Non-native palms (Arecaceae) as generators of novel ecosystems: A global assessment

Vincent Fehr1,2 | Robert Buitenwerf1,2 | Jens-Christian Svenning1,2

Abstract

Aims: Novel ecosystems are self-maintaining ecosystems that support species assemblages without historical precedent. Despite much interest and controversy around novel ecosystems, it remains poorly understood how they are generated, what their capacity to support biodiversity is and what the implications for society are. Here, we address these issues through a global synthesis of non-native palms, since palms are likely generators of novel ecosystems because they are introduced widely beyond their native range and have the capacity to act as ecosystem engineers.

Location: Global.

Methods: We gathered data on non-native palms from peer-reviewed literature/papers, grey literature and online databases. We extracted data on the biogeographic context of palm invasions, plant functional traits and anthropogenic drivers to quantify their effects on biodiversity, ecosystem functioning and ecosystem services.

Results: Of the 2,557 palm species, 3.4% (86 species) were recorded as naturalized and 1.1% (28 species) as invasive, which exceeds the average invasion success across all woody plants. Naturalized palms are present in most tropical and subtropical regions around the world, often in urban areas, reflecting the use of palms in horticulture. Many naturalized palms were taller and more likely to originate from open habitats or dry forest than non-naturalized palms. These features likely represent the naturalized palms’ competitive ability, high fecundity and dispersal ability along with ecological matching to human-disturbed environments. Overall, literature on ecological effects of palm invasions was sparse, but we found multiple cases in which palm invasions resulted in strong ecosystem changes or even biome shifts.

Main Conclusions: We found strong evidence that palm invasions can generate novel ecosystems. Although there are substantial knowledge gaps on the ecological effects of palm invasion, anthropogenic drivers like urbanization and ongoing global warming will continue to expand palm ranges and promote non-native palms as generators of novel ecosystems.

KEYWORDS

alien invasive species, Arecaceae, biological invasions, ecosystem effects, global change, invasion biology, non-native species, novel ecosystems, palms, urban ecology
1 | INTRODUCTION

Human agency is an increasingly dominant force in the assembly of ecological communities. An important component is the translocation of species to regions outside their native range (Seebens et al., 2017), with introductions sometimes resulting in species assemblages markedly without historical precedent (Hobbs, Higgs, & Harris, 2009). Such ecosystems have been termed “novel ecosystems” if they are self-sustaining without ongoing human intervention (Hobbs et al., 2009; Morse et al., 2014). Species invasions that trigger the emergence of novel ecosystems have far-reaching ecological—and in some cases also socio and economic—effects, as ecosystem functioning and services may be strongly affected (Hobbs et al., 2009).

The generation of novel ecosystems with non-native plants as the main drivers has been well documented within a wide range of habitats around the globe (Lugo, 2004; Rogers & Chown, 2014; Yu, Okin, Ravi, & D’Odorico, 2016). Despite awareness of the various mechanisms through which non-native plants can alter ecosystem composition and processes (Hejda, Pyšek, & Jarosík, 2009; Vilà et al., 2011), the degree of novelty that different taxonomic groups or functional types generate within an ecosystem remains unclear. This inability to generalize hampers the ability to make future projections of community assembly, structure and functioning and to forecast social and economic implications. Furthermore, the ecological dynamics of novel ecosystems, their ability to sustain biodiversity, and how this can be improved through conservation and restoration actions remain poorly understood (Svenning, 2018).

Tools to predict future ranges under different scenarios of global change exist, notably environmental niche models (Guisan & Zimmermann, 2000; Thuiller, 2003). However, these models typically ignore species interactions, which are crucial in species invasions. Even joint species distribution models (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Svenning et al., 2014), in which species interactions are considered through co-occurrence patterns (Ovaskainen et al., 2017), suffer from an intractability of the ecological processes through which species interact and typically focus on a single taxonomic or trophic level (Zurell, Pollock, & Thuiller, 2018). Evidence of the effects of species introductions across entire taxonomic groups may thus lead to new insights and generalizations that can be used to predict the degree to which invasions will create novel ecosystems.

Palm (Arecales) are potential generators of novel ecosystems as they (a) have the capacity to act as ecosystem engineers, and (b) have been widely introduced elsewhere for agri- and horticulture. Many palms have the capacity to act as ecosystem engineers within their native range, primarily because of their unique physiognomy and functional traits compared to other woody plants (Dransfield & Uhl, 2008; Tomlinson, Horn, & Fisher, 2011), combined with a capacity to become hyper-dominant (Steege et al., 2013). An example of a unique palm functional trait is the big, heavy and slow-decomposing leaves that modify the habitat in multiple ways (Farris-Lopez, Denslow, Moser, & Passmore, 2004). Many palms are considered as keystone species in their native range due to their important role for frugivores (Galetti, Keuroghlian, Hanada, & Morato, 2001; Henderson, 2002; Sica, Bravo, & Giombini, 2014). We therefore expect introduced palms to have disproportionate effects on ecological communities and ecosystem functioning. Palms have been widely introduced beyond their native range for ornamental purposes, food and other uses (Byg & Balslev, 2001, 2006; Campos & Ehringhaus, 2003; Martins, Filgueiras, & Albuquerque, 2014; Sosnowska & Balslev, 2009), resulting in the spread of many palm species (Figure 1). For example, the coconut palm (Cocos nucifera) has a pantropical distribution due to long-distance dispersal by humans (Gunn, Baudouin, & Olsen, 2011). The spread of palms to new environments is expected to accelerate due to ongoing global warming, which will allow palms to colonize higher latitudes and altitudes (Reichgelt, West, & Greenwood, 2018; Walther et al., 2007). Palms are also a practical model for studying novel ecosystems as they are one of the best known tropical plant families (Baker & Dransfield, 2016; Eiserhardt, Svenning, Kissling, & Balslev, 2011; Henderson, 2002; Kissling et al., 2019). This body of knowledge is key to move beyond descriptive work, and identify and quantify the mechanisms by which invasive species assemble novel communities and ecosystem processes.

