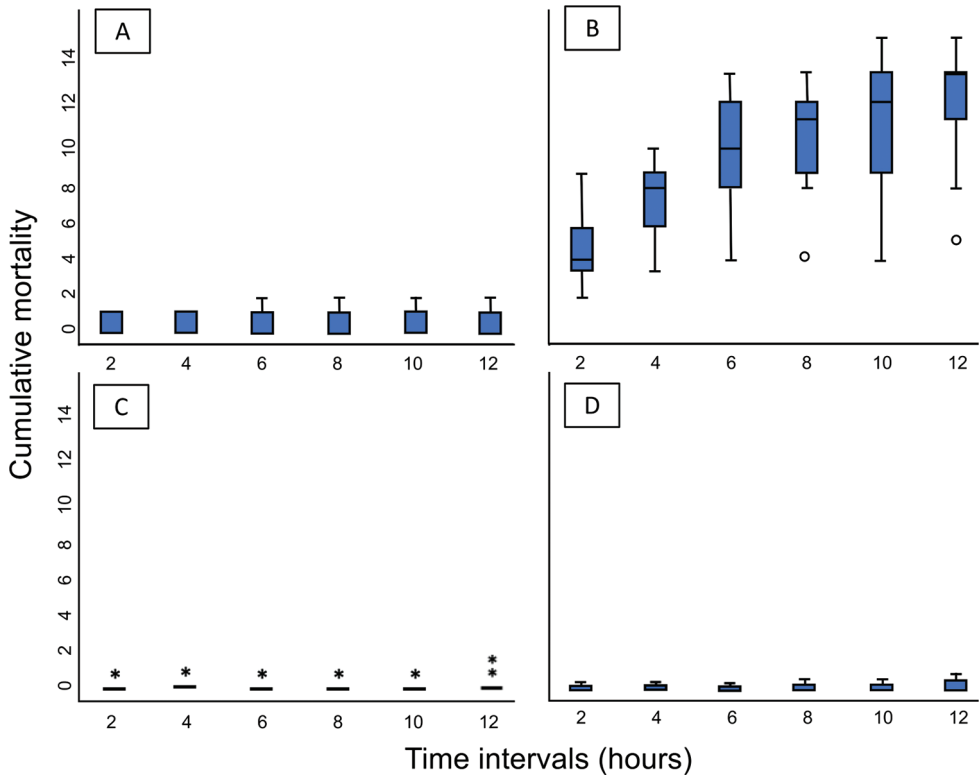
Figure 2. Boxplots depicting comparisons of cumulative mortality rates in predator-prey experiments over time (predator = *Thermonectus basillarus galapagoensis* larvae; prey = *Scinax quinquefasciatus* tadpoles) **A** cumulative non-predation-related mortality of tadpoles in predatory capacity experiments **B** cumulative predation-related mortality of tadpoles in predatory capacity experiments **C** cumulative larvae mortality in survival control experiments **D** cumulative non-predation-related mortality in tadpole survival experiments. Empty circles outside boxplots represent outlier values (1.5 times higher than box height). Asterisks represent extreme outlier values (3 times higher than box height).

Discussion

One way to determine the trophic effect of an introduced species is to carry out a stomach-content analysis. In this study, *Scinax quinquefasciatus* in the highlands of Santa Cruz are shown to have a diet that consists mostly of Lepidopterans, followed by Acarina (Table 1). These results are consistent with those found by Mieles (2006), who found that Lepidopterans were also one of the most common prey orders of *S. quinquefasciatus* on Isabela. However, that study did not specify the frequency of Lepidoptera consumption.

This apparent preference for Lepidopterans is likely due to their availability in the environment. Anurans are typically diet generalists (Duellman and Trueb 1994), which enables them to compete with native species that are likely specialised to local biotic conditions. Abiotic factors could also influence the availability of certain in-

Table 2. Results of the Bonferroni post-hoc test (α = 0.05), describing differences between time intervals in the cumulative number of *Scinax quinquefasciatus* tadpoles predated on by the beetle larvae *Thermonectus basillarus galapagoensis* during the execution of 12-hour predator capacity experiments (N = 9). Asterisks indicate significant differences between mean values of predated tadpoles with a 95% confidence level.

Time intervals	Cumulative # of predated tadpoles (mean value across trials)	Difference in predated tadpoles between time intervals		Significance
1st 0 h – 2 h	4.89	0–2 h vs. 2–4 h	-2.44	
2nd 2 h – 4 h	7.33	0–2 h vs. 4–6 h	-4.89	*
3rd 4 h – 6 h	9.78	0–2 h vs. 6–8 h	-5.11	*
4th 6 h – 8 h	10	0–2 h vs. 8–10 h	-6	*
5th 8 h – 10 h	10.89	0–2 h vs. 10–12 h	-6.67	*
6th 10 h – 12 h	11.56			

sects. In the highlands of Santa Cruz, various sources of artificial light (i.e. street lighting or home-generated light) attract a significant number of nocturnal Lepidopterans (Rydell 1992; Hölker et al. 2010), facilitating their predation (Rydell 1992; Tihelka 2019). In addition, the presence of rainwater repositories for irrigation purposes serve as an egg repository for many Lepidopteran insects (e.g. Noctuidae), thus supplying additional resources for their biological development (Roque-Albelo 2006). Since community compositions of terrestrial invertebrates vary across the Galápagos Islands (Peck 2001), we expected that results from the stomach analysis in our study would be different from those obtained on Isabela (Mieles 2006). However, despite presumed differences in the diets of *S. quinquefasciatus* on the two islands, this was shown to not be the case.

Sex did not influence the likelihood that a frog's stomach contained prey: 22.8% of females and 25% of males had prey items in their stomachs. This may be related to the fact that we sampled during the *S. quinquefasciatus* mating season (rainy season, December-May), when both sexes are expending energy on breeding. In many frog species, males invest more energy in behaviour related to reproduction than foraging during the breeding period (Wells 1978; Given 1988). The abundance of prey items in this anthropogenic system may mitigate the trade-off between eating and reproducing.

Even though most studies on introduced species focus on their effect on native prey communities (Fritts and Rodda 1998; Ricciardi and Cohen 2007), their role as prey is equally important. This study provides the first record of a *S. quinquefasciatus* predator in Galápagos: the endemic diving beetle *Thermonectus basillarus galapagoensis*. Our controlled predator-prey experiments indicated that the beetle larvae had a significant influence on the mortality rates of *S. quinquefasciatus* tadpoles. Studies in other ecosystems have also provided evidence of tadpole vulnerability to aquatic beetle

predators (i.e. Formanowicz 1986; Müller and Brucker 2015), but this is the first account for the Galápagos Archipelago.

If the feeding behaviour of *T. b. galapagoensis* larvae were selective (i.e. showing a strong preference for tadpoles) and/or if their populations were highly abundant, this endemic beetle could serve as a biological control for *S. quinquefasciatus*. However, our predator-prey experiments showed that the endemic beetle larvae stopped feeding before the tadpole resource was depleted, predating on a total mean value of 11.6 tadpoles after the 12-hour period. This 'feeding saturation' has direct implications for *S. quinquefasciatus* population control, suggesting that the predator-to-prey ratio is too skewed for the beetle to diminish populations of the invasive frog. This mirrors our observations in nature: there were far more tadpoles than beetle larvae in each surveyed water body on Santa Cruz. *T. b. galapagoensis* larvae presumably preyed on other animals prior to the arrival of *S. quinquefasciatus* to the island, but our finding also suggests that the beetle larvae have not developed a tadpole specialisation-decreasing its potential as a natural control agent. A recent study showed that an introduced bird, the smooth-billed ani (*Crotophaga ani*), feeds on *S. quinquefasciatus* adults in Galápagos, but predation rates are also too low to have an effect on the frog's population size (Cooke et al. 2020).

Population dynamics of introduced and invasive species depend on biological parameters (e.g. fecundity, growth, survival; Nakano et al. 2015)–and in this particular case, water reservoirs, prey availability and the expansion of agricultural sites. Our results suggest that *S. quinquefasciatus* populations are likely to remain stable or even increase on Santa Cruz. Their main prey items are common (Peck 2001) and, although tadpole predation occurs, it is currently not sufficient to decimate local populations. Additionally, the increasing occurrences of artificial ponds and rainwater reservoirs in the agricultural areas of Santa Cruz provide ideal habitats for reproduction and hydration-necessary components for anuran survival and growth (Rogowitz et al. 1999; Brand and Snodgrass 2010). As agricultural expansion continues in the highlands of Santa Cruz, the reproduction and proliferation of *S. quinquefasciatus* will likely follow suit.

Conclusion and future directions

Due to rapid development and the increasing human population, Santa Cruz is prone to invasive species events. *Scinax quinquefasciatus* is the first successfully invasive amphibian on the island; furthering our understanding of its ecological effect(s) is crucial for management, especially in such a fragile and unique ecosystem. As reproduction for both frogs and beetles in the highlands is apparently restricted to water sources provided in the rainy season and/or anthropogenic structures, we recommend that long- term research be conducted to investigate the frog's ontogeny, especially in relation to beetle presence/absence.

This diet composition study was limited to higher taxonomic identification levels due to the nature of digested stomach contents (exoskeletons, wings etc.) and economic constraints that prevented us from testing with molecular methods. Further research

should address the selection of native, endemic and introduced prey item ratios using DNA-metabarcoding approaches.

Our findings strongly suggest that *Scinax quinquefasciatus* population growth is likely to remain stable or increase on Santa Cruz. The dietary preferences and predation rates by natural predators on this introduced frog should be taken into account when considering management strategies in the Galápagos Islands.

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Supplementary material 1

Prey orders consumed by collected Scinax quinquefasciatus in the highlands of Santa Cruz island, Galápagos, Ecuador

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Data type: Table

Explanation note: Description of prey items identified in *Scinax quinquefasciatus* individuals, classified by order. Total number of prey items (n = 160) and total number of stomachs with food content (n = 54).

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RESEARCH ARTICLE

Marine hitchhikers: a preliminary study on invertebrates unintentionally transported via the international pet trade

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Abstract

The pet trade in aquatic organisms is a significant source of non-indigenous species introductions. In comparison with ornamental animals, unintentionally transported invertebrate assemblages are easily overlooked by traders and keepers. Moreover, hitchhiking species detection and identification is difficult even for experts. The densities of "hitchhikers" in aquaria may be relatively higher than those in the wild. These phenomena are known in freshwater aquaria but poorly studied in marine ones. We found 17 species of non-ornamental marine invertebrates in one of the leading importers of aquarium species in the Czech Republic in November 2017. The set comprised six gastropods, two bivalves, three cnidarians, two echinoderms, two crustaceans, and two polychaete worms. In one case, a symbiont was also detected, associated with the host "hitchhiker". No "live rocks" are traded by the surveyed wholesaler. Thus, the found animals were not imported together with this item as larvae or eggs. Contrary to the transport of targeted ornamental species, it is clear that transport of "hitchhikers" is occurring despite standard legislative regulations and should be brought to the attention of conservationists, wildlife managers, policymakers and other stakeholders.

Keywords

aquarium, biological invasion, invertebrate, non-ornamental species, symbiont

Introduction

While a majority of cultured and captured aquatic animals are exploited for human consumption, ornamental aquaculture is also an important and expanding sector of this industry (Padilla and Williams 2004). The keeping of aquatic animals and plants in aquaria is one of the most popular hobbies in the world (Tlusty 2002; Maceda-Veiga et al. 2016; Novák et al. 2020). In contrast with ornamental freshwater animals, marine fishes and invertebrates are mainly collected in the wild and millions of individuals of thousands of species are removed mainly from tropical coral reefs year by year (Rhyne et al. 2017). For this reason, researchers focussing on the exploitation of marine resources have proposed some suggestions on how to improve the sustainability of many harvested species, especially those not listed in the Convention on the International Trade in Endangered Species (CITES, www.cites.org), for example on the collecting of coral fish larvae in the wild for subsequent culture and stocking in aquaria as ornamentals (Bell et al. 2009; Lucas and Southgate 2019). The improvement of breeding in captivity is also highlighted but it is still only feasible for a few species due to a lack of proper methods and technologies (Tlusty 2002; Olivotto et al. 2011). Generally, decision-makers regulate the trade with marine biota including ornamental animals both locally and internationally, such as in the European Union (Duffy 2016) or the member countries in case of The International Council for the Exploration of the Sea (ICES) (Gollasch 2007).

However, some species may behave as invaders when they are released or they escape to a new locality beyond their native range. Even if there is still a debate on the pathway by which the species was introduced, the most highlighted invasive species in this regard, lionfishes (*Pterois volitans* and *P. miles*) invaded the Atlantic Ocean in the 1990s with devastating consequences for native benthic fauna (Albins and Hixon 2008, 2013; Green et al. 2012). Also, the aquarium origin of the green alga *Caulerpa taxifolia* introduced to the Mediterranean Sea can be mentioned (Jousson et al. 1998).

Aquatic organisms subjected to trade for ornamental purposes are transported intentionally (i.e., deliberately) and their invasion potential is known or could be evaluated. Unfortunately, the invasion potential of associated symbionts of intentionally transported species or faunal assemblages unintentionally transported with the targeted species (hereafter called "hitchhikers") are mostly overlooked. In comparison with the freshwater pet trade, where this phenomenon is well known (Rixon et al. 2005; Duggan 2010; Patoka et al. 2016a, b; Duggan et al. 2018), studies on unintentionally transported marine animals are lacking except for "live rocks" and locally transported organisms. The "live rocks" (marine rocks and old coral skeletons traded and used in marine aquaria for biological filtration as well as artificial reef substrate for other organisms and aesthetic functions) serve as a reservoir for a variety of marine microorganisms and invertebrates transported internationally as larvae or eggs (Padilla and Williams 2004; Calado and Narciso 2005; Walters et al. 2006). Various "hitchhikers" were found randomly transported with the locally traded popular marine aquarium green macroalga *Chaetomorpha* sp. in Florida (Odom 2012). The need for

further detailed study is essential because restrictions and regulation of unintentionally transported biota seem to be ineffective or simply impossible due to difficulties in species detection and identification. Interestingly the densities of "hitchhikers" in aquaria may be relatively high in comparison to the natural density of the same species in the wild (Ernst et al. 2011).

Many "hitchhiking" species have proven to be quite hardy. They are able to survive transport in sub-optimal conditions, as was documented by various aquatic animals found alive in boxes with water hyacinths (*Eichhornia crassipes*) shipped without water from Indonesia to the Czech Republic (Patoka et al. 2016b). Moreover, their invasion potential is in many cases high compared to ornamentals (Patoka et al. 2017). For the successful invasion of any aquarium species, individuals must overcome a series of sequential obstacles including transportation, release or escape from the tank to a new locality, and establishment of a new population in the wild. Although "hitchhikers" such as organisms from "live rocks" can generally improve the water quality in the tank (Yuen et al. 2009), some of them, typically species that pose a threat to fish and other aquarium inhabitants, are unwanted by hobbyists (Corsini-Foka et al. 2013). As a consequence, their release from the aquarium to a new locality is possible, as in the case of the toxic coral reef crab *Actaeodes tomentosus* in the Mediterranean Sea (Corsini-Foka and Kondylatos 2015).

Although there is no invasion risk of marine species in landlocked countries, animals can pass through the wholesaler-wholesaler or wholesaler-customer links and can thus be transported from an importer in the landlocked country to a coastal region where the invasion becomes a real threat as the secondary introduction. This is also true for "hitchhikers". It was previously noted that despite their small size, aquatic "hitchhikers" can significantly affect the ecosystems which they invade (Duggan 2010).

Improving knowledge about this overlooked part of the international pet industry can help to establish effective management strategies to reduce introduction rates. The Czech Republic is known as one of the leading importers for aquatic ornamental species and re-exporting many of these animals to other European countries (Kalous et al. 2015; Evers et al. 2019). Since we were alerted by the staff of the Czech wholesaler importing marine animals for ornamental purposes about an occurrence of "hitchhiking" creatures in their aquaria, we decided to survey the ornamental marine organisms there to determine which species are transported and stocked unintentionally as a preliminary study possibly resulting in future risk assessment of found taxa.

Methods

Data collecting

In 2017, we surveyed on two sampling occasions (on 6 and 20 November) 30 aquaria containing marine animals in the premises of the leading wholesale trader of ornamental organisms in Prague, in the Czech Republic, in business from 1990. First, we inter-

viewed staff (three persons) about "hitchhiking" creatures referred to as unintentionally imported. Subsequently, we visited the facility and these organisms were visually observed in tanks. Next, with the use of soft entomological tweezers, five individuals per species were sampled if possible. Finally, we did additional detailed searches to find more taxa in aquaria. The minimum size of organisms considered was 5 mm. These creatures were not transported with "live rocks" because these rocks are not traded in the surveyed wholesalers. Individuals were photographed and selected specimens were preserved in pure alcohol for later identification. The staff was asked about the origin of found organisms.

DNA analysis

For species identification, one individual of each collected taxon was separately DNA sequenced. DNA was isolated from ethanol-preserved tissue using DNeasy Blood and Tissue Kit (Qiagen GmbH, Hilden, Germany) according to the manufacturer´s instructions. The mitochondrial cytochrome oxidase subunit I (COI) gene was amplified using primers jgLCO1490 5'-TITCIACIAAYCAYAARGAYATTGG-3' and jgHCO2198 5'-TAIACYTCIGGRTGICCRAARAAYCA-3' (Geller et al. 2013). DNA extraction and amplification were processed according to (Patoka et al. 2016c). DNA was sequenced using the Macrogen sequencing service (www.macrogen.com). Chromatograms were assembled and checked for potential errors using BioEdit 5.0.9 software (Hall 1999). The obtained DNA sequences have been submitted to Gen-Bank (https://www.ncbi.nlm.nih.gov/genbank/). The Basic Local Alignment Search Tool (BLAST) was employed to find similarities in sequences in GenBank. The result was obtained in the form of a ranked list based on a normalized percent identity score, followed by individual sequence alignments (Madden 2013).