Here, we provide the first global synthesis on palms as potential generators of novel ecosystems, drawing on peer-reviewed literature, as well as non-peer-reviewed reports and verifiable anecdotal evidence in order to overcome data limitations. The study addresses three broad objectives. First, we assess the biogeographic and environmental context of palm invasions and quantify the role of functional traits and human-mediated dispersal. Second, we assess evidence that palm invasions generate novel ecosystems as well as effects more generally on other taxonomic groups, ecosystem functioning and human society. Finally, we discuss the future of palm-generated novel ecosystems under scenarios of societal and climate change.

2 | MATERIALS AND METHODS

2.1 | Data compilation and classification of non-native palm records

We gathered information on non-native palms from several sources including alien species databases, peer-reviewed publications, books and grey literature like inventory lists of alien species or factsheets from local authorities (see Appendix S1: Table S1.1 and S1.2 and Appendix S3) and examined the references from the retrieved sources for further records. A total of 302 records were gathered from the World Checklist of Arecaceae by Govaerts, Dransfield, Hodel, and Henderson (2015). We standardized the taxonomic names according to the nomenclature of Govaerts et al. (2015) and classified the species into three naturalization stages according to Richardson et al. (2000):

- **Casual species**: Seedlings, juveniles or reproductive individuals that spread locally and close to cultivated parent plants, but do not form self-sustaining populations (including species reported
as “casual alien species”, “not established”, “escaped”, “locally naturalised”, “semi-naturalised” or “introduced”).

- **Naturalized species**: Fertile individuals that exist over considerable distance from parent plants and form self-sustaining populations (including species reported as “naturalised” or “established”). All invasive species were also included in this category.

- **Invasive species**: Naturalized species that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants and for this reason could potentially have undesirable ecological, social or economic effects. This stage of naturalization was only assigned to non-native species if they were classified as such in a peer-reviewed publication or by an accepted authority (including species reported as “weeds”).

If we found contradicting information regarding the naturalization stage of a species in consulted peer-reviewed and grey literature, we adopted peer-reviewed records over grey literature. When equally reliable sources reported different naturalization stages, we assigned the most advanced stage of naturalization.

The criteria and the use of terms for categorizing non-native palm species varied considerably between different sources. We noticed several cases where the naturalization stage of a species was incorrectly adopted from the original source into a publication of a peer-reviewed journal or an online database. We also found entries in online databases where the climatic requirements of the non-native palm species did not comply with the climatic conditions in the introduced range (e.g. *Phoenix dactylifera* in Austria and Hungary; DAISIE, 2018). To ensure a high-quality data set, we checked each report for plausibility, verified the original source in doubtful cases and removed incorrect or implausible reports. In all the following analyses, we included only records of naturalized and invasive palms (i.e. excluding casual species records). All analyses were conducted using the R software (version 3.6.1; R Core Team, 2019).

### 2.2 Inventory, distribution and biogeography of non-native palms

To assess whether palm species from certain subfamilies are more likely to naturalize outside their native range, we compared the proportion of naturalized species (excluding casual species) and non-naturalized species in each subfamily with species from the remaining subfamilies using Fisher’s exact test.

To analyse the geographical distribution of non-native palms, we used the World Geographical Scheme for Recording Plant Distributions of the International Working Group on Taxonomic Databases (TDWG, Brummitt, 2001). Specifically, we used botanical continents (level 1), botanical regions (level 2) and botanical countries (level 3), which are units based on a combination of political boundaries and botanical traditions. For some parts of the world, comprehensive inventories of non-native biota were available including non-native palms, for example for Florida (FLEPPC, 2017), Australia...
Data on both maximum stem height and habitat type were available and were available for 1,741 species (87% of all non-climbing palms). To simplify the habitat types used by Henderson (2002), we created the following habitat classes: (a) moist forest, (b) dry forest, and (c) open habitat. To examine the relationship between the environment and non-native palm establishment, we assigned each occurrence record to “tropical” and “extratropical” climates based on the Köppen climate classification (Peel, Finlayson, & McMahon, 2007) and to eight habitat classes (IUCN, 2019), which were combined and renamed (see Table S1.3 in Appendix S1). Habitat classes were only applied to non-native palm records that specifically state the habitat type in the original source. Species may occur in multiple climatic regions and habitats. The climate and habitat information for many records were not detailed enough to assign species to biomes.

To determine the potential role of human-driven spread of non-native palm species, we assigned four human use categories to each naturalized palm species: (a) ornamental, (b) food, (c) rattan (i.e. the flexible stem of climbing palms used for furniture, wickerwork etc.), and (d) other uses (e.g. fuel, building material, handcrafts, erosion protection and medicine). We only included human uses that are likely to result in cultivation of palm species outside their native range. We thus ignored local uses of palms, as they generally do not contribute to an inter-continental range expansion of species outside their native habitat. The attribution of uses was mainly based on peer-reviewed papers. However, only few studies focused on the use of palms as ornamentals (e.g. Broschat, Elliott, & Hodel, 2014). To fill in these gaps, we relied on grey literature, personal observations and discussions with palm experts.

### 2.3 Functional traits of non-native palms

Height is a core trait in determining naturalization success as it relates to the plants’ ability to compete for light, their fecundity and their dispersal ability (Jelbert, Stott, McDonald, & Hodgson, 2015; van Kleunen, Weber, & Fischer, 2010; Thomson, Moles, Auld, & Kingsford, 2011). We also expected that palms originating from open environments are more likely to be pre-adapted for tolerating or benefitting from human disturbances and associated open- or semi-open anthropogenic environments. To test whether naturalized palms are on average taller than non-naturalized palms and are primed for anthropogenically disturbed habitats, we used a logistic regression. We excluded all climbing palms (i.e. 546 species, of which eight species were naturalized) because of their different functional attributes compared to non-climbing palms. Data on habitat types were derived from Henderson (2002) and were available for 1,069 species (53% of the non-climbing species [n = 2,011] of the palm family). To simplify the habitat types used by Henderson (2002), we created the following habitat classes: (a) moist forest (= lowland moist forest + montane forest), (b) dry forest, and (c) open habitat (= grassland, shrubland and savanna + desert and xeric shrubland). Data on maximum stem height were taken from Kissling et al. (2019) and were available for 1,741 species (87% of all non-climbing palms). Data on both maximum stem height and habitat type were available for 1,052 species (52% of all non-climbing palms). For species without recorded maximum stem height (n = 3) and habitat type (n = 25) in Henderson (2002) or Kissling et al. (2019), we substituted values using carefully selected records from (online) palm literature (Craft, Riffle, & Zona, 2014; Palmpedia, 2019; Palmweb, 2019). Pearson correlation tests were computed to assess how maximum stem height is related to maximum stem diameter, maximum blade length and average fruit length (Kissling et al., 2019).

To test whether palms with a conspicuous fruit colour are more naturalized (e.g. due to increased dispersal by birds), we compared the proportion of species with conspicuous fruit colour and species with cryptic fruit colour in naturalized and non-naturalized palm species using Fisher’s exact test. Data on fruit conspicuousness were available for 1,799 species (Kissling et al., 2019). We filled in missing values on fruits conspicuousness of naturalized species (n = 2) using Palmpedia (2019).

### 2.4 Ecological, social and economic effects of palm invasions

To estimate the ability of palms to generate novel ecosystems, we compiled information on their effects on different taxonomic groups, ecosystem functions and processes from our records (see Appendix 3). We collected information on their effects on aquatic fauna, birds, invertebrates, mammals, other plants and reptiles and ecosystem variables: fire regime, physical vegetation structure, soil moisture, soil nutrients, temperature regime and water regime. We classified these into desirable and undesirable effects based on the evaluation of the authors of the original source. For every reported case, we indicated if information was based on strong (experimental) or on weak (anecdotal or observational) evidence. It was not possible to evaluate the severity of these effects because many of the reported effects were not comparable among the different sources. Therefore, an “undesirable effect on native plants” can indicate an ecosystem-level threat or the suppression of a single native species.

### 2.5 Anthropogenic drivers of non-native palms

To determine the potential role of human-driven spread of non-native palm species, we assigned four human use categories to each naturalized palm species: (a) ornamental, (b) food, (c) rattan (i.e. the flexible stem of climbing palms used for furniture, wickerwork etc.), and (d) other uses (e.g. fuel, building material, handcrafts, erosion protection and medicine). We only included human uses that are likely to have resulted in cultivation of palm species outside their native range. We thus ignored local uses of palms, as they generally do not contribute to an inter-continental range expansion of species outside their native habitat. The attribution of uses was mainly based on peer-reviewed papers. However, only few studies focused on the use of palms as ornamentals (e.g. Broschat, Elliott, & Hodel, 2014). To fill in these gaps, we relied on grey literature, personal observations and discussions with palm experts.
We hypothesized that the level of urbanization in a region will be a major determinant of palm invasions because propagule pressure of non-native palms is usually high in urban settings due to the presence of ornamental palm plantings. To test this hypothesis, we used the human footprint index (HFI) from Venter et al. (2016) as a proxy variable for urbanization. For each TDWG level-3 country, we calculated the human footprint index by taking the 90th percentile of all 1 × 1 km HFI raster cells within the country. We used the 90th percentile instead of the mean, as we expect that the presence of highly modified areas (i.e. a high HFI value) better predicts palm invasions in a country. We selected the HFI of 1993 instead of the more current version from 2009 to take into account that the majority of currently naturalized palms are the result of introductions prior to 2009. We performed a logistic regression to test the effect of the HFI on the proportion of naturalized palms from the total number of palms (i.e. native + naturalized). We then calculated Nagelkerke’s $R^2$ to quantify the predictive power of the HFI for the proportion of naturalized palms.

### 3 | RESULTS

#### 3.1 | Inventory of non-native palms

We found 96 palm species and one hybrid (Phoenix sp.) that were introduced outside their native ranges. Of those 96 casual species (of 52 genera), 86 species (of 48 genera) were naturalized in their new range, with 28 species (of 21 genera) also classified as invasive (Table 1). Of the total number of palm species ($n = 2,557$, Govaerts et al., 2015), 3.4% were naturalized in the new range and 1.1% were invasive.

All five subfamilies included at least one casual species. The subfamilies Arecoidea, Coryphoideae and Nypoideae included significantly more naturalized species compared to the average relative frequency of naturalized species across the remaining subfamilies. The subfamily Coryphoideae with 37 species (7.3%, $p < .001$) contained the most naturalized species, followed by Arecoideae with 34 naturalized species (2.5%, $p = .008$) and Calamoideae with 14 naturalized species (2.2%, $p = .074$). The only species of the monotypic subfamily Nypoideae, Nypa fruticans, was also reported to be invasive (100%, $p = .034$). The subfamily Ceroxylloideae (0%, $p = .404$) contained no naturalized or invasive species, but one casual species.