Results

In total, we found 17 "hitchhiking" taxa from six animal groups; six gastropods, two bivalves, three cnidarians, two echinoderms, two crustaceans, and two polychaete worms, in the leading wholesale trader of ornamental marine organisms in the Czech Republic (Fig. 1). Based on interviews with staff, we immediately found most of the "hitchhiking" species in the suggested tanks with no difficulty, but some species were not found in numbers of five or more individuals (details in the next paragraph). Just one more taxon was subsequently found through detailed inspection of the tanks and this was of a tiny size less than 5 mm (*Cymodoce* sp., Fig. 1O). From all samples sequenced for species identification (Table 1), in six individuals the PCR amplification was not successful (samples Nos. 212–214, 218, 221 and 222, hence not included in Table 1; these taxa were identified morphologically on the certain level such as bivalves etc.). For the remainder, the obtained COI fragments matched with the publicly avail-
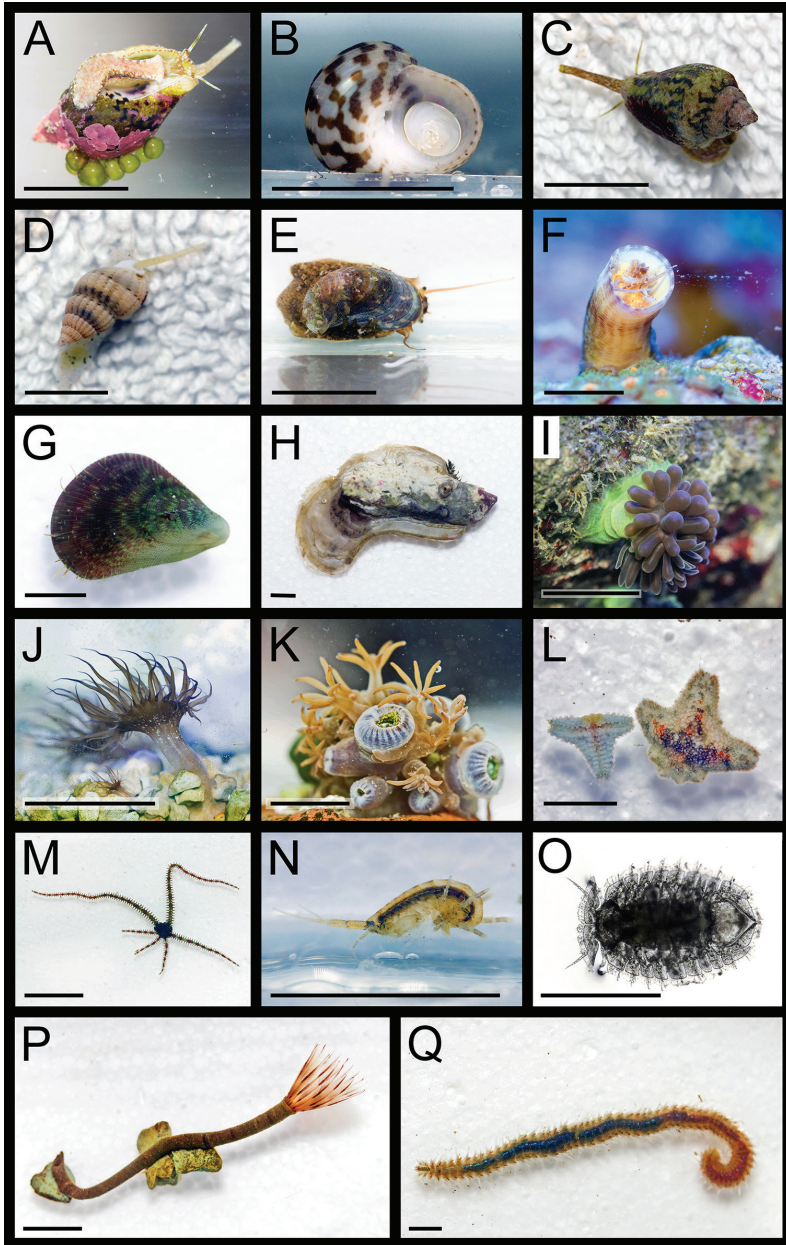
Figure 1. Found marine invertebrates **A** dove snail *Amphissa* / *Columbella* sp. with shell partly encrusted by algae **B** gastropod *Collonista* sp. **C** unidentified gastropod **D** unidentified gastropod **E** top-snail *Stomatella* sp. **F** worm snail *Serpulorbis* / *Thylacodes* sp. **G** unidentified bivalve **H** bivalve *Isognomon legumen* **I** unidentified sea anemone, possibly *Anemonia* cf. *manjano* **J** unidentified glass anemone, possibly *Aiptasia* sp. **K** soft coral *Acrossota amboinensis* **L** unidentified starfish, possibly *Asterina* sp. (left: typical three-armed regrown individual, right: individual with regenerated arms) **M** brittle star *Ophiocomella* sp. with four regenerated arms **N** amphipod *Niphargus* sp. **O** isopod *Cymodoce* sp. **P** fanworm *Bispira* sp. **Q** fireworm *Eurythoe* sp. Scale bars: 5 mm (**A–N**, **P–Q**), 1 mm (**O**).

Table 1. Identification of "hitchhikers" using DNA analysis; ID of the sample; GenBank: accession number; Taxon: name of the identified genus or species; BLAST: used Basic Local Alignment Search Tool and references.

ID	GenBank	Taxon	BLAST			Reference
			Query cover	Ident	Accession	
211	MT802127	*Columbella* sp. / *Amphissa* sp.	99% / 99%	87% 87%	KT753999.1 KF644285.1	Couto et al. (2016) / Layton et al. (2014)
215	MT802128	*Collonista* sp.	97%	92%	AM049345.1	Williams and Ozawa (2006)
216	MT802129	*Bispira* sp.	88%	83%	LT717721.1	Wood et al. (2017)
217	MT802130	*Stomatella* sp.	94%	98%	KX277585.1	Uribe et al. (2017)
219	MT802131	*Niphargus* sp.	98%	82%	KF719246.1	Esmaeili-Rineh et al. (2015)
220	MT802132	*Eurythoe* sp.	93%	99%	KY630466.1	Tilic et al. (2017)
223	MT802133	*Ophiocomella* sp.	100%	88%	KU895196.1	Hugall et al. (2015)
224	MT802134	*Thylacodes* sp. / *Serpulorbis* sp.	79%/90%	98% 85%	HM453709.1 AY296830.1	Faucci et al. (not published) / Colgan et al. (2003)
225	MT802137	*Isognomon legumen*	98%	100%	KX713469.1	Combosch et al. (2017)
226	MT802135	*Acrossota amboinensis*	95%	100%	GQ342379.1	Brockman and McFadden (2012)
227	MT802136	*Cymodoce* sp.	98%	80%	KJ410468.1	Khalaji-Pirbalouty and Raupach (2014)

able reference sequences (Table 1). The origin of sampled organisms was not clear but, based on information from wholesaler staff, the vast majority of them were imported "unseen" from Indonesia in several shipments with ornamental species. Subsequently, they were unintentionally released in aquaria where they grew and, in some cases, multiplied. Some found species had probably been living in the tanks for a long time.

In the surveyed tanks, we sampled five individuals of: *Columbella* sp. (Fig. 1A), *Collonista* sp. (Fig. 1B), two unidentified gastropod species (Fig. 1C, D), an unidentified starfish, possibly *Asterina* sp. (Fig. 1L), *Ophiocomella* sp. (Fig. 1M), *Niphargus* sp. (Fig. 1N), and *Cymodoce* sp. (Fig. 1O); two individuals of an unidentified sea anemone, possibly *Anemonia* cf. *manjano* (Fig. 1I); and one individual of: *Stomatella* sp. (Fig. 1E), a worm snail *Serpulorbis* / *Thylacodes* sp. (Fig. 1F), an unidentified bivalve (Fig. 1G), *Isognomon legumen* (Fig. 1H), an unidentified glass anemone, possibly *Aiptasia* sp. (Fig. 1J), *Acrossota amboinensis* (Fig. 1K), *Bispira* sp. (Fig. 1P), and *Eurythoe* sp. (Fig. 1Q).

Some of the unintentionally imported organisms were subsequently offered for sale (in the adult stage) by the wholesaler: a worm snail *Serpulorbis* / *Thylacodes* sp. (Fig. 1F), an unidentified sea anemone advertised as a majano anemone, probably *Anemonia* cf. *manjano* (Fig. 1I), a soft coral *Acrossota amboinensis* (Fig. 1K), and a fanworm *Bispira* sp. (Fig. 1P). The others were present in aquaria with ornamental species but not intended for trade. *Asterina* starfish were used as feed for the ornamental harlequin shrimp *Hymenocera picta* (Fig. 2). In many molluscs, the shells were partly encrusted with algae (Fig. 1A). Fireworms *Eurythoe* sp. (Fig. 1Q) were found in the substrate and also hidden in an empty snail shell.

In one case of the isopod *Cymodoce* sp. (Fig. 1O), a "hitchhiker of a hitchhiker" (probably ectocommensal) was detected since this isopod was associated with its host, the fanworm *Bispira* sp. (Fig. 1P). An assemblage of five *Cymodoce* individuals was collected on the surface of a single *Bispira* host.
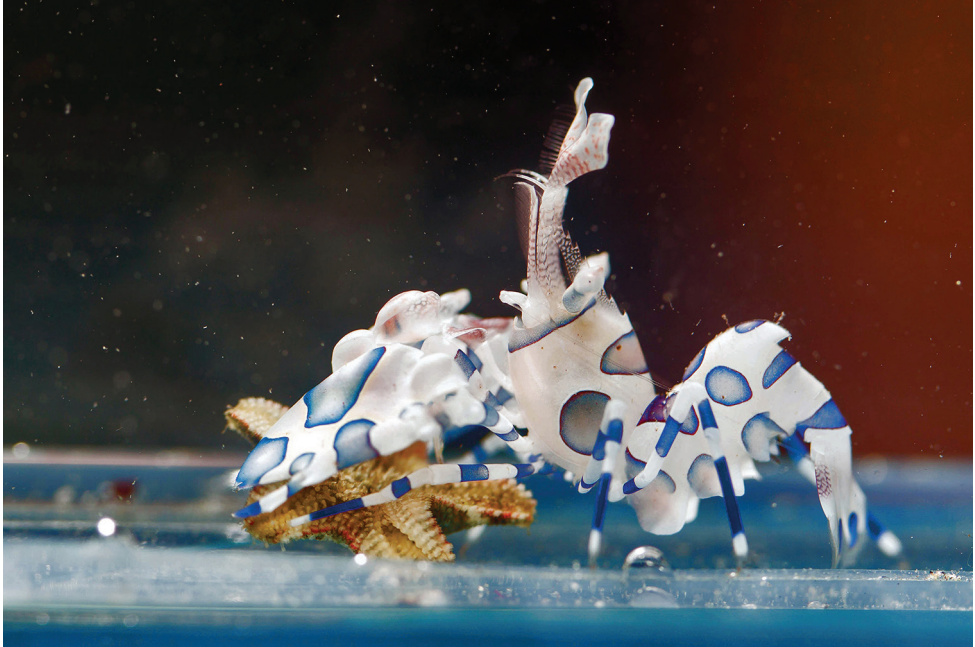
Figure 2. The obligate and voracious echinoderm predator *Hymenocera picta* (harlequin shrimp) turning an *Asterina* starfish upside-down and eating the soft tissue from the central disc.

Discussion

We found several imported marine "hitchhikers" occurring in tanks with ornamental species stocked by a wholesaler in the Czech Republic. Since no "live rocks", "bio-rocks" or any other such substrates are imported and traded by the surveyed wholesaler, the animals found could not have been imported together with this item as eggs or larvae. Some of the found "hitchhikers" were subsequently traded or used as feed for other animals, while the vast majority were living in the tanks as non-utilized animals. It is estimated that millions of marine animals are captured in coral reefs and associated habitats each year for ornamental purposes (Rhyne et al. 2017), nevertheless, there are no estimations of the quantity of unintentionally removed and transported "hitchhikers". Our preliminary findings suggest that this pathway of non-ornamental marine species introduction is important but mostly overlooked and that a quantitative analysis should be conducted in the future.

Moreover, some species may be harmful to other organisms in the tank and, in some cases, also to the keeper. The large and iridescent fireworms such as the found *Eurythoe* sp. (Fig. 1Q) are covered by dense setae capable of penetrating human skin upon epidermal contact and are responsible for skin inflammation and painful "bristle-worm stings" (Halstead 1978). Fireworms are therefore unwanted inhabitants in reef aquaria (Tilic et al. 2017). Although some authors have suggested that these polychaetes are urticating (covered by bristles which can be ejected toward a potential attacker) rather than toxic (Penner 1970; Eckert 1985; Tilic et al. 2017), a complex mixture of toxins

used by fireworms for their defence against predators was recently found (Verdes et al. 2017). Since fireworms were found hidden in an empty snail shell in the aquarium, their occasional unintentional translocation cannot be excluded.

"Hitchhiking" glass anemones from the genus *Aiptasia* (Fig. 1J) are small anemones some 3 cm in diameter. These highly resistant and aggressive cnidarians, described by some keepers as the worst "nightmare" one can have in the aquarium (McBirney 2013), are unpopular in reef aquaria because of their ability to dominate in the tank. In nutrient-rich tanks with good lighting, *Aiptasia* anemones quickly reproduce asexually by pedal laceration, and powerfully sting invertebrates and unwary fish to push them away, causing their mortality in many cases (Rhyne et al. 2004). The found majano anemones (*Anemonia* cf. *manjano*, Fig. 1I) are attractively coloured even as pest anemones in reef aquaria. They are less prolific than *Aiptasia* anemones and they are therefore generally perceived as ornamentals by hobbyists. However, similarly to *Aiptasia*, they may be very harmful to other sessile invertebrate inhabitants in the aquarium through their powerful stings (Ram 2013).

Ophiocomella brittle stars (Fig. 1M) and *Asterina* starfishes (Fig. 1L) can reproduce asexually by fragmentation (i.e., fissiparous reproduction); their bodies split apart losing one or two arms at a time, which regrow as new individuals of asymmetrical appearance (Mladenov et al. 1983; Wilkie et al. 1984; Achituv and Sher 1991). Therefore, both could be transported as overlooked fragments. Various *Asterina* species prey on corals but also grazing on algae covering the shells of "hitchhiking" dove snails *Amphissa / Columbella* sp. (Fig. 1A) was observed by wholesaler staff.

Very popular as an ornamental species in reef aquaria, mainly due to its attractive colouration, is the harlequin shrimp *Hymenocera picta* (Fig. 2). This shrimp is an obligate and voracious echinoderm predator (Wickler 1973). To feed it, hobbyists must have plenty of starfishes available (Prakash and Kumar 2013). For instance, the estimated annual costs of starfish for feeding one pair of harlequin shrimps in the USA is $260–390 USD per year. Therefore, the pest *Asterina* starfish is popular as low-cost food for these shrimps, and "hitchhiking" starfish can be spread in this way to other tanks. This was also the case with the surveyed wholesaler in the Czech Republic who advertised *Asterina* starfish as a suitable feed for traded harlequin shrimps.

The isopod crustacean *Cymodoce* sp. (Fig. 1O) found associated with the polychaete fanworm *Bispira* sp. (Fig. 1P) can easily be overlooked and transported with its host, which can be traded as ornamental despite its first importation as a "hitchhiker". Although we have no details about the ecological relationship of *Cymodoce* with the fanworm, this isopod did not occur elsewhere in the aquarium. It was previously suggested that isopods from the same family (Sphaeromatidae) may live in polychaete tubes (Müller 1990). Therefore, the possibility that the collected *Cymodoce* sp. is an obligate symbiont primarily introduced to aquaria with its host fanworm should be examined in future studies.

We have mentioned above some possible pathways by which marine "hitchhikers" can spread via the pet trade. There are some effective methods to mitigate or eradicate their occurrence in aquaria, such as stocking commonly traded shrimps of the genus

Lysmata in reef aquaria as effective predators of "hitchhiking" glass anemones (Rhyne et al. 2004; Calado and Narciso 2005). Nevertheless, some hobby keepers might decide to release unwanted pests into neighbouring seas. Ornamental aquatic animals are re-exported from the Czech Republic to other European countries (Ploeg 2007; Kalous et al. 2015; Patoka et al. 2015) including coastal regions where invasions of marine biota may take place. Some "hitchhiker" populations have expanded rapidly and become dominant species in coral reef tanks, such as the found gastropods of the genus *Collonista* (Fig. 1B); these molluscs are perceived as a menace by owners of marine aquaria (see http://www.reefcentral.com/forums/showthread.php?t=2284901) and could be released.

There is then the potential for released "hitchhiking" species to behave as invaders when introduced to a suitable new locality in the wild. Certain species collected in this study or closely related to these species can be seen as examples of successful and fast multiplying creatures even if their introduction pathway was not via ornamental aquaculture. For instance, the starfish *Aquilonastra burtoni* (family Asterinidae) invaded the Mediterranean Sea and consequently caused the decline of a native congener *Asterina gibbosa* (Achituv and Sher 1991; Galil 2007). Conversely, the fanworm *Sabella spallanzanii*, native to the Mediterranean, has invaded the ocean around southern Australia and northern New Zealand. It is currently abundant in these areas and both ecological and economic impacts are expected (Wood et al. 2017) because, in high densities, it has the potential to compete with cultured gastropods (Currie et al. 2000; Murray and Keable 2013). A third example is the non-native vermetid worm-snail, *Thylacodes vandyensis*, which was recorded attached to the wreck of the USNS *Vandenberg* sunk as an artificial reef close to the coast of Key West, USA, to reduce pressure on the surrounding natural reefs. As vermetid snails influence the growth of corals (Shima et al. 2010; Tootell and Steele 2014) and serve as intermediate hosts for turtle blood flukes (Cribb et al. 2017), they are of concern to wildlife managers (Bieler et al. 2017). On the other hand, the limited habitat match between source region (usually, tropical reefs) of traded or "hitchhiking" species and possible introduction regions reduces the probability of establishment in the wild in the temperate zone. Hence, tropical regions are most at risk from such species.

The replacement of potentially invasive species by low-risk species in aquaria is traditionally mentioned as a possible and safe way to mitigate the risk of biological invasions of ornamental organisms. Nevertheless, this approach is not feasible with "hitchhikers" which are mostly undetected due to their tiny size, and their release with wastewater is likely (Odom and Walters 2014). It must be noted that the problem is probably underestimated because, as well as macroinvertebrates, large quantities of microorganisms associated with their hosts are also likely to be transported unseen via the ornamental trade (Barille et al. 2017). In line with a previous publication on the effectiveness of legislative restrictions for aquatic pets (Patoka et al. 2018), the transportation of "hitchhikers", unlike ornamental species, is mostly uncontrollable by standard regulations. Since the majority of ornamental marine animals are imported into the United States, Europe, and Japan, their further monitoring and analyses of related risks at least in these countries are strongly recommended.