#### 3.2 | Distribution and biogeography of non-native palms

We found 86 species of naturalized palms that were spread over 185 TDWG level-3 countries, resulting in 567 unique species-country combinations. Non-native palm establishment was concentrated in the tropics and subtropics, where most countries had naturalized palm species (Figure 2a). However, the number of naturalized palms varied between continents. South America (including the Caribbean Islands) was the recipient of the most naturalized species (46 species), followed by tropical Asia (31), the Pacific islands (29), Africa (22), North America (22), temperate Asia (19), Australasia (14) and Europe (6). Of the 86 naturalized palm species, 64 species were naturalized outside their native continent (Table 1). Globally, the most widespread naturalized palms were commercially important species, that is coconut palm ($C. nucifera$; 97 botanical countries), date palm ($P. dactylifera$; 57 bot. countries), African oil palm ($Elaeis guineensis$; 38 bot. countries) and the betel nut palm ($Areca catechu$; 37 bot. countries).

The majority of naturalized species originated from tropical Asia (33 species) and South America (18 species). These two regions are also natural palm diversity “hotspots” (Figure 2b), and for this reason, we expected more naturalized species to come from these continents relative to other regions with fewer native palms. Indeed, we found a strong positive correlation between the number of native species on a continent and the number of naturalized species originating from that continent (Spearman’s $r = .78$, $n = 8$, $p = .023$, Figure 3). Naturalized palm species originating from tropical Asia were the most widespread and were present on every continent except Europe (Figure 4). Most naturalized species in tropical Asian countries originated from other parts of tropical Asia. The continental region receiving the largest number of naturalized palms was South America including the Caribbean, with most species originating from tropical Asia and from areas elsewhere in South America (Figure 4). In contrast to the records of species originating from tropical Asia and South America, the large number of naturalized palm records of African and temperate Asian species (Figure 4) stemmed from only a few widespread species (i.e. Livistona chinensis, $P. dactylifera$ and Trachycarpus fortunei from temperate Asia; $Dypsis lutescens$, $E. guineensis$ and $Phoenix canariensis$ from Africa).

The tropics contained the majority of naturalized palms (80 species) while the extratropics (including the humid subtropics, Mediterranean climate regions and deserts) were acceptors of only 31 species, reflecting the native distribution of the palm family per climate region (Figure 5a). However, the proportion of naturalized palm species was on average higher in the extratropical regions than in the tropics, and variation of this proportion was stronger in extratropical regions.
regions (Figure 5b). Naturalized palms were reported in forests (63 records), wetlands (35), anthropogenic areas (25), coastal areas (21), deserts (13), shrubland (6), grassland and savannas (3) and rocky areas (3). We found 248 and 319 records of naturalized palms on islands and continental landmasses, respectively.

3.3 | Functional traits of non-native palms

Naturalized palm species were significantly taller ($M = 16.94$ m) than non-naturalized species ($M = 8.43$ m) (see Appendix S2: Tables S2.1 and S2.2 for the logistic regression coefficients). The proportion of species becoming naturalized was higher in palms originating in open habitats (20.8%) and in dry forests (20%) compared to palms originating in moist forests (5.4%; Figure 6a). When grouping palms according to their native habitat type, naturalizing species were taller than non-naturalizing species in each habitat (Figure 6b). Stem height was positively correlated with stem diameter (Pearson’s $r = .67$, $n = 1,546$, $p < .001$), blade length (Pearson’s $r = .38$, $n = 1,500$, $p < .001$) and fruit length (Pearson’s $r = .27$, $n = 1,586$, $p < .001$). The proportion of palm species with conspicuous fruit colour was not significantly different between naturalized (39.5%) and non-naturalized palm species (41.1%; $p = .822$).

3.4 | Ecological, social and economic effects of palm invasions

Effects of naturalized palms on receiving ecosystems were reported for 18 of 28 invasive species. For the remaining 10 species, effects were either not mentioned or unclear. In total, we found 73 cases (a case is defined as a unique combination of an invasive palm species, an affected taxonomic group or an ecosystem function, a botanical region [TDWG-level-2] and the desirability of the effect) where an invasive palm was reported to affect a taxonomic group or an ecosystem function (Figure 7). The majority of the 73 cases were reported where
an invasive palm affected a taxonomic group or an ecosystem function in an undesirable way (evaluated as such in the original source). Approximately half of the undesirable cases were based on strong evidence. Reported undesirable effects of palm invasions ranged from effects on a single species to effects across several trophic levels. Competition with the native flora and alteration of the physical structure of the ecosystem were the most frequently reported effects. We found much fewer reports on effects on vertebrates, invertebrates and other ecosystem functions. However, our results illustrate that invasive palms were not only able to affect single species, but also can reduce the richness of an entire taxonomic group such as arthropods or birds and affect ecosystem functioning. In nine cases, naturalized palms were reported to have desirable ecological effects.

Reported social and economic effects of naturalized palms appeared limited as were only reported for six species and included ecosystem service provisioning, down- or upgrading the aesthetic landscape value, cost causation due to naturalized palm removal and posing a risk to human health.

### 3.5 Anthropogenic drivers of non-native palms

The most common human use of naturalized palms was cultivation as ornamental plants (61 species). A smaller number of naturalized palms are or have been cultivated for food (20), rattan (8) or other uses (13). For nine species, the reason for their introduction outside their native range was unclear, as no uses are known. The uses of all the naturalized palms are presented in Appendix S2: Table S2.3.

We found a positive relationship between the proportion of naturalized palm species relative to the total pool of palms.

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**FIGURE 4** Exchange of naturalized palm species between botanical continents (TDWG level-1 from Brummitt, 2001). Single species are counted multiple times in their region of origin if they have naturalized in multiple continents. For species with a native range that extends to more than one botanical continent \((n = 8\) spp.), the region in which the greatest proportion of the species’ distribution range is located was selected as the region of origin.
FEHR ET AL. (native + naturalized species) and the human footprint index (HFI) on a TDWG-level-3 country level (Figure 5c, for logistic regression coefficients, see Table S2.4 in Appendix S2). Nagelkerke’s $R^2$ showed that HFI explains 25% of the proportion of naturalized palms within TDWG level-3 countries. The association between harbouring naturalized palm species and human footprint is further illustrated by the fact that every TDWG level-3 country with a HFI > 20 had at least one naturalized palm species (Figure 5c). These findings strongly support our hypothesis that urbanization positively influences palm invasions, if the environmental conditions of a region match with the requirements of palms.

DISCUSSION

Our extensive literature review revealed that a relatively large proportion of the palm family has naturalized (3.4%, 86 species) or become invasive (1.1%, 28 species) in a wide variety of habitats in the tropics, subtropics and warm temperate regions. We found that naturalized palms were taller than non-naturalized palms and were more likely to originate from open habitats or dry forest than non-naturalized palms. The number of reported effects of naturalized palms was limited, but we found strong evidence that non-native palms can generate novel ecosystems in some contexts. Increased

FIGURE 6 (a) Proportion of naturalized and non-naturalized species for each native habitat type. (b) Kernel density estimate of the stem height distribution of naturalized and non-naturalized species for three native habitat types

FIGURE 5 (a) Number of native palm species in tropical and extratropical TDWG level-3 countries. b) Proportion of naturalized palm species of the total number of palm species (native + naturalized) in tropical and extratropical TDWG level-3 countries. (c) Proportion of naturalized palm species against the total number of palm species (native + naturalized) in TDWG level-3 countries as a function of the human footprint index (HFI) from 1993 from Venter et al. (2016). Low HFI values represent a low level of urbanization; high values represent a high level of urbanization. The black line shows the logistic regression curve (for logistic regression coefficients, see Table S2.4 in Appendix S2). Only TDWG level-3 countries with native palms (black points) were included in the logistic regression analysis.
urbanization and climate change will likely promote novel ecosystems generated by palm invasions in the future.

4.1 Distribution and biogeography of non-native palms

We found that the palm family has a higher proportion of invasive species (1.1%, 28 species) than the global pool of trees and shrubs (0.5%–0.7%, Richardson & Rejmánek, 2011), suggesting that the palm family is a major source of invasive woody plants within their climatic range (Rejmánek, 2014). South America (including the Caribbean Islands), tropical Asia and the Pacific islands were the major receivers of naturalized palms, likely because the climate of these continents matches the climatic requirements of many palm species. The number of naturalized species in Africa was lower, even though large regions of Africa are climatically suitable for palms, possibly reflecting lower propagule pressure of non-native palms due to a lower degree of urbanization. However, historical and cultural factors (e.g. colonization history) are known to strongly influence the distribution of non-native plants and data availability varies considerably between regions (Richardson & Rejmánek, 2011), making it difficult to interpret the geographical distribution of non-native palms. The largest number of naturalized species originated from tropical Asia and South America, reflecting the high number of native species on these continents. Overall, the number of naturalized species originating from a continent was proportional to the continents’ number of native species, suggesting that there are likely no continent-specific characteristics of palms promoting or preventing their naturalization.

The tropics contained a larger number of naturalized palm species (80 species) than the extratropics (31 species) reflecting the native distribution of palms per climate region. However, the proportion of naturalized palm species was higher in the extratropics than in the tropics because the number of native species in the extratropics is on average very low but the horticultural demand for having a variety of different species is similar in both climatic regions. Thus, the number of species that were introduced by humans is not proportional to the number of native species in the tropics and the extratropics. Naturalized palms were reported in a wide variety of habitats including forests, wetlands, anthropogenic habitats, coastal areas and deserts, indicating that many regions of the world could potentially be colonized by non-native palms. Likely more habitats per species would be suitable for naturalized palms than were reported. Islands can be considered major receivers of naturalized palms, with 42.6% of the naturalized palm records coming from islands, especially when taking into account their smaller area compared to mainlands. Islands are known to be more prone to plant invasions than mainlands likely due to their open niche space, increased ecological naiveté of native biota or simply higher numbers of introductions on islands (van Kleunen et al., 2015; Moser et al., 2018).

4.2 Functional traits of non-native palms

To become naturalized, a species has to overcome certain barriers, including survival, reproduction, dispersal and environmental barriers (Blackburn et al., 2011). The capacity of a species to overcome these barriers depends strongly on plant functional traits such as size and fecundity (Jelbert et al., 2015; van Kleunen et al., 2010). Our data show clearly that naturalized palms are on average taller than non-naturalized palms. This finding is consistent with the pattern found for plants in general that invasive plant species are larger than their non-invasive relatives (Jelbert et al., 2015). Height can promote naturalization in various ways. Tall palms were expected to be strong...
competitors for light and strong dispersers. We found that leaf size is positively correlated with height in palms likely resulting in a competitive advantage, with naturalized palms frequently reported to shade out native plants due to their large leaves (Ishii, Ichinose, Ohsugi, & Iwasaki, 2016; Starr, Starr, & Loope, 2003; Williams, 2008). We suspect that the capacity of tall palms to produce more propagules than smaller palms is likely favouring tall palms to naturalize more frequently as it is well known that tall plants usually exhibit a higher fecundity leading to increased propagule pressure, likely resulting in a competitive advantage (Jelbert et al., 2015; van Kleunen et al., 2010). Further, naturalization also depends on the dispersal ability of the species. Greater height increases the dispersal ability of plants as tall plants yield greater fecundity, resulting in an increased dispersal probability (Jelbert et al., 2015) and because greater height promotes greater dispersal distance (Thomson et al., 2011). Small fruit size and conspicuous fruit colour are known to favour the short-distance dispersal by birds (Levey, 1987; Schmidt, Schaefer, & Winkler, 2004). Although many naturalized palm species are dispersed by birds (e.g. Ishii et al., 2016; Mengardo & Pivello, 2012; Meyer et al., 2008; Spennemann, 2019), we did not find evidence that fruits with conspicuous colours are more frequent among naturalized palm species as expected. This may be because other dispersal agents and mechanism override the effect of bird dispersal, for example because some palm fruits are too big for extant birds (Furler & Willing, 2006; NSW Department of Planning, Industry, & Environment, 2019). Fruit size was indeed weakly positively correlated with stem height, indicating that naturalized palms have rather larger fruits than non-naturalized palms.