Acknowledgements

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RESEARCH ARTICLE

Non-native plants exert strong but under-studied influence on fire dynamics

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Abstract

Altered fire regimes are among the most destructive consequences of anthropogenic environmental change. Fires have increased in frequency in some regions, and invasion by fire-adapted non-native species has been identified as a major driver of this change, which results in a feedback cycle promoting further spread by the non-native species and diminishing occurrence of natives. We notice, however, that non-native species are often invoked in passing as a primary cause of changing fire dynamics, but that data supporting this claim are rarely presented. We therefore performed a meta-analysis of published literature to determine whether a significant relationship exists between non-native species presence and increased fire effects and risk, examined via various fire metrics. Our analysis detected a strongly significant difference between fire metrics associated with non-native and native species, with non-native species linked to enhanced fire effects and risk. However, only 30 papers discussing this linkage provided data to support it, and those quantitative studies examined only eight regions, five biome types, and a total of 22 unique non-native taxa. It is clear that we are only beginning to understand the relationship between non-native species and fire and that results drawn from an extremely limited set of contexts have been broadly applied in the literature. It is important for ecologists to continue to investigate drivers of changing fire regimes as factors such as climate change and land use change alter native and non-native fuels alike.

Keywords

Introduction

Anthropogenic global change has far-reaching consequences. Biodiversity is directly threatened by extinctions (Purvis et al. 2000; Barnosky et al. 2011). At the same time and perhaps more subtly, ecological processes are being altered as a result of both biotic and abiotic ecosystem transformation (Pausas 1999; Cramer et al. 2001; Grimm et al. 2013; Kraaij et al. 2018). These changes affect an increasing number of species and ecological communities – boosting some populations and reducing others (Clavel et al. 2010). Changing fire regimes exemplify such changes in process: fires are becoming more frequent in some contexts, more intense in others, and larger in extent in still others (Brooks et al. 2004; Rogers et al. 2011; Pausas and Fernández-Muñoz 2012; Balch et al. 2017; Schoennagel et al. 2017; Kelley et al. 2019). Each of these changes comes with significant potential to alter ecological systems and biodiversity as vulnerable species decline and other species replace them.

In places where fire has become more frequent in recent decades, fire regime changes are often the result of non-native species invasions increasing the local density of fine fuels, or of climate change bringing warmer temperatures and increasing the flammability of existing fuels (Wilson et al. 2010; Pyšek et al. 2012; Balch et al. 2013; Chambers et al. 2019). These drivers can also act synergistically (Bradley 2010). It can be difficult for native species in systems of low historical fire occurrence to recover after fire events, and decreases in native densities pave the way for increases in populations of non-native species that are adapted to frequent fires and capable of growing quickly following a burn event. This has occurred in, for example, the Sonoran Desert and the Great Basin of the western US, both of which have experienced invasion by Old World annual grasses bringing continuous fuels that recover readily after burning, replacing discontinuous and non-fire-adapted vegetation (Bradley and Mustard 2005; Balch et al. 2013; McDonald and McPherson 2013).

Such changes have been shown by multiple metrics to affect fire regimes (Brooks et al. 2004; Gill et al. 2013). Invasions have reduced the fire return interval at individual locations, impacting non-fire-adapted native plants and promoting still more invasion by non-natives (Van Wilgen and Richardson 1985; D'Antonio and Vitousek 1992; Le Maitre et al. 2014). Some non-native species also grow more quickly than natives because they lack the herbivores, competitors, and pathogens that would limit their growth in their regions of origin (Chun et al. 2010). Via these mechanisms, fires fueled by non-natives have been shown to hinder native species' regeneration, damage native soils, and otherwise result in ecosystem transformation and the replacement of native species with non-natives (Brooks et al. 2004). Where fires have become more intense (i.e., there has been an increase in heat at the fireline), this may be the result of fuels buildup following extended fire suppression or exclusion (Fulé et al. 1997) or of increased flammability of fuels as a result of climate change, or a combination of these factors. Additionally, introduced species may provide fuels that burn with higher intensity than native fuels, impacting seeds and soils and impeding recolonization by native plant species (Lippincott 2000; Brooks 2002; Esler et al. 2008; Le Maitre et al. 2014). Increases in fire extent caused by widespread invasions can also fundamentally alter vegetation communities. Recovery

after more extensive fire events can be delayed because seed or plant sources for such recovery are located a greater distance away (Cansler and McKenzie 2014). After severe fires, bare ground can persist for a longer period because of this distance, again promoting colonization by non-native weedy species that demonstrate disturbance-adapted traits enabling them to colonize sites with poor or eroded soils (Moles et al. 2008).

These changes in fire patterns can impact native biodiversity, ecological functions, and ecosystem resilience following disturbances (Johnstone et al. 2016). For example, non-native species that supply large quantities of flammable fine fuels may be promoted both by climate change and the fire cycle they perpetuate, generating feedback loops that can transform desert ecosystems into invasive grasslands (Abatzoglou and Kolden 2011). Heavily altered fire patterns can lead to degraded landscapes with reduced potential to support management objectives such as livestock grazing, conservation, recreation, and watershed maintenance (Allen et al. 2002). As a result, it is imperative for decision-makers and land managers to understand the key drivers of current changes in fire patterns so such changes can be better anticipated and prevented. This has led to increased focus on non-native species as sources of novel fuels and drivers of increased fire frequency and fire intensity (D'Antonio and Vitousek 1992; Brooks et al. 2004).

Although the link between non-native invasion and problematic shifts in fire is oft-cited in global change literature as an important invasion-fire cycle (e.g., D'Antonio and Vitousek 1992; Rossiter et al. 2003; Balch et al. 2013), that linkage depends on conditions that are not present in all systems at all times. Specifically, to alter fire regimes, invasion must alter fuels and/or flammability, thus altering fire frequency, intensity, or extent (Brooks et al. 2004; Bowman et al. 2011; Underwood et al. 2019; Bishop et al. 2020). Not all invasions result in such changes, which rely on characteristics of both the non-native species and the native communities. For any specific fire, for example, unusual precipitation and drought patterns associated with climate change may be as likely to result in increased biomass production and subsequent drying for native plant species as for non-native plant species (Liu and Wimberly 2016).

To understand how consistently non-natives have been quantitatively associated with increased fire effects and risk, we performed a meta-analysis of published quantitative studies examining the effect of non-native vs native plants on fire characteristics. Our goals were: (a) to determine whether non-native species, relative to functionally similar native species, quantitatively and consistently increase metrics of fire effects and risk in ecosystems, and (b) to gauge the range of contexts over which this has been quantitatively analyzed, in order to consider how broadly assumptions regarding these patterns can justifiably be applied. For this study, we define "fire metrics" as those quantifiable descriptors of fire patterns that can be compared across studies (i.e., fire frequency, fire intensity, flammability, fuels quantity, and fire spatial extent). Note that there have been previous meta-analyses that have examined related but different questions, contributing to our understanding of the link between fire and non-native species. Jauni et al. (2015) performed a meta-analysis examining the effect of disturbance on non-native species and found that fire events resulted in increased diversity of non-natives. Alba et al. (2015) found through meta-analysis that exotic species composition and performance were both enhanced following wildfires but not following prescribed burns.

Methods

To perform our meta-analysis, we began by searching ISI Web of Science (with coverage of years 1900–present) to find records of studies that have quantitatively compared non-native and native species' effects on fire metrics. We used the search terms fire + each of the following: plant + (native* OR exotic* OR non-native* OR alien* OR invasive*); plant + "functional group"; native + (tree* OR shrub* OR perennial grass* OR annual grass*); (severity OR frequency OR intensity OR extent) + (cause* OR attribute*), and applied them to all years inclusive. Additionally, we examined the Literature Cited sections of relevant papers to find additional studies – including from sources not referenced in Web of Science – that might contain relevant quantitative information. Searches were performed in summer 2020.

Although our search terms netted hundreds of references, only papers meeting the following criteria were useful in our meta-analysis: (1) they compared fire metrics stemming from native species (as a control group) with fire metrics stemming from non-native species; (2) they presented comparisons between the metrics of fire associated with native and non-native species from the same plant functional groups; (3) they included quantitative and original fire metrics. Many papers referenced fire effects in discussions of non-native species but did not include original quantitative information. Many other papers examined the effects of fire on non-native species (e.g., reporting experiments examining control measures for non-natives), but we sought the opposite metric: the effect of non-native species on fire. For each of the studies that suited our criteria, we derived from the reports treatment (effect of non-natives) and control (effect of natives) fire metrics as well as sample sizes and measures of variance for treatments and controls.

Across all of the studies we included in our analysis, fire metrics were the response variables of interest. However, there are many ways to measure the effect of a given factor (e.g., non-native fuels) on fire. We were able to include all of these in one common meta-analysis framework by using the ratio of means (ROM) to compare the treatment and control effects of all studies (Hedges et al. 1999; Schwartz et al. 2012). The ratio of means is calculated as the natural log of the quotient of the mean outcome from the experimental group divided by the mean outcome from the control group (Hedges et al. 1999). To parameterize the response ratio, we derived from each paper the average native vs. non-native plant effects on fire metrics; in the set of relevant studies we found, these metrics included fire frequency, fire intensity (i.e., heat at the fireline), fuels quantity (including biomass production, relative growth rate, and litter production), spatial extent, and flammability (including fuels moisture, heat of combustion, and volatility). We then calculated the natural log of the ratio of the experimental mean to the control mean fire metric within each study. The resulting set of ROMs, including ratios from all studies meeting our meta-analysis criteria, formed the set of values included in our analyses.

Categorical analysis can be used to further explore the population of studies included in the overall meta-analysis in order to ascertain whether significant treatment effects persist within certain limited contexts. As long as a given category is represented by at least two studies, it is possible to examine it separately from the other categories to measure the strength of the treatment effect within that categorical context. The categories

we examined as such included: biome type, geographic region, plant functional group, and fire effect metric. Because the total number of studies within each category was not always greater than 1, the total number of studies included in categorical analyses did not always equal the total number of studies included in the overall meta-analysis.

In meta-analyses, studies included in the calculation of effect sizes are weighted more heavily if they used a larger sample size in the original research. We included the variances and sample sizes of all studies in our response ratio meta-analysis by calculating fixed and random effects estimates and applying inverse variance weighting, thus allowing studies with larger sample sizes to carry greater influence on the effect estimates. We calculated heterogeneity Q statistics to evaluate whether effect sizes are homogeneous or, conversely, are suggestive of underlying unexplained structure in the data (Rosenberg et al. 2000). Using these models, we estimated effect size means and confidence intervals for the full meta-analysis as well as for categorical analyses of subgroups. As long as ROM means and confidence intervals exclude the value of 1, they can be considered significant effect sizes. We performed all calculations using the *meta* package in R version 3.6.3 (R Core Team 2020). For the overall model, significance was accepted at alpha = 0.05.

An important consideration in meta-analysis is that researchers and journals may be less inclined to publish studies that fail to show the expected effect, either because the results were non-significant (in our case, finding no difference between native and non-native species and their effects on fire metrics) or because they were significant in the opposite direction from predicted (in our case, finding that native species enhanced fire metrics more than non-native species). To estimate the potential quantitative effect of this phenomenon, we calculated a fail-safe analysis, which we performed using the *trimfill* function in the *meta* R package. Results indicated whether the outcome of our overall meta-analysis was likely affected by a lack of publication or "file drawer" problem and also estimated the likely overall effect size after producing a correction for such a publication bias. Note that sample sizes were not sufficient to conduct a similar fail-safe analysis for subgroup categories.

Results

Our search terms yielded 612 unique sources. We examined each of these for methodology and found only 30 papers, reporting results of 41 distinct studies, that included a usable quantitative comparison of the effects of native vs non-native species on fire metrics. This final sample of relevant papers displayed the following breakdown by subgroup categories: by region, nine studies took place in the Southwestern US, three in mediterranean California, five in the Western US more broadly, eight in Australia, six in the Eastern US, one in Europe, three in South Africa, and six in South America. By biome, six studies were performed in deciduous forest, 10 in desert, 16 in mediterranean systems, eight in savanna, and one in mixed shrubland/woodland. Functional groups included annual grasses (9 studies), forbs (1 study), perennial grasses (20 studies), shrubs (3 studies), and trees (6 studies). A total of five usable studies combined data from multiple species to report fire metrics of non-native vs native species, making it impossible to extract the contributions of individual species but allowing comparison between those two groups.

Table 1. The 16 species examined at the species level in quantitative comparisons of fire metrics stemming from native vs. non-native fuels, and key traits related to effects. Five analyzed studies compared groups of native vs non-native species and thus effects could not be ascribed to individual species, and these studies are excluded from this table.

Species	Traits related to fire effects in meta-analysis	Citation
Ampelodesmos mauritanica	Resprouts quickly after fire; produces flammable biomass more rapidly than native species	Grigulis et al. 2005
Andropogon gayanus	High growth potential relative to native species	Bilbao and Medina 1990
Bromus hordeaceus	Low quality litter decomposed less than native litter, contributing to regional fuels for a longer period of time; compared with native species, sustains dry biomass for a larger portion of the year	Hernández et al. 2019
Bromus rubens	Winter annuals that escape extreme summer heat, generating high fuel load production relative to native species	Brown and Minnich 1986
Bromus tectorum	Exploits soil water following fire, outcompeting natives in regeneration	Melgoza et al. 1990
Cenchrus ciliaris	Increases fuel loads relative to native species	Miller et al. 2010
Cytisus scoparius	Higher relative growth rate than native species	Fogarty and Facelli 1999
Eragrostis lehmanniana	Much faster biomass production than native species	Anable et al. 1992
Hakea sericea	Increased fuel loads relative to native species	Van Wilgen and Richardson 1985
Hyparrhenia rufa	Higher growth rates in fertile sites, relative to native species	Baruch et al. 1985
Imperata cylindrica	Increased fuel loads and fuel continuity relative to native species	Lippincott 2000
Melinus minutiflora	Higher growth rates in fertile sites, relative to native species	Baruch et al. 1985
Pennisetum setaceum	Increased fuel loads relative to native species	Rahlao et al. 2009
Pinus contorta	Increased vertical fire continuity and increased flammability of fuels relative to comparison native species	Cóbar-Carranza et al. 2014
Schinus terebinthifolius	Reduces fire frequency ecosystem-wide	Stevens and Beckage 2009
Tamarix sp.	Rapid biomass accumulation and rapid regrowth after fire	Ellis et al. 1998

Overall, our meta-analysis detected a strong, statistically significant link between non-native species and increased fire effect (random-effects model ROM = 2.21; 95% bias-corrected CI 1.52 to 3.20; n = 41; p < 0.0001). Heterogeneity was also significant (Q_T = 5.68 × 10^5, df = 40, p < 0.0001), which highlights the large amount of unexplained data structure in the dataset. The many different approaches to comparing fire stemming from natives and non-natives that were employed by the various studies we examined likely contributed to this heterogeneity, emphasizing the importance of subgroup comparisons. The relevant studies found for this analysis contained clear evidence of a link between non-native species and enhanced fire metrics. However, the total number of species and the total number of contexts covered is extremely limited. The 41 studies reported species-level fire metrics reported for only 16 taxa (Table 1). Usable studies took place in only eight regions and four biome types (Table 2).

The significant response ratio of non-natives to natives held across almost all examined subgroups, as well. Among metrics of fire effects and risk, non-natives generated significantly higher fire metrics of flammability (random-effects model ROM = 1.50; 95% bias-corrected CI 1.39 to 1.62; n = 15; Q_B = 1923.69), fuels (ROM = 2.27; CI 1.30 to 3.97; n = 18; Q_B = 6.48 × 10^4), and spatial extent (ROM = 10.02; CI 3.19 to

Table 2. Usable studies took place in eight regions and four biome types.

Region	Biome type	Study
Southwestern US	Savanna	Anable et al. 1992
	Desert	Brooks 1999
		Brown and Minnich 1986
		Busch 1995
		Eilts and Huxman 2013
		Ellis et al. 1998
		Stevens and Fehmi 2009
Western US	Savanna	Balch et al. 2013
		James and Drenovsky 2007
		Wilsey and Polley 2006
	Desert	Melgoza et al. 1989
		Whisenant 1990
Australia	Mediterranean	Fisher et al. 2009
		Fogarty and Facelli 1999
		Miller et al. 2010
		Rossiter et al. 2003
		Setterfield et al. 2010
Eastern US	Deciduous forest	Dibble et al. 2007
		Lippincott 2000
		Stevens and Beckage 2009
Europe	Mediterranean	Grigulis et al. 2005
California	Mediterranean	Keeley 2001
		Keeley and Brennan 2012
South Africa	Mediterranean	Rahlao et al. 2009
		Van Wilgen and Richardson 1985
South America	Savanna	Baruch et al. 1985
		Bilbao and Medina 1990

31.48; *n* = 2; Q_B = 30.30) (Fig. 1). Fire frequency did not differ significantly between native and non-native species (*ROM* = 2.22; *CI* 0.30 to 16.43; *n* = 5; Q_B = 1544.80) (Fig. 1). Among biomes, non-natives generated significantly higher fire metrics for deserts (*ROM* = 3.02; *CI* 2.17 to 4.20; *n* = 10; Q_B = 1532.06) and mediterranean biome (*ROM* = 2.82; *CI* 2.54 to 3.14; *n* = 16; Q_B = 2376.90), but not for savannas (*ROM* = 1.60; *CI* 0.48 to 5.28; *n* = 8; Q_B = 2.26 × 10^5), or deciduous forests (*ROM* = 1.04; *CI* 0.90 to 1.19; *n* = 6; Q_B = 26.76) (Fig. 2).