We found that palm species associated with open habitats and dry forests are more likely to naturalize than palms occurring in moist forest. Palms from these habitats may have traits that favour rapid establishment within a broad range of environmental conditions (e.g. physiological traits promoting fast growth and drought tolerance) and would be pre-adapted to tolerate the high light levels and often relatively dry conditions in urban or other anthropogenic environments. Some palms have been reported to flourish in their native range as a result of human-induced disturbances (Smith, 2015). The expansion of anthropogenically disturbed habitats in the tropics due to ongoing deforestation would be expected to open up niche space for non-native palms adapted to open or disturbed habitats. Two traits, long-lived seeds and remote germination may help palms of the Coryphoideae subfamily to establish in anthropogenic dry habitats, explaining why this subfamily is particularly over-represented among naturalizing palms. The longer-lived seeds in coryphoid palms relative to other subfamilies (Jones, 1995) are likely an adaption to climate seasonality (Casas et al., 2017) and might facilitate establishment in disturbed habitats, creating seedbanks persisting several months. In remote germination, the radicle is pushed down deep before sending up the first leaves (Broschat et al., 2014). As a result, the meristem and the sensitive zone where the roots emerge are located deeper in the soil, an adaption that is likely advantageous in drought-prone settings (Pinheiro, 2001).

The abundance of certain traits in naturalizing palms, such as size, fast growth, ease of propagation and good performance in different environments and climates, is coupled to selection criteria for ornamental palms. We expect this to have a strong influence on naturalization patterns, as it is well known that traits that make plants attractive for horticulture also promote naturalization (van Kleunen et al., 2018), and, as we found here, the majority of naturalized palms were introduced for ornamental purposes. Notably, a complementary explanation for the height effect on naturalization could be that tall palms are more likely to be introduced outside their native range, as they are used in higher numbers in horticulture than short palms due to the popularity of large palms in landscaping (V. Fehr & J.-C. Svenning, personal observation). Overall, we expect an increase in the number of naturalized palm species as new species are being introduced to horticulture on a frequent basis. Knowing which traits are over-represented in naturalized palms will be crucial for predicting the naturalization potential of new species in cultivation.

4.3 Do non-native palm invasions generate novel ecosystems?

We found support for the hypothesis that non-native palms generate novel ecosystems. For example, the coconut palm (C. nucifera) invasion of a Pacific island triggered a trophic cascade (Young, Miller-ter Kuile, McCauley, & Dirzo, 2017). Because birds did not nest on the non-native coconut palms, reduced nutrient input by guano altered plant community composition, which in turn affected herbivorous invertebrate communities. In another example of ecosystem effects, the Chinese windmill palm (T. fortunei) has transformed the understory of deciduous forests in Southern Switzerland into evergreen, palm-dominated thickets, which may classify as a biome shift (Figure 1d, Fehr & Burga, 2016). Further evidence for the ability of palms to generate novel ecosystems includes the modification of habitats by changing the physical habitat structure (e.g. Talley, Nguyen, & Nguyen, 2012; Young, McCauley, Pollock, & Dirzo, 2014), by altering key ecosystem functioning like the water regime (e.g. flow reduction of desert springs [Furler & Willing, 2006] or reduction of plant-available water [Young et al., 2017]), by inducing nutrient depletion (Young, McCauley, Dunbar, & Dirzo, 2010) or by triggering wildfires (DiTomaso & Kyser, 2013; Ortiz-Uribe, Salomón-Torres, & Krueger, 2019). Such habitat modifications can lead to cascading community effects and result in a strong ecosystem change (Buma, 2015).

However, direct measurements of ecosystem effects of non-native palms were scarce, and for more than one third of the 28 invasive palm species, no ecological effects were reported. This is surprising, as invasive species by definition should have negative effects on ecosystems and native species. The lack of data on ecosystem effects may partly stem from logistical challenges in generating such data for long-lived species (Stricker, Hagan, & Flory, 2015). However, we suspect that several naturalizing palm species are incorrectly classified as invasive, for example, because palms are highly noticeable and there is a tendency among biologists to regard non-native biota in general as negative for the native biodiversity (Davis et al., 2011; Gbedomon, Salako, &
Schlaepfer, 2020; Warren, King, Tarsa, Haas, & Henderson, 2017). This biased view emerged as invasion biologists traditionally focus on non-native species perceived to pose a threat to ecosystems or society to inform policy, in order to guide potential management actions (Davis, 2009). The focus of invasion biologists on undesirable effects might also explain the paucity of reported desirable ecosystem effects of naturalized palms. However, we found limited evidence of non-native palms benefiting the invaded ecosystem by creating habitats and providing food for the native biota and contributing to a higher biodiversity. For example, in Brazil’s Atlantic rain forest, the long-term survival of endangered primates depends on the non-native oil palm (E. guineensis) (Canale, Kierulff, & Chivers, 2013; de Jesus Rodrigues Malta & Pontes, 2013). Overall, we expect that desirable ecosystem effects of naturalized palms are more common, especially cases where naturalized palms benefit native frugivores, as many palms are part of mutualistic relationships with frugivores in their native range (Galetti et al., 2001; Henderson, 2002; Sica et al., 2014).

Besides the reported ecological effects of naturalized palms, there is evidence of palms acting as ecosystem engineers within their native range through various ways. For example, palm leaves can reduce the light availability (Farris-Lopez et al., 2004), senescent falling palm leaves can cause disturbances in the forest understory (Peters, Pauw, Silman, & Terboorgh, 2004) and the slow decomposition of palm leaves can result in thick litter layers hindering the establishment of small-seeded (tree-) species (Farris-Lopez et al., 2004). Palms are widely hyper-dominant members of their ecosystems, for example in the Amazonian rain forest, where 227 tree species (1.4%) account for 50% of all stems, with 15 of these species being palms, nearly five times as many hyper-dominant species for the family than expected by chance (Steege et al., 2013). It is likely that naturalized palms have the ability to affect the invaded ecosystem through similar pathways.

In summary, considering the ecological key role of palms within their native ecosystem and the few, but strong, examples of non-native palms as ecosystem engineers, we expect that ecosystem effects of palm invasions are far more diverse and that many mechanisms through which they can affect native biota or ecosystem functioning are still unknown (Svenning, 2018).

4.4 | Social and economic effects of palm invasions

We found six studies that provided information on the social and economic effects of naturalized palms, which is surprisingly scarce. Palms are valued for aesthetic reasons, as evidenced by a lively horticultural trade in palms (Broschat et al., 2014), but sometimes also by the appreciation of wild naturalized palms (Lindemann-Matthies, 2016). In contrast, naturalized palms can also be perceived as an undesirable, foreign landscape element (Williams, 2008). In one case, naturalized palms were suggested to provide ecosystem services including food, fibres and wood to local communities (de Grenade, 2013). One palm species was reported as posing a risk to human health (albeit likely a small one): The barbs on the leaf bases of P. canariensis can cause injuries that often have a protracted course and multiple surgical procedures may be required to remove all of the foreign material (Adams, Timms, & Hanlon, 2000). Further, the pollen of the same species has been reported to cause asthma and rhinoconjunctivitis (Blanco et al., 1995). The only substantial economic costs of non-native palms that we found reported were costs for controlling or eradicating non-native palms.

4.5 | Future of palm-generated novel ecosystems

We expect that increased urbanization (United Nations, Department of Economic and Social Affairs, Population Division, 2017) and associated horticultural trade will promote future palm invasions and thus the emergence of novel ecosystems, especially in regions without (many) native palms. On a country-level scale, we found strong evidence that most palm invasions occur within or close to urbanized regions, that is every country with native palms and areas with a high human footprint index (HFI > 20) had at least one naturalized palm species (Figure 5c). This is most likely due to the high density of gardens and parks that host a large number of cultivated, ornamental palms in urbanized areas and therefore propagule pressure is high. This is consistent with the results of van Kleunen et al. (2018), who showed that between 75% and 93% of the global naturalized alien flora is grown in domestic and botanical gardens, which are typically located in urbanized regions. Given the long generation time of palms, long lags between the first introduction and subsequent spread are expected. The four most widespread naturalized palm species (coconut palm, date palm, African oil palm and betel nut palm) are all agricultural crops that have been cultivated for centuries (Harries, 1978; Mathew et al., 2015) compared to many ornamental palm species that have been disseminated more recently, again illustrating the importance of time but also propagule pressure in the process of naturalization of palms. Overall, we expect a strong increase in the reports of palm invasions in the near future, as many regions of the world may still be within this lag phase and propagule pressure will likely increase due to increased urbanization.

From a biogeographic perspective, we expect that palm invasions will increase around the globe in tropical, subtropical and warm temperate regions. Areas with exceptionally high diversity of naturalized palms might become more frequent in the tropics in the future (Svenning, 2002). In the subtropics and temperate regions, the naturalized palm richness is unlikely to increase strongly, as the pool of species adapted to cooler, more seasonal climate is relatively small.

Some subtropical and warm temperate climates are currently able to support palms, but have no native palms, for example, due to past extinctions during ice ages or post-glacial dispersal limitations (Kissling et al., 2012), as is the case for the Southern European Alps where the Chinese windmill palm (T. fortunei) is spreading. This unoccupied niche space for palms might further facilitate palm invasions. Open niches for non-native palms might also be available in Africa where palm richness is low, potentially due to climate change during the Neogene and Quaternary (Blach-Overgaard, Kissling,
Ongoing global warming will promote the spread of non-native palm species in the subtropics, warm temperate regions of the Northern Hemisphere (>30°N) and higher elevations (Reichgelt et al., 2018). The expansion of the Chinese windmill palm (T. fortunei) in Southern Switzerland (Figure 1d) is an example where global warming expanded palm niche space, increased urbanization increased propagule pressure and less intensive forest management allowed establishment (Conedera, Wohlgemuth, Tanadini, & Pezzatti, 2018; Fehr & Burga, 2016; Walther et al., 2007).