Among functional groups, non-natives generated significantly higher fire metrics for perennial grasses (*ROM* = 2.53; *CI* 1.55 to 4.10; *n* = 20; Q_B = 4.66 × 10^4), shrubs (*ROM* = 1.41; *CI* 1.34 to 1.49; *n* = 3; Q_B = 0.27), trees (*ROM* = 1.73; *CI* 1.51 to 1.99; *n* = 6; Q_B = 1695.02), and annual grasses (*ROM* = 2.39; *CI* 1.24 to 4.60; *n* = 9; Q_B = 1. × 10^4) (Fig. 3). Finally, among regions, non-natives generated significantly higher fire metrics for the Southwestern US (*ROM* = 3.85; *CI* 1.80 to 8.21; *n* = 9; Q_B = 2.10 × 10^4), Australia (*ROM* = 3.65; *CI* 2.77 to 4.81; *n* = 8; Q_B = 132.71), South Africa (*ROM* = 1.78; *CI* 1.14 to 2.78; *n* = 3; Q_B = 29.49), and South America (*ROM* = 1.59; *CI* 1.38 to 1.83; *n* = 6; Q_B = 2515.47), but not for the Eastern US (*ROM* = 1.04; *CI* 0.90 to 1.19; *n* = 6; Q_B = 26.76), California (*ROM* = 3.25; *CI* 0.66 to 15.94; *n* = 3; Q_B = 460.80), or Western US (*ROM* = 1.06; *CI* 0.40 to 2.80; *n* = 5; Q_B = 1.01 × 10^4) (Fig. 4).
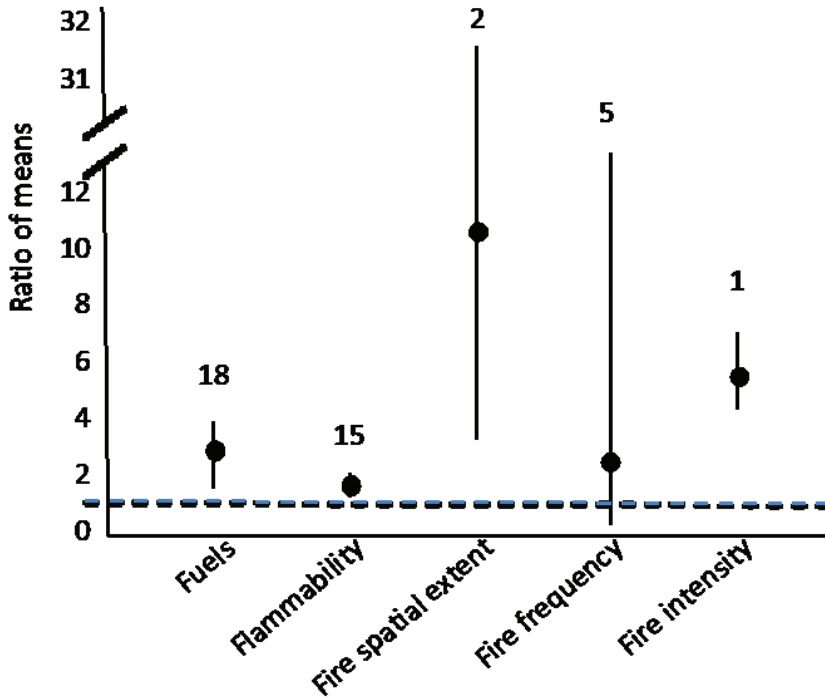
Figure 1. Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for fire metric subgroups analyzed using Hedges' d response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

The fail-safe analysis detected a significant file drawer problem (t = –2.49; df = 39; p = 0.017). Upon correcting for this problem via an estimate of the effect size in the absence of a file-drawer problem, the *trimfill* recommended analysis assumed an addition of 19 non-significant studies but predicted that with such studies included the overall effect would remain significant (*ROM* = 5.46; *CI* 3.83 to 7.77; p < 0.0001) and that the link between non-native species and increased fire metrics would persist.

Discussion

Our meta-analysis found a significant link between non-native plant species and fire metrics broadly, and specifically found that non-natives are associated with increased fuels, fire intensity, flammability, and fire extent, compared with native plant species, where the two have been contrasted. That is, quantitative research finds evidence that non-natives alter fire regimes by shifting the characteristics, quantity, and/or flammability of fuels. At the same time, our search terms netted a very small number
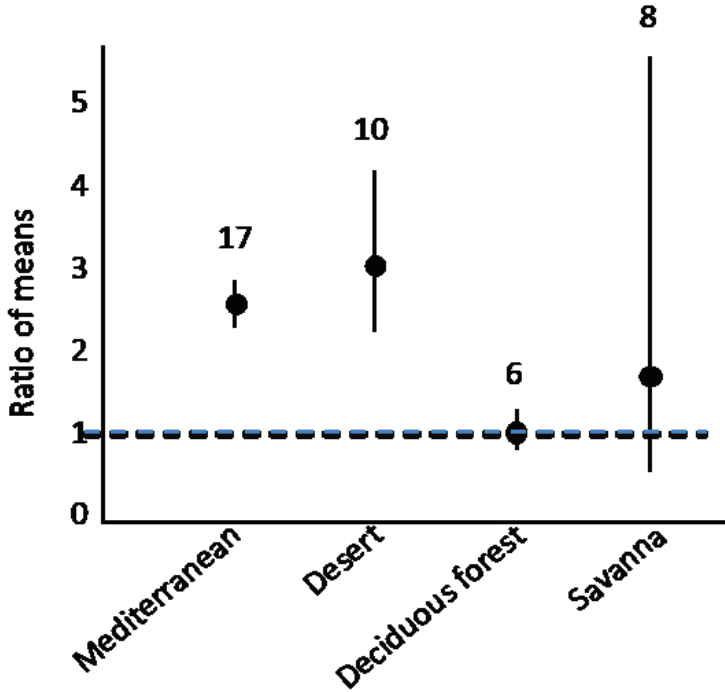
Figure 2. Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for biome subgroups analyzed using Hedges' d response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

of quantitative studies examining an even smaller number of species. Approximately a twentieth of the studies that met our search criteria compared native and non-native plant species quantitatively; most of the others simply referenced the relationship between non-natives and fire.

Together, these results suggest that we are only beginning to understand the role of non-native species in fire regimes under environmental change, globally. Effects are quite strong where they have been quantitatively analyzed, but analyses have been limited to a few contexts. By one estimate, there are almost 17,000 species that have been established outside their native range (Seebens et al. 2017). As of 2016, just under 5,000 plant species were classified as "invasive," suggesting that they exert a negative impact in the systems where they are introduced (Kew 2016). It is clear that the 16 taxa included in these studies are merely a fraction of all invasive species, and the effects of the remainder of those species on fire have not been examined with reference to native species. In most cases, the difference in fire conditions between sites before and after invasion is unknown. Since fire interacts with other environmental change drivers, in addition to biological invasion, the future consequences of many invasions remain uncertain or unpredictable.
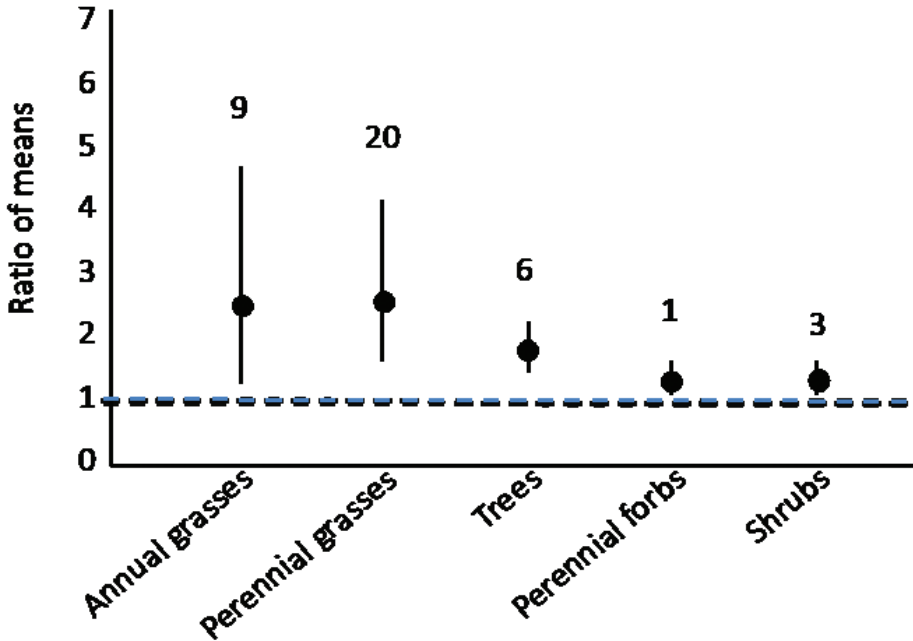
Figure 3. Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for functional group subgroups analyzed using Hedges' d response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

The 16 taxa that were examined at a species level in these studies included annual and perennial grasses, trees, shrubs, and a forb. Nearly all of them contributed to increases in fire metrics; the sole exception was *Schinus terebinthifolius*, which is associated with decreased fire frequency that promotes further invasion by this non-native tree (Stevens and Beckage 2009). In the quantitative research reviewed here, higher biomass production relative to native species were associated with the grasses *Ampelodesmos mauritanica*, *Andropogon gayanus*, *Bromus rubens*, *B. tectorum*, *Cenchrus ciliaris*, *Eragrostis lehmanniana*, *Hyparrhenia rufa*, *Imperata cylindrica*, *Melinus minutiflora*, and *Pennisetum setaceum* (Table 1). Similarly, the shrubs *Cytisus scoparius* and *Hakea sericea* and trees in the genus *Tamarix* were associated with increased fuels production relative to native species (Table 1). Other important factors included continuity and flammability of fuels (for example, *Pinus contorta* exhibited greater vertical continuity and volatility of biomass than did comparison native species; Cóbar-Carranza et al. 2014), as well as phenological drivers; *B. rubens*, for example, accumulated biomass during the winter months and thereby escaped damage from extreme summer heat and produced higher total fuels than comparison natives (Brown and Minnich 1986) (Table 1). In each case where fire frequency was increased
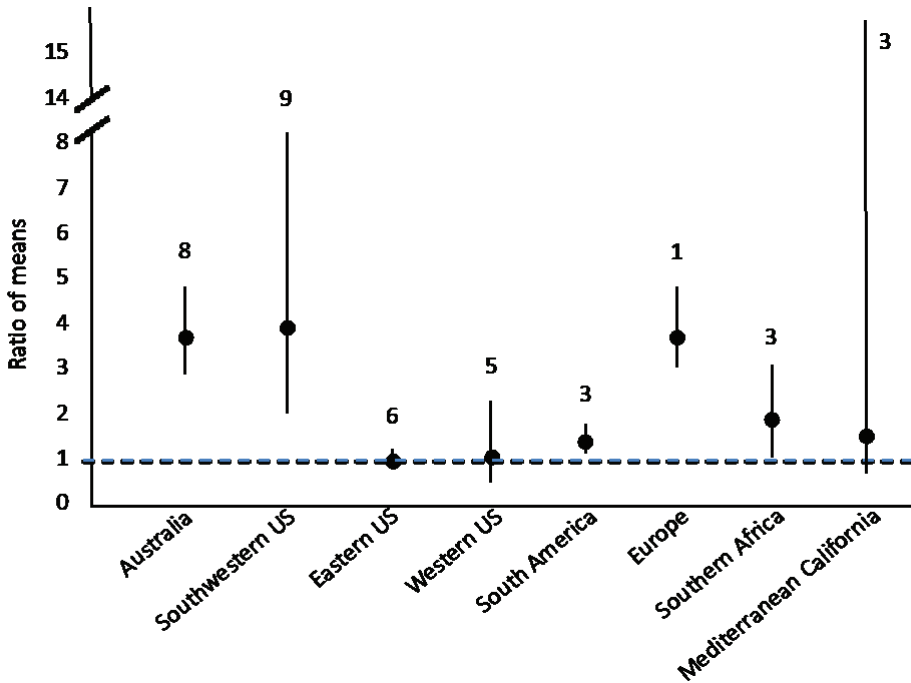
Figure 4. Ratios of means (dark circles) and 95% confidence intervals (denoted by lines) for region subgroups analyzed using Hedges' d response ratios. Positive means and confidence intervals excluding 1 (indicated by a dashed, horizontal line) can be considered to indicate significantly higher fire metrics for native than non-native species. Sample sizes of each subgroup are denoted with numerals above each line.

by the presence of non-native species, the critical factor distinguishing invaded sites from non-invaded sites was the exceptional continuity (in space or over time) of fuels produced by the non-natives, increasing fire frequency and risk.

Non-native plants have led to novel fire disturbances in the studied systems. Our results demonstrated that fires in invaded sites recur with greater frequency, burn with higher fireline intensity, or burn over greater extent than in native-dominated sites. Such systems are subject to significant ecological transformation: when native species are non-fire-adapted or unable to recover from severe fires, a positive invasive species-fire feedback cycle emerges (D'Antonio and Vitousek 1992; Rossiter et al. 2003). This cycle can threaten native communities over very large areas, fundamentally reshaping ecosystems and ushering in alternative, non-native-dominated stable states (e.g., Brooks et al. 2003; Godfree et al. 2017).

Altered fire regimes are evidently a strong component of global change. Furthermore, they interact with other drivers of environmental change. Climate change alone can boost the growth rate (i.e., production and thus total quantity of fuels) and flammability of biomass both native and non-native (Myneni et al. 1997; Westerling et al. 2006; McGranahan et al. 2018). Unusual fire patterns stemming from climate change

may or may not depend on non-native species invasion, although system-specific characteristics (such as historical fire frequency, timing of precipitation, and fire adaptations among native species) may elevate the likelihood that non-native fuels carry particular significance during any given fire year. Land use changes and resulting increases in human footprints in natural areas can also transform fire regimes, increasing the rate of intentional and accidental ignitions (e.g., 95% of all annual ignitions in California are caused by humans; Syphard et al. 2008).

Disentangling the effects of climate change, land use, and non-native fuels will be important for spatially-explicit fire risk assessment and management and restoration decision-making (Gray et al. 2014; Westerling 2016; Balch et al. 2017; Syphard et al. 2017). Improved forecasting to guide such assessments will require continued and extended research of the quantitative fire metrics associated with non-native species across functional groups, regions, and biome types, as well as the response of those fire metrics to climate change and land use change. As conditions change in any given system, the relative fire risk driven by each of these factors is also likely to change (McWethy et al. 2013). Classic adaptive management requires sequential use of management activities to meet certain objectives, and also requires careful study of the effectiveness of each activity (Holling 1978; Gunderson 1999; Williams and Brown 2012), highlighting the importance of continued research in complex systems. Study of the relative roles of native vs non-native plants in fire regimes within any particular location will be necessary to facilitate effective management decisions over time.

Conclusions

Global change today consists of multiple drivers operating both individually and in synergy. The combined influence of biological invasions, land use change, and climate change can result in dramatic changes in fire dynamics within particular systems, yet understanding how each driver contributes to fire regime change is essential for effective management decision-making in response. Our study identified a clear role of non-native species in increased fire metrics, but also highlighted the limited scope of our understanding – only a small number of species and systems have been quantitatively examined to this point. Both native and non-native fuels must be considered in light of changing climatic patterns and land uses, and increased empirical assessment of the respective roles of climate, land use, and invasion are necessary for appropriate responses.

Acknowledgements

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REVIEW ARTICLE

Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts

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Abstract

Sustainably managed non-native trees deliver economic and societal benefits with limited risk of spread to adjoining areas. However, some plantations have launched invasions that cause substantial damage to biodiversity and ecosystem services, while others pose substantial threats of causing such impacts. The challenge is to maximise the benefits of non-native trees, while minimising negative impacts and preserving future benefits and options.

A workshop was held in 2019 to develop global guidelines for the sustainable use of non-native trees, using the Council of Europe – Bern Convention Code of Conduct on Invasive Alien Trees as a starting point.

The global guidelines consist of eight recommendations: 1) Use native trees, or non-invasive non-native trees, in preference to invasive non-native trees; 2) Be aware of and comply with international, national, and regional regulations concerning non-native trees; 3) Be aware of the risk of invasion and consider global change trends; 4) Design and adopt tailored practices for plantation site selection and silvicultural management; 5) Promote and implement early detection and rapid response programmes; 6) Design and adopt tailored practices for invasive non-native tree control, habitat restoration, and for dealing with highly modified ecosystems; 7) Engage with stakeholders on the risks posed by invasive non-native trees, the impacts caused, and the options for management; and 8) Develop and support global networks, collaborative research, and information sharing on native and non-native trees.

The global guidelines are a first step towards building global consensus on the precautions that should be taken when introducing and planting non-native trees. They are voluntary and are intended to complement statutory requirements under international and national legislation. The application of the global guidelines and the achievement of their goals will help to conserve forest biodiversity, ensure sustainable forestry, and contribute to the achievement of several Sustainable Development Goals of the United Nations linked with forest biodiversity.

Introduction

Non-native trees (hereafter NNTs) and sustainably managed plantation forests of NNTs provide a wide range of forest goods and services and help to reduce the pressure on natural forests (FAO 2010a, b). Because of their often greater hardiness, faster growth rates, and resistance to climate change, pathogens, and pests compared to native species (Bolte et al. 2009; Seidl et al. 2017), the standardisation of silviculture techniques (e.g., nurseries, seedling establishment, and thinning), and industrial processes for their products (e.g., timber and pulp), certain NNTs are favoured over native species in tree planting programmes (Wang et al. 2013; Papaioannou et al. 2016; Brus et al. 2019; Vítková et al. 2020). As a result, NNTs make up 44 percent of plantation forests globally (approximately 58 million ha) (FAO 2020). The prevalence of NNT forestry plantings varies significantly between regions. For example, plantation forests in North and Central America mostly comprise native species whereas those in South America consist almost entirely of NNTs (FAO 2020).

This large extent of NNTs is, in part, due to the rapid decrease in the extent of natural forests. Many on-going large-scale planting initiatives, sometimes with NNTs, aim to compensate for the loss of natural forests. Some examples of drivers of this loss are the reduction of natural forests caused by human activities in tropical regions of Brazil (Seymour and Harris 2019; Klug et al. 2020), in Chile (Braun et al. 2017), and in cold regions of Russia (e.g., Trunov 2017), and the loss of conifer forests in North America and Europe due to recent bark-beetle outbreaks (Morris et al. 2017; Hlásny et al. 2019). The expansion of NNT plantations has been highlighted as a major land use/cover change worldwide, leading both to deforestation and loss of agricultural land (Hua et al. 2016; Benra et al. 2019), although this varies by country and depends on underlying policies and economic situations (Pirard et al. 2017).

NNTs also represent a significant component of urban forests and are widely planted in urban greening projects worldwide (Bauduceau et al. 2015; Sjöman et al. 2016; Castro-Díez et al. 2019; Escobedo et al. 2019). The continuous growth in urban populations creates demands and opportunities for urban forests to deliver ecosystem services critical to human wellbeing and biodiversity (dos Santos et al. 2010; Potgieter et al. 2017; Endreny 2018; Riley et al. 2018; Kowarik et al. 2019). NNTs are often promoted in cities because of their aesthetic value, easy and well-known requirements for maintenance, higher growth rate than native species, and the reliability of achieving greening and the associated ecosystem and social services (Dickie et al. 2014; Potgieter et al. 2017).

Botanic gardens and arboreta, all hosting a large variety of NNTs, are increasingly recognised as key components of global plant conservation efforts through their living collections of endangered species, long-term archiving of seeds, taxonomic training, and public outreach (Hulme 2011). Yet, an increasing body of evidence highlights the role of botanic gardens in facilitating plant invasions worldwide (Hanspach et al. 2008; Hulme 2011, 2015; van Kleunen et al. 2018), albeit at a much smaller scale than through commercial horticulture and forestry practices. A number of botanic gardens now apply stringent measures to prevent the spread of invasive species and to promote the use of native species in ecological restoration efforts, but most do not (Hulme 2015).