Factors that have been hypothesized to regulate many plant invasions are diseases and pathogens. Invasive species are suggested to become less invasive over time as they accumulate pests and pathogens in their new locations (Flory & D’Antonio, 2015). We are aware of one example in Southern California, where a population of naturalized P. canariensis was infested and decimated by (non-native) palm weevils (Milosavljević et al., 2019; V.Fehr, personal observation, Figure 1f). Considering the large number of diseases and pests that can affect palms (Gitau, Gurr, Dewhurst, Fletcher, & Mitchell, 2009), cases where naturalized palms are infested by diseases and pests are likely to increase in the future and eventually benefit native plants. Hence, such ecological dynamics may increase the biodiversity of novel ecosystems in the long term (Svenning, 2018), similar to what has been achieved through the introduction of biological control agents in cases such as Opuntia spp. in Australia (Novoa et al., 2019).

4.6 Management of non-native palms

Where non-native palms are perceived as negative, various management approaches have been implemented. However, information on control techniques for invasive palms is scarce (Dyer et al., 2019; Enloe, Langeland, Ferrell, Sellers, & MacDonald, 2018) and only scattered cases of local attempts to control invasive palms exist. In Southern California, Washingtonia robusta is removed at significant costs (removal with helicopter; Anderson & Castellanos, 2014; DiTomaso & Kyser, 2013), despite no strong evidence for negative biodiversity effects or additional economic costs (National Park Service & U.S. Department of the Interior, 2015). The economic investment into eradicating W. robusta is even more surprising as it is native only 350 km further south, and the closely related Washingtonia filifera occurs only 80 km to the east (Minnich, Franco-Vizcaíno, & Salazar-Ceseña, 2011). In Indonesia, the invasive arenga palm (Arenia obtusifolia) is controlled by both cutting the palm down and using herbicide in an attempt to restore the habitat for the Javan rhino (Rhinoceros sondaicus) (Konstant, 2014). In southern Switzerland, the Chinese windmill palm (T. fortunei) is cut down regularly in certain areas as it is suspected to negatively affect the native flora and the protective forest to prevent erosion (Info Flora, 2014). We suggest that management should be based on careful assessments of the extent to which the non-native species cause major net negative ecological or social effects and if control is likely to be effective in the long-term, notably to not waste scarce resources for environmental management (Svenning, 2018). Given the over-representation of open habitat-associated palms among the naturalizing species, reducing human disturbance may be in many cases an effective long-term strategy. In some cases, expansions could also reflect defaunation, notably losses of large herbivores (Ripple et al., 2015) that could otherwise limit palm populations (Mandle & Ticktin, 2012; Watson, Cameron, & Ilo, 2020), and here trophic rewilding (Svenning et al., 2016) could be a long-term solution (cf. Guyton et al., 2020).

4.7 Knowledge gaps and the way forward

Our review revealed important knowledge gaps. First, data on non-native palms were geographically and taxonomically biased, suggesting potential under-reporting of non-native palms. Second, studies on ecological, social and economic effects of non-native palms were scarce and available studies focused on palm effects on specific taxa rather than on ecosystem-level effects. Based on the ecological importance of palms within their native range, we anticipated that desirable ecosystem effects, that is where non-native palms benefit the native biota and contribute to a higher biodiversity, could be common. However, we did not find many reported desirable effects, which could reflect that such outcomes of novel ecosystem formation may simply be underexplored due to a bias in non-native species research towards focusing on undesirable effects. Hence, there is a strong need for more field-based studies aiming to uncover if and how non-native palms modify habitats and affect key ecosystem functioning and biodiversity in different climate and land use settings. Here, it will be important to address the temporal dynamics and spatial scaling of the ecological effects, as effects that are locally negative for other species could be transient or lead to higher biodiversity at larger scales.

Novel ecosystems are on the rise, in large part driven by introductions of non-native species, but also promoted by ongoing global warming, increased atmospheric carbon dioxide (CO₂) and land use change (Feng et al., 2014; Hobb et al., 2009; Perring & Ellis, 2013). The new species assemblages and ecosystem functions of these novel ecosystems are likely to alter ecosystem services (Collier, 2014; Evers et al., 2018; Hobb et al., 2009; Millenium Ecosystem Assessment, 2005) may threaten native species (Bellard, Genovesi, & Jeschke, 2016; Pyšek et al., 2012) but could also generate new habitats for native species (Padowani, Salisbury, Bostock, Roy, & Thomas, 2020). An improved understanding of the functioning of novel ecosystems to these increasingly widespread natural environments should clearly be an important research priority (e.g. Svenning, 2018). Further, to restore these novel ecosystems to a historical baseline would in many cases be an unfeasible task (Hobbs et al., 2009), for example due to climate change (Ordonez & Svenning, 2016). Hence, adapting conservation and restoration practices to promote the biodiversity value of these novel ecosystems may be the most feasible approach in many cases (Svenning, 2018).
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DATA AVAILABILITY STATEMENT
The literature-based dataset on non-native palms used in this study can be found in Appendix S3. All other data used are available publicly from the sources given in the manuscript.

ORCID
Vincent Fehr https://orcid.org/0000-0002-9609-6873
Robert Buitenwerf https://orcid.org/0000-0003-3356-2301
Jens-Christian Svenning https://orcid.org/0000-0002-3415-0862

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BIOSKETCH

Vincent Fehr is a PhD student at the Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) at Aarhus University in Denmark. Beside his enthusiasm for the diversity and ecology of palms, he is interested in how non-native species are driving the emergence of novel ecosystems in a human-dominated world.

Robert Buitenwerf is a broadly interested ecologist, with a research focus on the impacts of global change on ecosystem functioning and biodiversity.

Jens-Christian Svenning is an ecologist and biogeographer with strong interests in palms and novel ecosystems, among many other aspects of the biosphere.

Robert Buitenwerf is a broadly interested ecologist, with a research focus on the impacts of global change on ecosystem functioning and biodiversity.

Jens-Christian Svenning is an ecologist and biogeographer with strong interests in palms and novel ecosystems, among many other aspects of the biosphere.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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