A major change in the planting of trees has emerged recently, as massive tree-planting campaigns using NNTs are beginning to gain momentum globally as an assumed silver bullet to mitigate the impacts of climate change and for other purposes such as poverty alleviation (Table 1). In response to climate change, trees, regardless of their biogeographical status (native or non-native), are being presented as a general panacea (Bastin et al. 2019). However, emerging research suggests that trees might not help offset carbon emissions as much as some would expect (e.g., Popkin 2019), and plantations in inappropriate sites can have disastrous consequences for sustainable development, biodiversity conservation, and ecosystem functioning (Bond 2016; Bond et al. 2019; Temperton et al. 2019), and even may lead to a loss of soil organic carbon (Jackson et al. 2002). Silveira et al. (2020) highlighted the myth that tree planting is always good for biodiversity and ecosystem services and that the use of trees in the restoration of tropical and subtropical old-growth grassy biomes is misguided. The notion that the presence of trees indicates good ecosystem health is a driver of tree planting initiatives (Table 1) in many parts of the world (Richardson et al. 2014). In many cases, increased tree cover is clearly at odds with objectives of biodiversity conservation and the sustained delivery of ecosystem services (e.g., Jackson et al. 2005).

Although sustainably managed NNTs can and do deliver economic and societal benefits with limited risk of escape and spread from planting sites into adjoining areas in many contexts, some widely used NNTs are invasive or have high potential to become invasive, sometimes causing substantial damage to biodiversity and related ecosystem services and functioning (Richardson 1998; Richardson et al. 2000; Richardson and Rejmánek 2011; Castro-Díez et al. 2019). Many of the traits that are desired in NNTs are the same as those that have been recognised as promoting invasiveness (e.g., fast growth rate, high seed production, and high seedling survival) (Pyšek and Richardson 2007). The number of NNTs that are being reported as spreading and causing negative effects on biodiversity and ecosystem services is increasing rapidly globally (Rejmánek and Richardson 2013; Krumm and Vítková 2016).

Invasive NNTs (INNTs) can be important ecosystem engineers, i.e. they "directly or indirectly modulate the availability of resources to other species by causing physical state changes by biotic or abiotic materials" (Jones et al. 1994; Mitchell et al. 2007; Ayanu et al. 2015). They can also cause regime shifts in invaded ecosystems (altered states of ecosystem structure and function that are difficult or impossible to reverse), alter the identity of dominant species and therefore change dynamics on all levels, lead-

ing to impacts that ripple across trophic levels such as in the case of ecosystems invaded by *Acacia cyclops*, *A. longifolia*, and *A. saligna* (Gaertner et al. 2014; Souza-Alonso et al. 2017) or by *Tamarix* sp.pl. affecting the flood and sediment regime (Zavaleta 2000). INNTs can also radically change fire regimes by increasing fuel availability and flammability (Paritsis et al. 2018; Davis et al. 2019), which can have disastrous effects on ecosystems and people (e.g., in Chile, Portugal, South Africa, and Spain). The impacts of such invasions are particularly notable in naturally treeless ecosystems (Jäger et al. 2007; Rundel et al. 2014). Moreover, the spread of INNTs are among the invasions with the greatest impacts on ecosystem services such as water provision (Richardson 1998; Le Maitre et al. 2002; van Wilgen and Richardson 2012; Richardson et al. 2014).

As for many other groups of non-native species, perceptions regarding NNTs differ across interest groups, sometimes creating conflicts around their use and management (Starfinger et al. 2003; van Wilgen and Richardson 2014; Woodford et al. 2016; Vítková et al. 2017). For example, among some of the most widely planted genera such as *Acacia* s.l., *Eucalyptus* s.l., and *Pinus* there are many invasive species that have severe impacts on biodiversity and ecosystem services (Richardson 2011; Richardson and Rejmánek 2011; Cazetta and Zenni 2020). *Prosopis* species were introduced by NGOs and government organisations to countries like Kenya in the 1970s and 1980s to provide wood and animal fodder, and to stabilise soils in degraded ecosystems (Swallow and Mwangi 2008; Maundu et al. 2009). There is continuing advocacy for the utilisation of these NNTs (Choge et al. 2007), despite clear evidence that these species have devasting effects on human livelihoods and biodiversity (e.g., Mbaabu et al. 2019; Linders et al. 2019). Kenya is, as far as we know, the only country that has enshrined in its constitution the goal of achieving a particular level of national tree cover (10%). According to the corresponding National Strategy, the achievement of this goal will require the planting of NNTs, including INNTs which are among the worst invasive species worldwide. This is particularly troublesome in the case of *Prosopis juliflora*: while the area covered by this notoriously INNT is included in Kenya's estimates of current tree cover, the country has recently also launched a National Prosopis Strategy which aims to bring the invasion of this species under control in order to protect Kenya's nature, people, and the economy (http://www.environment.go.ke/).

The challenge is to maximise the socio-economic benefits and opportunities of NNTs, while minimising risks and negative impacts on the environment or compromising future benefits and land uses (Richardson 2011; Brundu and Richardson 2016). Addressing this challenge requires collaborations between governments, non-governmental organisations, environmental managers, forestry and horticultural industries, and other parties to develop and promote tailored policies, coordinate existing legislation tools, ensure capacity building, promote the preferential use of native trees, ensure the responsible introduction and sustainable use of NNTs globally, and to identify and share best-management practices to deal with INNTs. Such measures are essential to mitigate and reduce the negative impacts from unregulated and poorly informed use and dissemination of NNTs. To increase the awareness of issues associated with the use of NNTs and the potential risks, this paper proposes a set of

Table 1. Examples of massive tree planting campaigns.

Name of the initiative	Geographical scope	Aim of the initiative, tree species considered	Web site / Reference
The Great Green Wall initiative (African Union)	Africa (the Sahel)	Restore degraded land, sequester carbon and create green jobs by 2030 to reduce desertification; no indication for species used.	http://www.unccd.int/actions/great-green-wall-initiative (Bond et al. 2019) http://time.com/5669033/great-green-wall-africa
The Trillion Trees campaign (NGO)	Global	Plant and protect one trillion trees to mitigate climate change and promote prosperity by 2050; native tree species are preferred, but planting NNTs is considered when there is a clear socio-economic, ecological, or climatic reason.	http://www.trilliontrees.org/home (Cernansky 2018)
Tree Nation (NGO)	Global	Citizens and companies can compensate CO_2 emissions by supporting tree planting projects worldwide; trees are being chosen of a list of 300 species, but without further information if native trees are preferred over NNTs.	http://tree-nation.com
Plant for the Planet (NGO)	Global	Platform enables to support tree planting projects worldwide with the goal to plant 1.000 billion trees; no indication for species used.	http://www.plant-for-the-planet.org/en/home http://www.unenvironment.org/news-and-stories/press-release/planting-trees-has-never-been-easier
The Bonn Challenge (launched by German Government)	Global	Restore 150 million hectares of deforested and degraded land by 2020 and 350 million hectares by 2030 worldwide; no indication for species used.	http://www.bonnchallenge.org
The "Seed Bombing" initiative (Thai Government)	Thailand	Reforestation programme in Thailand throwing "seed bombs" from planes; only native species are considered.	http://thelondonpost.net/tree-seeds-tree-seeds-bombing-thailand
The Billion Tree Tsunami Afforestation Project (BTTAP) (Khyber Pakhtunkhwa Government)	Pakistan	The BTTAP in Pakistan's northern Khyber Pakhtunkhwa province was launched in 2015. It has surpassed its target by restoring and planting trees in 350,000 hectares of degraded forest landscapes; no indication for species used.	http://ejatlas.org/conflict/billion-tree-tsunami-afforestation-project (Nazir et al. 2019)
The Billion Trees campaign (NGO)	Global	Afforestation campaign with the goal to plant a billion trees across the planet to mitigate climate change; no indication for species used.	http://www.nature.org/en-us/get-involved/how-to-help/plant-a-billion http://www.unenvironment.org/resources/publication/plant-planet-billion-tree-campaign
The One Billion Trees Programme (New Zealand Government)	New Zealand	Afforestation and reforestation programme with the aim to plant one billion trees to diversify existing land uses across New Zealand and to improve socio-economic performance; planting native species is encouraged to improve biodiversity.	http://www.mpi.govt.nz/funding-and-programmes/forestry/one-billion-trees-programme/about-the-one-billion-trees-programme/
The Three-North Shelter Forest Program (Chinese Government)	China	More than 66 billion trees were planted since 1978 to stop expansion of arid regions; NNTs and native species have been used so far, but native vegetation will be preferred in future.	http://www.nature.com/articles/d41586-019-02789-w http://news.bbc.co.uk/2/hi/world/monitoring/media_reports/1199218.stm (Ge et al. 2020)
The 300,000 Trees in Nicosia initiative (Cyprus Government)	Cyprus	Afforestation programme with the aim to plant about 50,000 trees to combat climate change and protect biodiversity; planting indigenous species, such as endemic and rare varieties, is encouraged.	http://www.themayor.eu/fr/nicosia-launches-large-scale-tree-planting-campaign
The 60 Million Trees initiative (Madagascar Government)	Madagascar	Reforestation project with the aim to plant 60 Million trees across 40,000 hectares; endemic and agroforestry species, including NNTs and INNTs, are being used to balance economic and ecological interests.	http://www.ecowatch.com/madagascar-tree-planting-2644879937.html
The 50 Million For Our Forests campaign (NGO)	USA	Reforestation campaign with the aim to plant about 50 million trees to combat forest loss due to natural disturbances; only native trees are being used.	http://www.nationalforests.org/get-involved/tree-planting-programs
The 73 Million Trees in the Amazon initiative (NGO)	Brazil	Reforestation programme with the aim to plant 73 million trees in the Amazon rainforest to combat forest loss; only native tree species are being used.	http://www.smithsonianmag.com/smart-news/brazil-begins-effort-plant-73-million-trees-amazon-180967086/
The 350 million trees in 12 hours Guinness record (Ethiopia Government)	Ethiopia	Afforestation project with the aim to plant 4 billion trees to combat deforestation and climate change effects; 350 million trees were planted in 12 hours setting a new world record; no indication for species used.	http://albertonrecord.co.za/221373/afforestation-project-ethiopia-recently-resulted-350-million-trees-planted-one-day/

Name of the initiative	Geographical scope	Aim of the initiative, tree species considered	Web site / Reference
Conversion of Cropland to Forest Program (also called Grain for Green) (Chinese government)	China	Tree-planting enterprise (since 1999) that pays farmers to plant trees on their land and provides degraded land to rural families to restore; native and NNTs are being used.	http://forestsnews.cifor.org/52964/grain-for-green-how-china-is-swapping-farmland-for-forest?fnl=en http://www.cifor.org/publications/pdf_files/articles/APutzel1601.pdf (TheOneEartheditorial team 2020)
Millennium show forest (Chinese government)	China (new city "Xiongang New Area")	Massive urban afforestation project to construct a close-to-natural urban forest with the aim to minimise invasive species impacts; prioritisation of local species and seedlings.	(Li et al. 2020)
Eden Reforestation Programme (NGO)	Global	Reforestation project with the aim to reduce poverty and restore forests by hiring local villagers to plant trees; no indication for species used.	http://edenprojects.org
WeForest Making Earth Cooler (NGO)	Global	Forest and landscape restoration programme with the aim to mitigate climate change, conserve biodiversity, and reduce poverty of local communities; no indication for species used.	http://weforest.org
OneTreePlanted (NGO)	Global	Reforestation programme to protect biodiversity, restore degraded soils, improve climate, and reduce poverty; no indication for species used.	http://onetreeplanted.org
60 Million trees (60 Milioni di Alberi)	Italy	Planting one tree for each Italian citizen to fight climate change. It is recommended the use of native or non-native non-invasive trees.	http://www.alberitalia.it

Global Guidelines for the use of Non-Native Trees (GG-NNTs). These GG-NNTs were developed, discussed, and elaborated at a workshop in Prague, Czech Republic, in September 2019 that was attended by many of the co-authors of this paper. The guidelines and supporting text were further developed in consultation with a large number of researchers and other interested and affected parties in the fields of arboriculture, forestry, nature conservation, and invasion science. In compiling the working team, consideration was given to geographic and gender balance and diversity of age and expertise. However, we recognize that certain areas, especially in low and lower-middle income countries, are underrepresented and should be considered in future efforts.

Global Guidelines for the use of Non-Native Trees (GG-NNTs)

The GG-NNTs set out in this paper are addressed to all relevant stakeholders (including policy makers, the forestry and agroforestry industries, national forest authorities, certification bodies, environmental organisations, organisations and individuals involved in urban greening, landscape architecture, climate change mitigation, and all other endeavours that rely on the planting and management of trees). The GG-NNTs aim to reduce the risk of introduction of new INNTs and the negative impacts that might originate from their unregulated and/or unscrupulous use. To do so, these guidelines aim to enlist the co-operation of all relevant stakeholders to identify both robust scientific knowledge and technical knowledge and experience regarding the use and management of NNTs. Containment of NNTs to areas set aside for their cultivation or use must become an integral part of silviculture. Managers and planners need

to consider the species and the environmental context and therefore should develop a stratified approach to take into account regional and habitat-specific management (van Wilgen and Richardson 2012; Pergl et al. 2016; Sádlo et al. 2017; Campagnaro et al. 2018).

The eight recommendations (Rec.) in the GG-NNTs are clustered according to three overarching goals (Fig. 1): (1) preventing the introduction of INNTs; (2) preventing and mitigating the risk of escape of NNTs from plantation sites to adjoining areas; and (3) mitigating the negative impacts of INNTs. They are not an exhaustive list of recommendations, but rather provide the first step towards building a global consensus on the precautions that should be taken when introducing and planting NNTs, particularly over large areas. The GG-NNTs are voluntary, and are intended to complement and guide statutory requirements under international or national legislation. Private forestry enterprises, local authorities, arboreta, and public forest managers might wish to publicise their adherence to the GG-NNTs through adopting a symbol or logo indicating this commitment (Fig. 2). The GG-NNTs could be incorporated in national or regional strategic documents or plans dealing with non-native species.

The GG-NNTs aim to implement and expand the geographical context of most of the principles and recommendations of the European Code of Conduct for Invasive Alien Trees as endorsed by The Standing Committee to the Convention on the Conservation of European Wildlife and Natural Habitats, acting under the terms of article 14 of the Bern Convention, on the 8th of December 2017 (Rec. No. 193/2017). The Bern Convention has endorsed two other Codes that included overlapping principles addressing NNTs used as ornamental species, i.e. the Code of Conduct on Horticulture and Invasive Alien Plants published by the Council of Europe (Heywood and Brunel 2011) or kept in botanic garden and arboreta (European Code of Conduct for Botanic Gardens on Invasive Alien Species, Heywood and Sharrock 2013). Therefore, in proposing the GG-NNTs we mainly focus on NNTs used in forestry, in other types of large-scale plantings, restoration projects, and in urban forestry.

Terminology and structure of the GG-NNTs and their recommendations

In the context of the present GG-NNTs, and in accordance with the Convention on Biological Diversity (CBD) principles and definitions (Decision V/8 of the Conference of the Parties to the CBD), the term non-native trees (NNTs) has exclusively a biogeographical meaning, i.e. it refers to tree species, subspecies, lower taxa, or genotypes, introduced through human activity outside their past or present natural distributions, and includes any part, seeds or propagules of such taxa that might survive and subsequently reproduce. As such, the term NNTs carries no *a priori* connotation (negative or positive) relating to risks to biodiversity (or to the economy or public health). For a detailed discussion of the terms used in these GG-NNTs and how they relate to those used internationally see Annex 1, Glossary/Acronyms.
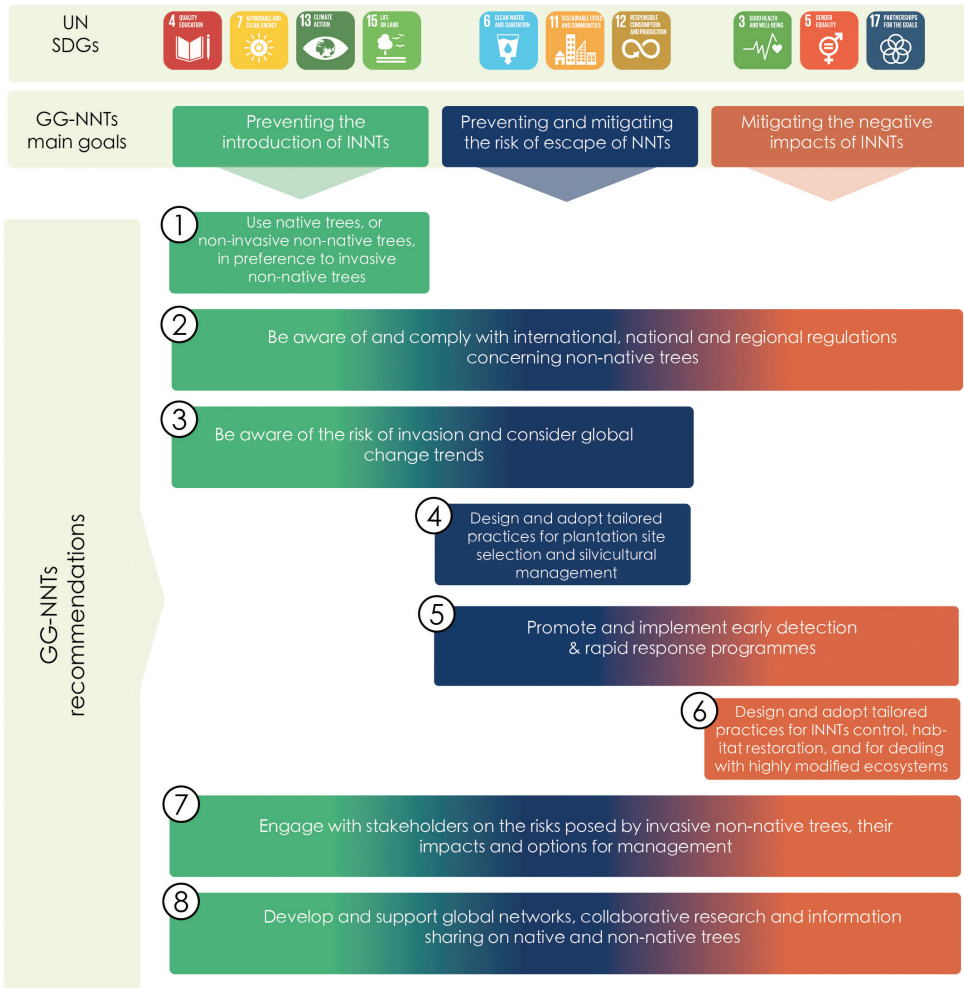
Figure 1. Main goals and recommendations of the Global Guidelines for the use of Non-Native Trees (GG-NNTs) in relation to the Sustainable Development Goals of the United Nations (UN SDGs).

In the context of the GG-NNTs, the terms alien, allochthonous, non-native, non-indigenous, exotic, and introduced are considered synonymous. These synonyms are all used in international and national legislation and in various technical documents, although with different frequency and with sometimes subtle differences in the meaning they convey. Therefore, for consistency, we use the term NNTs in accordance with the CBD definition, and for the purposes of the GG-NNTs, the term invasive non-native trees (or INNTs) is herewith defined as a NNTs whose introduction and/or spread threatens or adversely impacts biodiversity and related ecosystem services, or causes ecosystem disservices (Vaz et al. 2017), recognising that negative impacts on the economy and on public health might occur as well (Bacher et al. 2018).

Figure 2. Private forestry enterprises, local authorities, arboreta and public forest managers might wish to publicise their adherence to the GG-NNTs through adopting a symbol or logo indicating this commitment.

Recommendation 1: Use native trees, or non-invasive non-native trees, in preference to invasive non-native trees

Native tree species should be preferred over NNTs, and consideration should be given to the precise provenance of seeds and germplasm. If native tree species are not suitable, the consequent recommendation is to evaluate the use of NNTs with low invasion risk.

Within a country or region, native tree species rather than NNTs, should be used, in planning and establishing large-scale plantings, afforestation or reforestation projects, planted forest, and agroforestry (Douglas et al. 2014; Peltzer et al. 2015) wherever possible. This approach is particularly important in massive and global projects such as the Trillion Trees campaign, the African Green Wall initiative (Goffner et al. 2019), the China's Grain-for-Green Program (Hua et al. 2016), and the Bonn Challenge (Temperton et al. 2019) (Table 1).

Multiple organisations have suggested, under certain conditions, the promotion of native trees over NNTs, including, for example, FAO (FAO 2006; FAO 2010 – Principle 9 – "if native trees are equal to or better than introduced species for the intended purpose") and UNFCC (Aarrestad et al. 2014). FSC certification comprises 10 principles and 70 criteria that cover environmental, social, and economic aspects of forest management. The FSC standard uses the CBD definition of alien species and criterion 10.3 (Principle 10 "Implementation of Management Activities") states that "The Organisation shall only use alien species when knowledge and/or experience have

shown that any invasive impacts can be controlled and effective mitigation measures are in place". Before introducing NNTs, FSC certification requires the presence of a management plan and scientific evaluations (Indicator 10.3.1), a stakeholder consultation and the use of effective mitigation measures to avoid the spread of NNTs outside the management unit area (Indicator 10.3.2), and the cooperation with competent authorities/bodies (Indicator 10.3.3).

PEFC certification system sets international Sustainable Forest Management benchmarks (see PEFC ST 1003:2018, Sustainable Forest Management – Requirements); within the framework provided by these benchmarks (11 criteria and 48 guidelines), national stakeholders develop their own national standards with the open participation of interested parties in a consensus-driven decision making process. All 54 recognised national standards require that origins of native species that are well-adapted to site conditions shall be preferred for reforestation and afforestation. Only those NNT species, provenances or varieties shall be used whose impacts on the ecosystem and on the genetic integrity of native species and local provenances have been scientifically evaluated, and if negative impacts can be avoided or minimised (Stupak et al. 2011). PEFC national standards recognise as guidance for avoidance of non-native invasive species CBD Guiding Principles for the Prevention, Introduction, and Mitigation of Impacts of Alien Species that Threaten Ecosystems, Habitats or Species.

Native tree species exhibit multiple local adaptations to the climate of their habitat, guaranteeing optimal growth and survival under stable environmental conditions (Aitken et al. 2008). For example, in the hot arid North African desert belt, the conservation of stands of the native *Vachellia tortilis* subsp. *raddiana* and augmentative restoration plantings of seeds or seedlings may promote invasion resistance through establishment of shade to limit the invasion of *Prosopis glandulosa* (Abbas et al. 2019). The seedlings of *V. tortilis* subsp. *raddiana* are able to implement important shifts in key functional traits in response to altering abiotic stress conditions, behaving as a stress-tolerant species that is well-adapted to the habitat it occupies in the hot arid deserts of North Africa.

With global change, the link between climate and local adaptation may be disrupted, leading to local provenances of native tree species no longer providing the required ecosystem services (Alfaro et al. 2014; Podrázský et al. 2020). Different provenances of tree species with wide natural distribution ranges are adapted to different conditions. Thus, a possible match for a planting site in terms of vitality and productivity should first be sought among provenances of already present native tree species, drawing from the vast network of provenance trials and models built upon them. In a second step, provenances of other native species that are predicted to be better adapted to the planting site should be considered. Only if both alternatives have been exhausted, should NNTs be considered for planting to sustain the required ecosystem services (Bolte et al. 2009; Allen et al. 2010; Brus et al. 2018; Frischbier et al. 2019). According to Climate-Smart Forestry (CSF), an emerging branch of sustainable forest management, one option to further resilience and adaptability of native forest diversity is to improve

connectivity and migration corridors of key species and forest structures to sustain the availability of seed sources, as well as genetic variation (Bowditch et al. 2020).

When native tree species cannot be used, it is necessary to evaluate the use of NNTs with an expected low risk of invasiveness. Standard weed risk assessment tools can be successful at distinguishing between INNTs and non-invasive NNTs; see Gordon et al. (2012), and Ziller et al. (2019) for *Eucalyptus*, and McGregor et al. (2012) for pines. New data and information on the biology and ecology of species may result in a change of the risk assessment and evaluation outcomes. However, the use of weed risk assessment tools might not be familiar to practitioners and risk assessment and management approaches should be carefully communicated among relevant stakeholders (Stokes et al. 2006). Lorentz and Minogue (2015) remarked that trait selection during breeding is potentially a very effective containment approach for managing the risk of invasiveness in non-native *Eucalyptus* taxa. The likelihood of spread can be reduced by decreasing fecundity or by increasing the age to maturity, although the latter method may negatively influence productivity (Gordon et al. 2012). This strategy has been successfully implemented in other taxonomic groups, including a triploid *Leucaena* hybrid in Hawaii (Richardson 1998). Likewise, elimination of seed production is considered a feasible goal for *Eucalyptus* (Gordon et al. 2012), and elimination of fertile pollen production has been accomplished in the transgenic hybrid *E. grandis* × *E. urophylla* (AGEH427) (Hinchee et al. 2011). There have been some suggestions that polyploidy may be related with invasiveness of forestry species, as in the case of *Prosopis juliflora* (Kaur et al. 2012). Polyploids may have an advantage over their diploid progenitors in having higher growth vigour but are often sterile (Pandit et al. 2011). In the case of *Robinia pseudoacacia*, there are many cultigens that are generally less invasive than the typical form (Sádlo et al. 2017). For some species of Pinaceae, there is a good understanding of the invasiveness of the different species, with some species having low invasion risk (Rejmánek 1996; Carrillo-Gavilán and Vilà 2010; McGregor et al. 2012). This understanding has been used in some areas to promote plantations with fewer invasive species and to discourage the plantation of highly invasive species (Nuñez et al. 2017). However, a careful assessment and evaluation of risk and benefits is always necessary. For example, male individuals of non-native *Populus* clones suitable for fast growing bioenergy plantations might be recommended to prevent seed dispersal to natural areas, but it is important to locate the site so as to avoid the risk of hybridisation with native poplars. A similar recommendation was proposed for the planting of male plants of *Acer negundo* in urban areas to mitigate the risk of spread by samaras, although the production of allergenic pollen must be considered (Ribeiro et al. 2009).

Trees for urban environments are generally selected on the basis of pragmatic criteria, such as suitability for the site, pest resistance or tolerance, availability of stock, and the cultural and aesthetic preferences of local people (Spellerberg and Given 2008). Evidence from Northern and Central Europe shows that in some regions the catalogue of native tree species might be too limited to fulfil ecosystem services and resilience in harsh urban environments (Sjöman et al. 2016). Thus, it might be unrealistic to generally exclude NNTs from consideration for urban greening. Further work is required to

quantify the diverse benefits of native species in many contexts. Therefore, we recommend to (a) plant more native trees in urban areas; (b) avoid NNTs if they pose risks to biodiversity or ecosystem services; and (c) plant NNTs only if invasion risk in the surrounding areas is low or can be managed effectively.

At a country level, the recommendation of using native trees in preference of NNTs should be based on sound knowledge of the natural ranges and distribution of native tree species within the country and its regions, to limit translocations across biogeographical regions and safeguard biological integrity of Important Plant Areas (Mehrabian et al. 2020), protected areas, and hot-spots of endemism for trees.

Recommendation 2: Be aware of and comply with international, national, and regional regulations concerning non-native trees

Those engaged in the introduction, breeding, and use of NNTs and in the planted forest sector in general need to be aware of and comply with their obligations under regulations and legislation to prevent the introduction of INNTs and to minimise conflicts with regulatory authorities.

There is a substantial corpus of legally binding and non-binding conventions, regulations, and agreements on invasive non-native species at international, national, and regional levels. The CBD and its Parties recognised that there is an urgent need to address the impact of invasive alien species, and have adopted guidance on prevention, introduction, and mitigation of impacts of alien species that threaten ecosystems, habitats or species, and have taken a number of relevant decisions on invasive alien species, and forest biodiversity (e.g., COP 9 Decision IX/5). The CBD, the UN Climate Change, and UN Desertification Conventions may act synergistically to reduce the negative impacts of INNTs, promoting integrated, coherent, and multi-disciplinary approaches to these related issues and guiding the national forest authorities.

These international conventions have direct and indirect impacts on the everyday work in the planted forest sector and in the use of NNTs. Indeed, international conventions addressing issues of invasive alien species have been ratified by many countries (Shine 2007; Ormsby and Brenton-Rule 2017) and a significant number of NNT species are banned or are subject to restrictions. At national (or subnational) level, many countries have legislation and/or regulations aimed at preventing possession, transport, trade or use of specific (invasive) NNTs (e.g., for Europe see Brundu et al. 2020; Pötzelsberger et al. 2020).

The Regulation (EU) No. 1143/2014 has included in the "list of invasive alien species of [European] Union concern" a number of NNTs – *Acacia saligna*, *Ailanthus altissima*, *Prosopis juliflora*, and *Triadica sebifera* (syn. *Sapium sebiferum*) – totally banning any use of these species in the European Union. This is a very stringent ban, as invasive non-native species of concern in the European Union may not be intentionally: (a) brought into the territory of the Union, including transit under customs supervision; (b) kept, including in contained holding; (c) bred, including in contained

holding; (d) transported to, from or within the European Union, except for the transportation of species to facilities in the context of eradication; (e) placed on the market; (f) used or exchanged; (g) permitted to reproduce, grown or cultivated, including in contained holding; or (h) released into the environment.

An example of national-level regulation is that of Mesquite (*Prosopis juliflora*) in the Sudan. This species, native to Mexico, Central America, and northern South America, was introduced to the Sudan in 1917 from South Africa and Egypt and was planted in Khartoum for research purposes. The success of this species in tolerating drought and stabilising sand dunes led to it being introduced to more drought-prone areas. In the 1990s, *P. juliflora* was introduced as part of dune stabilisation programmes in the spate irrigation systems of the Gash and Tokar. However, soon after its introduction *P. juliflora* became invasive. Tens of thousands of hectares were invaded in these areas and a 1995 presidential decree pledged to eradicate the species from Sudan (Laxén 2007). Similarly, *Melaleuca quinquenervia* (a tree native to Australia and Malaysia) was introduced into Florida in 1906 as a potential commercial timber and was later widely sold as an ornamental tree. This species is now on the Federal Noxious Weed List (USDA 2012) because it has invaded all types of terrestrial and wetland habitats, including undisturbed pine flatwoods, sawgrass-dominated communities and cypress swamps, but also roadsides, pastures, and urban sites (Porazinska et al. 2007). For these examples, earlier pro-active regulations on the sale or use of these INNTs could have reduced rates of invasions and impacts.

Recommendation 3: Be aware of the risk of invasion and consider global change trends

Those engaged in the planted forest sector and otherwise in the introduction and use of NNTs need to be aware of the potential for NNTs to become invasive and/or have negative impacts, and to use such information to inform decisions about the selection of trees and the management of plantations. This awareness should be based on the best available knowledge, on experience from elsewhere, and on appropriate assessments of risk, taking into account the existence of time lags in NNTs species spread and impacts (i.e. the "invasion debt", Essl et al. 2011; Rouget et al. 2016) and global change trends.

The fact that some NNTs have not yet spread from the sites where they were planted should not be taken as definitive evidence that spread and negative impacts will not occur in the future. Experience with the same NNTs in planted forests or gardens in other parts of the world, including areas where the species have long residence times (Richardson et al. 2015), should be evaluated to assess the extent of invasion debt since NNTs often have long lag-phases (up to 200–300 years or longer; see Kowarik 1995). There is strong evidence that INNTs can replicate invasive behaviour and impacts in environmentally similar conditions in different parts of the world (Essl et al. 2010).

INNTs included in legally-binding prohibited species or in advisory lists (such as the IUCN list of "100 of the world's worst invasive species", which includes, e.g., *Acacia mearnsii*, *Cinchona pubescens*, and *Leucaena leucocephala*) should not be used

in the countries or regions where they are listed, nor released in the environment, nor planted along transport networks, nor used for new planted forests. For example, all new plants (including trees) currently not in New Zealand are banned unless permitted (Hulme 2020). Each new NNT species or provenance planned to be introduced for the first time in a given country or to be planted over large scales which has not yet been evaluated, should be subject to a comprehensive risk analysis to consider opportunities, risks, and management options, with uncertainties explicitly recognised. Moreover, regions or countries should consider not planting NNTs if these taxa are restricted in neighbouring jurisdictions, as NNTs can easily spread across national borders making biosecurity a regional issue (Faulkner et al. 2020). For example, the list of the Israel's "least wanted alien ornamental plant species" includes numerous NNTs which may be relevant for various countries around the Mediterranean, experiencing Mediterranean, semiarid, and arid climates (Dufour-Dror et al. 2013).

More than 100 risk assessment and risk analysis schemes for plant species have been proposed (Křivánek and Pyšek 2006; Leung et al. 2012), and decision-support schemes have been developed specifically for trees or woody plants (Reichard and Hamilton 1997; Pheloung et al. 1999; Kumschick and Richardson 2013; Wilson et al. 2014). Although no global repository currently exists, the European and Mediterranean Plant Protection Organisation (EPPO) platform on pest risk analysis (PRA) contains more than 400 PRAs produced since the early 1990s, including a few for NNTs, and additional documents related to PRA activities. A number of Weed Risk Assessments for NNTs (e.g., *Vachellia nilotica* and *Ligustrum sinense*) are available on-line, e.g., the Noxious Weeds Program Risk Assessments of USDA APHIS (https://www.aphis.usda.gov/aphis/), the PIER (Pacific Island Ecosystems at Risk – Plant threats to Pacific ecosystems; http://www.hear.org/pier/), and the UF/IFAS Assessment of Non-native Plants in Florida's Natural Areas (https://assessment.ifas.ufl.edu/). The result of risk assessments conducted for NNTs in Brazil are available on the web page of the Horus Institute (https://institutohorus.org.br/).

It has been suggested that importers, breeders, and growers who are responsible for introducing potentially invasive non-native species should be responsible for damages to the environment (i.e. the "polluter pays" principle), rather than allowing the burden to be borne by tax payers or neighbouring private landowners (Richardson 1998; Hulme et al. 2008; Buddenhagen et al. 2009; Chimera et al. 2010; McCormick and Howard 2013; Lorentz and Minogue 2015). In addition, contingency plans (EPPO 2009) and effective rapid response measures in the event of escape of NNTs should be in place before the introduction takes place (Rec. 5).

Climate change could affect the dynamics of invasions of NNTs in many interacting ways, for example: (a) by causing modification in the ecosystems that potentially modify opportunities for establishment, naturalisation, and spread of both native trees and NNTs (e.g., Iverson et al. 2008; Bezeng et al. 2017; Fei et al. 2017; Aubin et al. 2018); (b) by favouring individual traits of particular NNTs (e.g., Kawaletz et al. 2013; Castro-Díez et al. 2014); and (c) by modifying introduction pathways, potentially promoting the increased use of certain NNTs (Lindenmayer et al. 2012; Frischbier et al. 2019), thereby challenging the recommendation to preferentially use native trees

(Rec. 1). Climate matching between native and non-native ranges of tree species is often crucial for the outcomes of introducing NNTs (Petitpierre et al. 2012); it is therefore important to incorporate climate change into risk-analysis models for an anticipatory evaluation of scenarios for invasiveness of NNTs. Risk maps that incorporate the effects of climate change should guide land and forest managers and stakeholders with longer-term planning. Land-use change (not only related to the establishment of plantings) is also an important driver of NNTs invasions. Abandonment of land can increase the potential for invasion of NNTs or lead to the establishment of plantations (Lugo 2004, 2015; Sitzia et al. 2012; Mullah et al. 2014; Bravo et al. 2019; Vaz et al. 2019).

Under climate change, outbreaks of pests on native trees might increase, giving a greater momentum to planting NNTs, but these NNTs are also susceptible if pest/pathogens are subsequently accidentally introduced. For example, there has been an alarming increase in impacts of bark beetle outbreaks in conifer forests in recent years in Austria, the Czech Republic, Germany, Slovakia, and in North America (Hlásny et al. 2019). Synchronised by extreme weather, recent bark beetle outbreaks have already reached a supranational scale. Outbreaks are likely to further increase in extent and severity in the future due to climate change (Hlásny et al. 2019). A study in France (Bertheau et al. 2009) supports the assertion that native phytophagous insects adapted rapidly to conifers introduced in Europe. Non-native conifers in France are now colonised by native bark beetles. For risk assessment of native bark beetle attacks on newly introduced conifers, tree taxonomic relatedness appears to be a good predictor of shifting probability and the simplest one to consider in forest management. Planting NNTs within stands of taxonomically unrelated species might therefore reduce the rate of bark beetle shifts into novel hosts (Bertheau et al. 2009). NNTs species are widely used in planted forests for their high productivity and performance compared to native trees. However, these advantages may be compromised by insects and microbial pathogens which were introduced accidentally or have adapted to new host trees (Branco et al. 2015; Wingfield et al. 2015).

Managed relocation or assisted migration has been proposed as an approach to mitigate climate change impacts on biodiversity by intentionally moving species to climatically suitable locations outside their natural range (Richardson et al. 2009). It has also been proposed as a means to maintain forest productivity, health, and ecosystem services under rapid climate change (e.g., Gray et al. 2011; Kreyling et al. 2011; Pedlar et al. 2012; Benito-Garzón and Fernández-Manjarrés 2015; Peterson St-Laurent et al. 2018). This practice has the potential to launch invasions and should be subjected to the same level of risk analysis as for any other type of NNT planting.

Recommendation 4: Design and adopt tailored practices for plantation site selection and silvicultural management

All stakeholders involved in the many activities related to NNTs use, from the nursery industry to the design of plantation, and from silvicultural management to timber har-

vest, should design and adopt tailored practices to ensure the sustainable use of NNTs and minimise the risk of the escape of NNTs. The nursery industry and public nurseries are key stakeholders (Table 2), as the sustainable supply of germplasm of planting material and its quality is crucial for any tree-based project, from afforestation to restoration and to urban forestry (Broadhurst et al. 2015; Whittet et al. 2016). Nurseries are key stakeholders also for sharing information on native and NNTs (Rec. 8). Commercial horticultural and forest nurseries can act as important hubs of non-native species dissemination to planting sites and urban forest sites. Many weeds and forest pests, both insects and pathogens, have also entered new lands via nursery stock (Liebhold et al. 2012) e.g., *Phytophthora* (Sims et al. 2019), and *Hymenoscyphus fraxineus* (Nielsen et al. 2017). Nurseries are one of the most important sources of unintentional introductions of non-native plants (Hulme et al. 2008). Best-practice methods relating to species and provenances of seed or clones (Karlman 2001), seedling production, weed, pest and disease control should be adopted (FAO 2011). Invasive non-native species and pests should be detected, identified, recorded, notified to competent authorities if mandatory or suggested by the local regulations, and eradicated where possible, before transfers and planting.

Table 2. Stakeholder groups and their expected involvement in the implementation and use of Global Guidelines for the use of Non-Native Trees (GG-NNTs). The classification of stakeholder groups is modified from Raum (2018) and Kleinschmit et al. (2018). Y = Involvement of the stakeholder group in a recommendation (R).

Stakeholder Group	Description	R1	R2	R3	R4	R5	R6	R7	R8
Regulators/Governors/ Public Administrators	National, regional and local governments involved in policy, law making, law enforcement, and incentives. National and regional environmental and forest authorities, public forest agencies, public forest nurseries, protected areas.	Y	Y	Y	Y	Y	Y	Y	Y
Commercial agro-forestry business & industry	Private businesses involved in timber production, harvesting, processing, transport, and trade; water companies; and energy suppliers. Includes confederations of industries.	Y	Y	Y	Y		Y		
Commercial nursery industry	Private businesses involved in tree collection, breeding, trade, etc. Turf and substrata industry.	Y	Y	Y	Y				Y
Forest certification organisations	Independent, non-profit organizations setting standards under which forests and companies are certified.	Y	Y	Y	Y			Y	
Professionals and their organisations or confederations	Individuals providing specialist advice and support, urban forest professionals, landscape architects.	Y	Y	Y	Y	Y	Y		
Academia, science and education	Broad group of individuals and organisations conducting research on biodiversity, forest ecosystems related issues, urban forestry, and providing education. National or international scientific associations such as IUFRO.	Y	Y	Y	Y	Y	Y	Y	Y
Botanic gardens and arboreta	Public or private institutions, including historical gardens where trees are grown for scientific study and display to the public. Confederations such as BGCI.		Y	Y		Y	Y	Y	Y
Private forest owners and their organisations or confederations	Broad groups of individuals and organisations responsible for plantations and woodland management.	Y	Y	Y	Y	Y	Y		
Local or indigenous communities	Local, tribal, and indigenous groups involved either formally or semi-formally in running or managing local woodlands.	Y	Y	Y		Y			
Individuals	Individuals (local) who use (the nearby) woodland or urban forest for numerous purposes, e.g. recreational activities, collection or non-wood forest products, as bee-keepers, hunters, agriculture and grazing.			Y					
General public	Citizen and consumers and their organisations, non-directly using the plantations or the urban forests.			Y					
Media and social media	Media professionals and their organisations, private individuals and organisations, broadcasting and social media platforms.	Y		Y		Y		Y	

Standard biosecurity protocols (Sharma et al. 2014) and phytosanitary measures should be followed and applied, such as the International Standards for Phytosanitary Measures (ISPMs) which are standards adopted by the Commission on Phytosanitary Measures (CPM), which is the governing body of the International Plant Protection Convention (IPPC) (Ormsby and Brenton-Rule 2017). Scouting principles such as those used in integrated pest management are relevant; these require growers to follow a standardised sampling plan to scout large numbers of NNTs efficiently, focussing on key NNT species and vectors that are most susceptible to important pests. Any nursery growing or maintaining ornamental and forest NNTs should have an invasive non-native species and pest control program to prevent the growth of non-native species and NNTs outside sites demarcated for cultivation and around growing areas. Similarly, accidental dispersal of NNT propagules, e.g., through the movement of soil, growing media, equipment, machinery, water, should be avoided. Correct labelling of the nursery material (species and provenances) using scientific names is essential. It is also good practice to use double labels for all seed lots – one label fixed outside the bag, the other inside (Schmidt 2007).

Standards, guidelines, criteria, and indicators for sustainable forest management (SFM) have been developed by intergovernmental processes, international organisations, certification schemes (e.g., Forest Stewardship Council, FSC, and Programme for the Endorsement of Forest Certification schemes, PEFC) (Masiero et al. 2015) and national governments. These recommendations, which apply to all forests including planted forests, have resulted in forestry being recognised as a sustainable form of land-use essential to combatting climate change by storing carbon and preventing deforestation. Activity was increased considerably after the Statement of Principles for the Sustainable Management of Forests was adopted in 1992 at the Earth Summit in Rio in response to global concerns about deforestation and the unsustainable exploitation of natural forests (Stupak et al. 2011). At the European level, the 46 signatories of the Ministerial Conference on the Protection of Forests in Europe agreed on a definition of sustainable forest management in a Ministerial Process dating from 1990 and have developed and refined a set of criteria and indicators. These criteria are regularly updated and adapted to new challenges (https://foresteurope.org/).

Best-management practices include criteria such as that biodiversity issues must be considered in the design of planted forests (Conference of the Parties COP 11 Decision XI/19, 8–19 October 2012, Hyderabad, India). For example, the shape of planted forests comprising NNTs should minimise edges at right angles to prevailing winds during the seed-release season. The establishment of representative natural forest should be encouraged within planted forests and, where possible, natural forests should be restored on appropriate sites (Secretariat of the Convention on Biological Diversity 2009). Plantings of NNTs should be avoided near protected areas or endangered habitats. Because the seeds or other propagules of many INNTs are dispersed in water, consideration must be given to the proximity of planting sites to streams and rivers. Suitable practices for planted forest and urban forestry should also include all available methods to limit the spread of pathogens and pests within planted forests and

from infested sites to native forest and other ecosystems (e.g., Engelmark et al. 2001; FAO 2011).

Land managers and owners of planted forests should be informed of forestry activities that favour or limit the spread of NNTs outside plantations (Sitzia et al. 2016). For example, coppicing is known to encourage the spread by *Ailanthus altissima* and *Robinia pseudoacacia.* In South Tyrol, Northern Italy, Radtke et al. (2013) concluded that the currently applied coppice management, involving repeated clearcuttings every 20–30 years, favours the spread of both NNTs. They proposed adaptation of the system to avoid further spread. Vítková et al. (2017) confirmed that, in the absence of forestry interventions, the abundance of *R. pseudoacacia* would decrease during succession in European forests with highly competitive and shade-tolerant trees. However, nearly all lowland forests in Central Europe are managed, which means that these findings are of little value for forestry management in this region unless management plans are totally overhauled. In fact, the limited pool of native woody species, the lack of serious natural enemies, and a dense cover of grasses and sedges can suppress forest succession and favour the development of *R. pseudoacacia* monodominant stands. A stratified approach, combining both tolerance in some areas and strict control at sites of high conservation value, provides the best option for achieving a sustainable coexistence of *R. pseudoacacia* with people and nature (Motta et al. 2009; Vítková et al. 2017, 2020; Sádlo et al. 2017).

The New Zealand guidelines for the use of the Decision Support System (DSS) "Calculating Wilding Spread Risk from New Plantings" (Paul and SCION 2015) are intended to guide individual landowners, consultants, and planners in carrying out initial assessments of wilding spread risk for new afforestation projects. The assessment applies a DSS known as the Wilding Spread Risk Calculator to assess wilding spread risk in a transparent, consistent and repeatable manner using the step-by-step description and examples.

Calviño-Cancela and Rubido-Bará (2013) suggested the establishment of a safety belt around *Eucalyptus* plantations in Spain to reduce the spread of eucalypts from plantations. This measure requires the elimination of all newly recruited individuals in this safety belt (e.g., a 15-m wide belt could reduce the probability of *Eucalyptus* spread by more than 95%) before they start producing seeds, thereby hindering the advance of the front line of invasion. For this purpose, Calviño-Cancela and Rubido-Bará (2013) recommended managing operations at 1–2-year intervals, so that saplings can be removed (uprooted), thus preventing resprouting. Their recommendations apply to situations without fire. Fire stimulates regeneration (Gill 1997; Calviño-Cancela et al. 2018) and could increase dispersal distances, which means that additional measures would probably be needed to control *Eucalyptus* spread after fires. According to Nereu et al. (2019), keeping dense competing vegetation is probably the most cost-effective option to minimise unwanted *E. globulus* recruitment and maximise seedling mortality inside and around plantations. In Portugal, *Eucalyptus* wildlings are more abundant in plantations in moist aspects, coppiced, with older tree stems and corresponding to intermediate site growth indexes (Águas et al. 2017). Silva et al. (2016) undertook an

experiment in six regions in Brazil, under different climatic/ecological conditions, with five pure species (*E. camaldulensis*, *E. pellita*, *E. grandis*, *E. urophylla*, and *E. saligna*) and three hybrids. Factors such as competition with other plant species and seedlings predation drastically limited *Eucalyptus* establishment suggesting low ecological adaptation as an invasive species.

Tailored management practices should be followed in the case of planted forests with NNTs for bioenergy production (Short Rotation Forestry SRF, Short Rotation Coppice SRC): choosing new planting sites; mitigating negative impacts on biodiversity (Weih 2008; Framstad et al. 2009; Vanbeveren and Ceulemans 2019); preventing spread into surrounding habitats e.g., using buffer zones (Crosti et al. 2016); protecting hydrology (Christen and Dalgaard 2013); conserving landscape values; and planning for the restoration of the site after the cultivation cycle (Hardcastle et al. 2006; Neary 2013; Caplat et al. 2014). For example, experience with *Eucalyptus* plantations under intensive short-rotation regimes in China (Zhou et al. 2020) suggests that, in the long term, the intensively managed monospecific plantations under short-rotations should be progressively converted into mixed plantations with short-, medium- and long-term rotations. This strategy could be accomplished by interplanting with high-value native tree species such as *Castanopsis hystrix*, *Dalbergia odorifera*, and *Parashorea chinensis*.

Finally, it is very important to design and adopt good practices for harvesting and transport of timber and other forest products or materials, to mitigate the unintentional spread of reproductive material of NNTs by harvest and transport of timber, to reduce the spread of seeds of other weeds, pathogens, and pests inside and outside the plantations. A key requirement of best practice in this regard is to keep forestry machinery out of water bodies and riparian margins. Machinery needs to be cleaned and checked regularly where the transfer of propagules of NNTs species is an identified risk. Although the role of such dispersal has only been studied in a few cases (e.g., Kaplan et al. 2014) it is probably a major factor in invasions of NNTs in many situations. Appropriate water and sediment controls need to be installed to reduce runoff directly into waterways to reduce opportunities for the spread of propagules of NNTs.

Forest personnel and city council staff responsible for working with urban trees should be trained to recognise and report unusual pests and symptoms of diseased or infested trees, to report escape events, and to carry out practices that reduce the risk of pest, NNTs and other non-native species or propagules moving to other locations (Rec. 6). Personnel should wear outer layers of clothing and footwear that are not "seed friendly" (*sensu* USDA 2012) to minimise the risk of spreading INNTs and other invasive non-native species propagules accidentally.

Forest roads (usually built with the primary aims of supporting forest management and harvesting), fire-control ditches, and road and railways networks should be periodically monitored to prevent the escape of NNTs, especially during harvesting or other silvicultural operations that can promote the accidental spread of propagules (Nereu et al. 2019; Chmura 2020). Transport of timber, and other forest products of materials, removing trees or coppice, arboricultural work in urban forestry and mechanisation movement are also responsible for unintentional transport of NNT propagules and other (non-native) species, such as invertebrates, pathogens, and pests.

Recommendation 5: Promote and implement early detection and rapid response programmes

It is very important to regularly monitor plantings for the spread of NNTs and to act rapidly to control spread so that invasions can be managed before they become widespread and costly to control. Early detection and initiation of management to promptly remove INNTs can make the difference between being able to prevent invasions and having to either spend substantial resources controlling widespread invasions or accept or mitigate against whatever negative impacts they have (Nuñez et al. 2017). Proactive measures to reduce the chances of NNT and INNT spread and for dealing with problems at an early stage must be included in standard silvicultural practices, large-scale plantation plans, and urban forestry policies, such as the design of buffer zones around NNT plantations where the potential spread can be monitored more accurately.

The relatively long initial lag phase between introduction and naturalisation/invasion (Kowarik 1995), relative long life span and age of maturity, and slow dynamics observed in many INNTs, compared to other non-native invasive plant species (e.g., aquatic invasive non-native plants), offers opportunities to control the INNTs while escaped populations are still small (Finnoff et al. 2007; Dodet and Collet 2012). Developing "alarm lists" or "alert lists" of possible new invasive NNTs can also enable more rapid reaction (Richardson 2011; Faulkner et al. 2014) as can horizon scanning exercises (e.g., Roy et al. 2014).

Any NNTs detected outside cultivation areas – especially NNTs recognized elsewhere as invasive and/or if occurring in areas of high conservation value – should be georeferenced, reported, and controlled or contained. All records and sightings will help to determine the extent of the INNT problem in a given area and facilitate a rapid response where necessary. They can also help to better understand species distribution, habitat suitability, and thus support better management. Such data should ideally be collected and quality-controlled by a (national / state) coordination centre, so that it can directly inform policy and management. Owing to the huge number of species observations that can be collected by non-professional scientists, citizen science has great potential to contribute to data collection, scientific knowledge on invasive non-native species, and to support early detection for NNTs outside cultivation areas. The recent adoption of information and communications technology in citizen science (e.g., web or mobile application-based interfaces for citizen training and data generation) has led to a massive surge in popularity, mainly due to reduced geographic barriers to citizen participation (Adriaens 2015; Johnson et al. 2020).

A rapid response capacity implies the availability of skilled personnel, contingency plans (where responsibilities are clearly determined), and technical guidelines for controlling invasive NNTs. Guidelines exist for many NNTs (e.g., PM-9 for *Ailanthus altissima*, EPPO 2020) but they need to be incorporated into a unified framework and databases (Rec. 8). It should be stressed that controlling small foci of escaped NNTs, generally saplings, does not require heavy equipment and costly investments. In most cases control can be easily achieved either by cut-stump, drill-fill or hack and squirt techniques that do not require sophisticated tools. In addition, controlling a limited number of NNTs

with direct application methods, i.e. without spraying, enables using very small quantities of herbicides. The recent development of new herbicides with high ecotoxicological profiles gives the opportunity to perform INNTs control with a maximum effectiveness and a minimum risk for the environment (Dufour-Dror and Yaacoby 2019).

Establishing a new sentinel garden or joining a network of sentinel sites is an important tool for supporting early detection and early waring strategies. This approach provides the unique opportunity to monitor NNTs in sentinel site networks (Kenis et al. 2018) both for their susceptibility to pathogens and pests, and for their ability to naturalise and to escape from cultivation. Other areas that worth monitoring as they are likely to act as sources of propagules and sites of entry for new invasions are urban areas, areas of human habitation outside large towns where gardens have been established (Alston and Richardson 2006; McLean et al. 2017), experimental plantings, arboreta or botanical gardens containing NNTs (Dawson et al. 2008), networks of non-native monumental trees. They can also be included in sentinel networks (Roques et al. 2015).

Kenis et al. (2018) and Visser et al. (2014) believe that sentinel site networks as described above could help to: (1) identify emerging trends in NNT invasions; (2) provide valuable mapping for particular NNTs; (3) monitor changes in NNT abundance and distribution over time; (4) help ensure legislative compliance of land managers and plantation owners; and (5) track management efforts over time. The International Plant Sentinel Network (IPSN; https://www.plantsentinel.org/), was developed to facilitate collaboration amongst institutes around the world, with a focus on linking botanic gardens and arboreta, National Plant Protection Organisations (NPPOs), and plant health scientists, focusing on pests and pathogen, but it might also help in monitoring NNTs.

Efficient monitoring activities require carefully planning, large and permanent funding and skilled personnel, but important contributions can be done even with limited resources. For example, Visser et al. (2014) showed that Google Earth can be used to establish a global sentinel site network for NNT invasions, because imagery is continuously being updated, is free to access and is low-tech. The ease of accessing Google Earth, potentially linked with projects in platforms such as iNaturalist (https://www.inaturalist.org/), means that effective monitoring of networks of sentinel sites could be achieved as part of citizen science initiatives. Google Street View has been used to detect eucalypt wildlings along roads in Portugal (Deus et al. 2016).

Recommendation 6: Design and adopt tailored practices for invasive non-native tree control, habitat restoration, and for dealing with highly modified ecosystems

If an INNT species has been introduced and started to spread beyond a planting site, early detection and rapid response is crucial to prevent its establishment. The preferred response is to eradicate the INNTs as soon as possible (UNEP/CBD/COP VI/23, principle 13). If eradication is not feasible, containment, and long-term control measures should be implemented. It is often not clear how INNTs can be successfully managed,

but there are examples from Australia and South Africa where integrated management approaches are applied, including chemical, physical, biological (Hill et al. 2020), and cultural control (Richardson et al. 2015; van Wilgen et al. 2020). As with other invasive non-native species, a clear definition of the management goals and a spatially coordinated management strategy are key for successful management of INNTs.

It is necessary to develop and adopt species-specific and site-specific guidelines for the restoration of sites previously occupied by INNTs or by planted forests of NNTs, to minimise or reverse disturbances caused by the previous land use or INNTs. In fact, recent international commitments have paved the way for the implementation of large-scale ecological restoration programs in the upcoming decades (https://www.decade-onrestoration.org/), such as the Initiative 20×20 in Latin America and the Caribbean (https://initiative20x20.org/) that seeks to restore 20 million hectares of degraded land by 2020, the AFR100 African Forest Landscape Restoration Initiative (afr100.org) that aims to bring 100 million hectares of degraded land under restoration by 2030 (Chazdon et al. 2017), and the Atlantic Forest Restoration Pact, which aims at restoring 15 million hectares in the Brazilian Atlantic Forest until 2050 (Pinto et al. 2014).

Restoration objectives have been broadly classified into overarching strategies, such as rehabilitation, reconstruction, reclamation, and replacement (see Stanturf et al. 2014). Native tree species can grow in the understory of planted forests of NNTs. However, not all planted forests of NNTs develop species-rich understories; some remain NNT monocultures. Low light intensity below the canopy, distance to seed sources, inhospitability to seed dispersers, altered soil and litter conditions affecting seed germination or seedling growth, intensive root competition with the planted NNTs, other forms of plant-soil interactions, plantation design, or periodic disturbances by organisms or any external factor are likely causes of the lack of native species diversity in NNT planted forests that require careful consideration (Lugo 1997). Thus, human-mediated restoration is likely necessary after the presence of NNTs. One option is the continuous change of the plantation by reducing the abundance of NNTs and simultaneous replanting with native species.

Sádlo et al. (2017) proposed a stratified approach to the management of eight types of *Robinia pseudoacacia* stands growing in Europe, based on decisions that reflect the local context. Specific guidelines for restoration of sites previously occupied by planted forests of *R. pseudoacacia* have been produced in the Piedmont region of Italy and in China (Zhang et al. 2018). Sturgess and Atkinson (1993) suggested management strategies for the restoration of near-natural sand dune habitats following the clearfelling of *Pinus* planted forests in Britain, and Brown et al. (2015) proposed approaches for restoring areas previously planted with non-native conifers on ancient woodland sites. Szitár et al. (2014) assessed the recovery of open and closed grasslands over five years after the removal of planted forests of non-native pine species through burning in an inland sand dune system in Hungary. Arévalo and Fernández-Palacios (2005) proposed the continuous elimination of the non-native *P. radiata* and augmentation with the native *P. canariensis* on Tenerife, Canary Islands (Spain). Hughes and Richards (2003) and Moss and Monstadt (2008) proposed management guidelines for the restoration

of floodplain forests in Europe. Detailed guidelines are available for the restoration of South African fynbos vegetation following the clearing of NNTs (Holmes et al. 2000, 2005, 2008; Hirsch et al. 2020; Holmes et al. 2020a, b).

The Atlantic Forest in the Brazil biodiversity hotspot is being threatened by its replacement for *Eucalyptus* plantations (Joly et al. 2014). In many regions, small remnants of Atlantic Forest currently persist in a matrix of *Eucalyptus* plantations (Tavares et al. 2019). Restoration plantations in this biome must be established with nursery-grown seedlings of high genetic diversity (Sujii et al. 2017). Inbreeding depression in trees may lead to reduced tree population viability in forest restoration areas. This issue may play an even more relevant role in restoration plantations in the tropics because most tree species are pollinated by animals, and their maximum flight distances are not considered when distributing seedlings in the field (Sujii et al. 2017).

Active restoration of ecosystems degraded by INNTs to pre-invasion or pre-degradation conditions is impractical in some situations for logistical or financial reasons. In such cases, options for managing such ecosystems sustainably to optimise biodiversity and considerations relating to key ecosystem services should be explored, and guidelines should be formulated for integration into regional management plans (e.g., Schwartz et al. 2012). Management interventions involving inexpensive measures to encourage spontaneous succession following the removal of NNTs or other degrading disturbances are removed or reduced ("passive restoration") have been successful in many regions (see Holmes et al. 2020b for a review). Engagement with all stakeholders is crucial in restoration and control programmes pertaining to NNTs (Rec. 7).

Recommendation 7: Engage with stakeholders on the risks posed by invasive non-native trees, the impacts caused, and the options for management

Stakeholder engagement and public participation are key in the management of risks posed by NNTs and INNTs. The crucial role of stakeholder engagement is increasingly recognized globally, but engagement still implemented mostly in a top-down fashion (Shackleton et al. 2019); much more attention is needed to co-design, co-create and co-implement research and management. Social learning and feedback to stakeholders also need to be promoted, and multidisciplinary collaboration and partnerships are also highly beneficial (Rec. 8).

Forest and forestry issues have become more complex in recent decades. The many uses of forests, of NNTs, and the related types of land uses, now benefit a wider stratum of people than ever before, and is subject to a large range of social and environmental demands. An example of one possible classification of the major stakeholder groups involved in forest and forestry issue, and which are differentially affected by the GG-NNTs, is reported in Table 2. It is a general classification, to be applied only to the GG-NNTs, and cannot substitute national and local analysis of the forest and forestry systems and dedicated stakeholder's maps for local implementations of the GG-NNTs.

It is always important to consider that many NNTs, planted for production or for other purposes, have strong direct positive economic impacts on the local and national

economies of many countries, including poverty alleviation, but often lead to sharp conflicts of interest when the NNT species become invasive, and have negative impacts on the ecosystem (Dodet and Collet 2012; van Wilgen and Richardson 2012; Dickie et al. 2014; Sladonja et al. 2015). Such conflicts can be reinforced if risk assessment methods are not transparent or do not give adequate consideration to the context-dependence of impacts (Bartz and Kowarik 2019).

Besides land managers, forest owners, and local or indigenous communities, engagement with the general public is very important for issues related to NNTs, from their use in gardening and landscaping to forests and forestry. The active and informed participation of communities and stakeholders affected by planted forest management decisions is critical to the credibility and acceptance of management processes. Public awareness-raising and communication activities play critical roles in informing and educating the public (Andreu et al. 2009; Marchante et al. 2011; Schreck Reis et al. 2013), thereby allowing them to participate more effectively in decision-making and in the management of NNTs and INNTs (Dechoum et al. 2019). Public support for eradication, management or control efforts directed at INNTs must be sought through carefully planned, long-term ongoing outreach initiatives involving, among other things, meetings with stakeholders, local village leadership, employment of villagers from areas adjacent to invasions, and the effective use of media outlets (Novoa et al. 2018).

An increasing number of tourists are interested not only in experiencing unique natural and cultural environments and landscapes but also learning more about them. Forest-based tours are an ideal opportunity to share information about different types of forest environments, native and NNT species, restoration actions, wildlife and landscapes, how they function, and how they came to be. Visitors are also likely to be interested in the lifestyles, cultures, and social and political histories of local communities living near forest areas and making use of local tree species. Citizen science projects such as online apps for collecting data on distribution and impacts of INNTs (Groom et al. 2017, 2019) should be utilized. Wider engagement and education regarding impacts can be through online sources or field guides (Rotherham and Lambert 2012; Veenvliet et al. 2019).

Since 1992, the UNCED Statement of Forest Principles (Galizzi and Sands 2004) states that the provision of timely, reliable, and accurate information on forests and forest ecosystems is essential for public understanding and informed decision-making and should be ensured (principle 2, letter c). Similarly, the CBD COP 6 Decision VI/23 "Alien species that threaten ecosystems, habitats or species", within its Guiding Principle no. 8 stresses the importance of the process of the exchange of information on invasive alien species.

In formulating legislation on NNTs and INNTs a further application of the participatory approach from regulators, governors, and the public administration in general is envisaged. The aim of participatory forestry is to ensure that all stakeholders are included in all aspects of forest management, decision-making and policy formulation (FAO 2010a). It is often remarked that the public is more likely to comply with regulations that they have actively participated in creating (Sudirman et al. 2004). However, there is diverse criticism regarding the ability to successfully design participatory forest

policy processes (Kleinschmit et al. 2018). For example, in Ghana, it has been suggested that involving the public can be disruptive, costly, time consuming, and inefficient, because they are "unable to participate effectively" (Mohammed 2013). On the contrary, many publications identify key factors for successful participation (Kleinschmit et al. 2018), dedicated novel tools, such as the Participatory Technology Assessment (Griessler 2012), Co-Design (Blomkamp 2018), or show how participatory tools in forest policy, legislation making and forest management (e.g., in Tanzania; Magessa et al. 2020) can also help in achieving a number of UN Sustainable Development Goals (https://sdgs.un.org/).

Participatory forestry in the context of NNTs should include professionals from the invasion science sector, as scientific knowledge and evidence are usually conceived outside of policy systems and legislation corpus, and then brokered or disseminated into the policy process, with varying degrees of success (Cairney and Oliver 2017; Pineo et al. 2020).

Recommendation 8: Develop and support global networks, collaborative research and information sharing on native and non-native trees

Global networks, collaborative research, and information sharing are crucial for supporting the implementation of the recommendations of the GG-NNTs and for achieving their goals. Thus, this final recommendation is cross-cutting and relevant to all the other recommendations.

For example, the preferential use of native trees has to be supported by large-scale efforts for the conservation and evaluation of forest genetic resources (Sigaud 2000), from dedicated research in forest tree breeding and improvement, particularly in developing countries. These collaborations and research programmes are essential for the adaptation and the evolutionary processes of trees and forests, for improving their resilience and productivity, and for providing suitable materials and information to the nursery sector on native and NNTs. To date, forest trees are underrepresented among available plant genome sequences (Holliday et al. 2017).

Another important field, and a critical aspect of collaborative research in the management of NNTs and INNTs, is the need for defining and identifying NNT species, since species are the unit tied to regulatory policies and management (Hamelin and Roe 2020). However, a large number of NNTs are used, including thousands of cultigens (hybrids, clones, etc.); for many NNTs, further studies on biosystematics, phylogenetics, taxonomy, nomenclature, and biogeography (e.g., an accurate delineation of native, neonative *sensu* Essl et al. (2019), non-invasive, and invasive geographic ranges) are vital to reproducibility, documentation, and prediction. Lack of concern for nomenclature can undermine science and management of NNTs, and it can lead to serious mistakes. Furthermore, the CBD has long recognised that taxonomy is crucial for the implementation and monitoring of the CBD itself (Global Taxonomy Initiative, Decision IV/1).

Fast and reliable identification of NNTs and INNTs is also a prerequisite of early detection and rapid response (Rec. 5). Global networks and collaborative research can

advance application of novel techniques, such as remote microscopy facilitating real-time identification of NNTs (Thompson et al. 2011). This task is achieved by using web-enabled video cameras mounted on microscopes, allowing live streaming of images to a web address. This web link can then be accessed by anybody (e.g., a specialist taxonomist for that NNT species) with access to the Internet. Direct communication between an expert and a specimen holder using remote microscopy equipment facilitates a very high level of interactivity (Thompson et al. 2011).

Global networks (Packer et al. 2017) are critical for the future of invasion science, and to ensure effective planning and management of NNTs to deal with, among other things: identifying global priorities for research and management agendas; coordinating data collection over space and time; assessing risks and emerging trends; understanding the complex influences of biogeography on mechanisms of invasion; predicting the future of invasion dynamics; and using the insights on all of the aforementioned issues to improve the efficiency and effectiveness of evidence-based management techniques.

The scientific community should support the improvement of standard and accepted methods to assess negative impacts of INNTs, establish priorities for intervention, and provide improved tools for comparing species (Bindewald et al. 2019), habitats and regions at the global level. In 2020 the IUCN adopted as a formal standard the Environmental Impact Classification for Alien Taxa (EICAT) methodology (Hawkins et al. 2015; IUCN 2020). Consideration should be given to assessing the impact of INNTs using EICAT. Results of such assessments should be shared using freely accessible platforms such as the IUCN Global Invasive Species Database. An important example of global network is the CONTAIN project, supported by a group of more than 20 researchers from four countries (Argentina, Brazil, Chile, and the UK) with diverse research focuses, such as invasion ecology of plants and animals, ecological restoration, economy, statistics, and social dimensions of invasions, which aims to design, and introduce to stakeholders a user-friendly decision making tool that will help to guide the long-term management of invasive species (Lambin et al. 2020).

Cavender and Donnelly (2019) called for greater involvement of botanical gardens and arboreta with urban forestry to improve sustainability of cities and human lives. These institutions have a significant public reach, maintain strong professional networks, and can make important contributions to addressing key priorities including protecting existing trees; improving tree selection, diversity, and age structure; and improving planning, standards, training, and management. Improving urban forests is one of the solutions to achieving several of the UN SDGs, such as making cities healthier and more liveable (Fig. 1). With the cooperation of practitioners involved in forest and urban forest management, best practice manuals for control or eradication for the most important INNT species can be prepared for different world regions and taxa.

Information on NNTs and INNTs and strategies for dealing with them is critical for the implementation of all the recommendations in the GG-NNTs. Science-based strategies to tackle biological invasions depend on recent, accurate, well-documented, standardised, and openly accessible information on non-native species (Hulme and Weser 2011; Groom et al. 2017). Information is becoming more easily accessible (e.g.,

IUCN Global Invasive Species Database, www.iucngisd.org, IUCN Global Register of Introduced and Invasive Species, http://www.griis.org/, and CABI Invasive Species Compendium, www.cabi.org/ISC). For INNTs of concern in the European Union, IUCN provided comprehensive information on costs and available methods of appropriate management actions. Such science-based reviews are also available from the EPPO website; an example is the PM/9 Standard on *Ailanthus altissima* (EPPO 2020). The European National Forest Inventory Network (ENFIN) is a facilitator for enhancing harmonisation and comparability of national data and the ancillary information required to monitor European forestry-related policies (Vidal et al. 2016). Similarly, the *Observatoire des Forêts d'Afrique Centrale* (OFAC) is an association of public and private bodies, researchers and NGOs whose goal is to help set up the convergence plan of *Commission des Forêts d'Afrique Centrale* (COMIFAC). It provides COMIFAC and country members a powerful steering and national or remote sensing data sharing platform to promote better governance and the sustainable management of forest ecosystems (Vidal et al. 2016).

However, there is the need to improve the quality and quantity of the available information, and support and use systems for information sharing. For example, the precise geographical distribution of plantations of NNTs is not available for many countries. Harmonised and quality-controlled data at the regional scale (e.g., for the European Union) are needed for robust assessments of responses of forest tree species to climate change (Serra-Diaz et al. 2018; Reyer et al. 2019; Ruiz-Benito et al. 2020).

Information sharing systems would greatly improve the ability of authorities to prevent the introduction and spread of INNTs (Katsanevakis et al. 2013; Tsiamis et al. 2016). Up-to-date and accurate data are also particularly relevant for "horizon scanning" initiatives, which are an essential component of invasive species management, to prioritise potential new invaders that are not yet naturalized in a region (Groom et al. 2015).

Global networks, collaborative research, and information sharing are also crucial to adequately design and promote forest and forestry biosecurity training programmes, in building and developing capacity. In fact, the effective management of NNTs and INNTs, from prevention to early detection and rapid response, from habitat restoration to stakeholder engagement, requires a breadth of expertise from field to laboratory, and specialised knowledge and skills that can only be developed over time. The capacity and awareness of landowners, forestry officials, nursery personnel, and other stakeholders are crucial for effective implementation of the recommendations of the GG-NNTs, as is their hands-on experience to help design training programmes or adjust and improve existing guidelines.

A number of universities offer graduate and postgraduate certification and diplomas on plant biosecurity. Skill development includes, for example, knowledge of the legislative frameworks underlying the regulation of transboundary movement of potentially invasive non-native species, the identification and analysis of pathways and vectors, writing risk assessments for new species (pre-border and post-border), developing incursion response plans, biodiversity management plans, and research proposals, as well as gaining advanced science communication skills. Other important topics include training on pest and pathogen risks to forestry (Marzano et al. 2017), and the

use of plant protection products. A single full curriculum dedicated to biosecurity for NNTs is not yet available; there is thus scope for collaborative research aimed at implementing and sharing online training for everyone who might be interested.

Conclusions

A large and growing number of NNTs are invasive in their new ranges and have diverse negative impacts on biodiversity and ecosystem functioning, as well as on Nature's Contribution to People (Díaz et al. 2018). The GG-NNTs call for the preferential use of native trees whenever possible, aims to raise awareness and contribute to reducing the further introduction and spread of new INNTs and further dissemination of known invaders. Where the use of NNTs is unavoidable, the GG-NNTs call for the application of best practices to guide NNT cultivation to minimise the risk of escape from areas set aside for plantings and to ensure that measures are in place to control wildings in the early stage of the invasion process. The application of the GG-NNTs and the achievement of their goals will help to conserve forest biodiversity, ensure sustainable forestry, and contribute to the achievement of a number of Sustainable Development Goals linked with forest biodiversity.

The GG-NNTs outlined in this paper are general; they need to be modified for implementation in different national, regional, and local-scale contexts, in consultation and with full engagement of all relevant stakeholders. Different groups of stakeholders have different fundamental and unreplaceable roles in formulating workable management strategies. For example, in the stakeholder group that includes regulators, governors, and public administration, key expectations are to: make pledges to mobilise resources; build and develop capacity; mainstream the GG-NNTs into national and sub-national policies, regulations, strategies and plans, to prevent NNTs invasions and ecosystem degradation; and to support collaborative scientific research and delivering of technical solutions for the sustainable management of plantations of native trees and NNTs.

The GG-NNTs offer general recommendation on NNTs and provide a basic framework and suggestions on tools for planning and implementing sustainable use of NNTs in nationally appropriate and scientifically sound practices that account for national and sub-national needs. It is important to bear in mind that national circumstances vary considerably in terms of biophysical conditions (e.g., NNT species, forest types, and forest and forestry utilization practices), institutional and legal frameworks, economic challenges and possibilities, management, and use, among other factors. Therefore, no "one-size-fits-all" approach can be applied in the implementation of the GG-NNTs. Instead, various technical and organisational options must be combined to achieve efficient implementation of the guidelines.

Global networks, collaborative research, and information sharing are crucial for supporting the implementation of the recommendations of the GG-NNTs and for achieving their goals. This is the main cross-cutting recommendation. However, other recommendations or parts of them are somewhat cross-cutting and relevant to the whole set of GG-NNTs, such as the need to consider global change trends and to en-

gage with all relevant stakeholders. In fact, tree species, provenance, and site selection, plantation management, evaluation of risks and benefits in the use on NNTs, restoration, and conservation activities are all expected to be strongly influenced by changes in climate and land use.

Finally, in the implementation phase, intersectoral collaboration within the country or within regions should be promoted. Sectors such as agriculture, environmental protection, biodiversity conservation, ecotourism development, and other social fields will be interested in the process of local implementation and in the results of applying the GG-NNTs to the country scale. This involvement may lead not only to greater value at the national level, but also to greater understanding, acceptance of and support for the guidelines. Ideally, the goals of the GG-NNTs should be embedded in national strategies on biodiversity and invasive non-native species. Forest certification schemes are important instruments for mainstreaming the recommendations in the GG-NNTs.

Acknowledgements

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Supplementary material 1

Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts (GG-NNTs) Background information (Annex to the GG-NNTs)

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Data type: additional materials

Explanation note: Terms and definitions, Acronyms, and additional Tables: Non-native tree species in planted forests and for other uses: historical and recent pathways of introduction; Main types of negative impacts of INNTs (after Richardson et al. 2000); Major international initiatives and legislation pertaining to invasive alien species and INNTs.

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