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Are Introduced Alien Species More Predisposed to Invasion in Recipient Environments If They Provide a Wider Range of Services to Humans?

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Abstract: The drivers of invasion success of alien species remain, to some extent, a matter of debate. Here, we suggest that the services (the benefits humans obtain from a species) provided by alien plants could predict their invasion status, such that alien species providing more services would be more likely to be invasive than not. The rationale for this expectation is that alien species providing multiple services stand a better chance of being introduced in various numbers and multiple times outside their native range (propagule pressure theory). We investigated this hypothesis on alien woody species in South Africa. First, we defined 12 services provided by all the 210 known naturalized alien woody plants in South Africa. Then, we tested for a phylogenetic signal in these services using a DNA barcode-based phylogeny. Finally, we tested for potential links between the services and invasion status by fitting GLM models with appropriate error families. We found a phylogenetic signal in most services, suggesting that closely related species tend to provide similar services. Counter-intuitively, we consistently found that alien non-invasive species tend to provide more services, or even unique services, in comparison to alien invasive species. Although alternative scenarios are plausible to explain this unexpected finding, we speculate that harvesting alien plants for human benefits may limit their invasion ability. This warrants further investigation.

Keywords: alien woody plants; horizon scanning; DNA barcode; predicting invasion success; environmental policy; propagule pressure

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1. Introduction

Over the past four centuries, some alien woody plants were introduced intentionally into South Africa to meet the growing human demands for various goods and services (charcoal, timber production, ornaments, dune stabilization, medicine, etc.; [1–5]). The selection and use of plants by humans have been shown to be non-random, but this non-randomness has been widely demonstrated for native plants (e.g., [6–10]). However, it is increasingly shown that alien species intentionally selected and introduced into new environments for human use (e.g., medicine) are also non-random selections from local floras (e.g., [11]; see [12] for further references). While some of the introduced alien plants fail to establish a viable population in their recipient environments, many others have naturalized, and some of the naturalized species have become invasive [13]. Alien invasive plants are naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from their points of introduction, and thus have the potential to spread over a considerable area [14]. Although some of the invasive species pose a severe ecological threat to their recipient systems [15–17], the levels of threat are not equal; some species are strong invaders and pose high ecological and economic threats, while others are weak invaders [12,18,19].

In the face of these threats, a massive research effort has focused on understanding the predisposition of alien plants to invasion success in a foreign environment [5,20–23]. The findings reported in these studies are, to some extent, contradictory. This is because the drivers of invasion of some taxa in an environment do not explain the invasion of other taxa or the same taxa in different habitats [23–27], thus revealing the environment-dependent nature of invasion and the need for case-specific management solutions. Here, we propose that the services that alien species provide, and which motivate their introduction into a new environment, should better predict the invasion status of these species (naturalized vs. invasive) in their recipient ranges. There are two reasons underlying this expectation.

Firstly, since functions (ecological or physiological) generate services, and functional traits correlate with the invasion status of species in South Africa [21], services should also predict the invasion status of alien species. Several studies have tested, albeit indirectly, this potential link between services and invasion by focusing only on the link between functional traits and invasion [21,28]. Secondly (and this is the most critical basis for our expectation), an alien species that provides a diverse array of services is more likely to be introduced independently multiple times and in various numbers into new environments than an alien species that provides only one or a few services [9,29]. However, we also acknowledge that multiple independent introductions in large numbers may not necessarily be due to a diverse array of services, but rather could be driven, for some species, by a single service of high use-value for local communities. These alternative scenarios match the prediction of the propagule pressure theory [30], also termed “introduction effort” [31], which is the number of individuals introduced into a new environment and how often the introduction events occur [30,32].

In the present study, our aim is to link the services of naturalized woody plants to their invasiveness status in South Africa. Specifically, we ask the following questions: Are plant species selected and used by humans a random selection with regard to the services they provide? Does the total number of services (used as a proxy for propagule pressure) of alien species predict their invasion status? We explored these questions using the alien woody flora recorded as intentionally introduced to South Africa [21].

2. Materials and Methods

2.1. Native and Alien Woody Flora of South Africa

The present study focuses on South Africa but literature across Southern Africa, which includes Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, and Zimbabwe, was also consulted for the purpose of a comprehensive documentation of information. For example, native and alien plants to South Africa and their uses have been reported in various sources across Southern Africa. The Southern Africa’s woody flora comprises approximately 2200 native species [21,33,34]. Of this native flora, 1190 species are included in the present study. This list includes 210 intentionally introduced alien species now documented as naturalized in South Africa. In total, 1400 species are included in our study, of which 1190 species are native, and 210 species are naturalized alien species.

2.2. Categorization of Alien Species

First, naturalized alien species were categorized into invasive and non-invasive following Bezeng et al. [20,21] as their study provides the most recent and comprehensive record and categorization of alien woody species in South Africa. In South Africa, the NEMBA list of alien plants is the official list of species considered as invasive and non-invasive (naturalized) in South Africa. The list is generated, through a lengthy process, by the government of South Africa through the Department of Environment, Forestry and Fisheries (DEFF). The process through which the list of alien species is generated can be summarized as follows: An Alien Species Risk Analysis Review Panel (ASRARP) is established and tasked to conduct the invasion risk analysis of alien species in the country. This panel, formed of various experts in the field of biological invasion, uses the framework of [35] for alien invasion risk analysis. This framework is grounded on the following five risk assessment criteria: background (of the alien species), likelihood (of the species being introduced to the country, naturalized and invasive), consequences (environmental and socio-economic), management (of the alien species) and reporting (summary of the risk assessment and risk recommendation). Before ASRARP makes a final decision on the risk status of a given species, the opinions of at least two experts, generally one local and one international, are consulted. The list of South Africa's alien species used in the present study emanated from this process and additional expert consultations [21].

2.3. Record of Services of Woody Flora (Native and Alien) in South Africa

We documented through an intensive literature search the different services these species (native and alien) provide to humans in South Africa. First, we used the Web of Science (WoS) to retrieve existing scientific ethnobotanical studies in the region. Second, we searched for each species by using combinations of keywords such as "scientific name of species", "Southern Africa", "Botswana", "Mozambique", "Namibia", "South Africa", "Swaziland", "Lesotho", "Zimbabwe", "uses", "usages", and "benefit". We also made use of Google and Google Scholar for scientific and grey literature using similar keywords to retrieve online resources such as regional and country-specific journals, proceedings, technical reports, herbarium and commercial websites informing on the uses of woody plants in our dataset. The Southern African Plant Invaders Atlas (http://www.agis.agric.za/wip/, accessed on 1 March 2017) was also consulted. In addition, we consulted key books on the regional flora such as *Trees of Southern Africa*, *Field Guide to Trees of Southern Africa*, and *Guide to Trees Introduced into Southern Africa* [33,36,37]. Additionally, plant uses in South Africa were retrieved from the *Prelude Database for Medicinal Plants in Africa* (http://www.africamuseum.be/collections/external/prelude; accessed on 10 February 2017), a unique database where medicinal plants and uses across the entire African continent since 1847 are documented and frequently updated. Finally, services of plants were updated by consulting the global dataset of plant uses of plants documented on the WEP database (National Plant Germplasm System GRIN-GLOBAL; https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearcheco.aspx, accessed on May 2021) and Diazgranados et al. [38]. All the different services (uses) retrieved from this wide and intensive literature search were grouped into 12 distinct categories of services (Table S1).

2.4. Phylogeny of the Southern Africa's Woody Flora

The phylogenetic tree used in this study is the most comprehensive DNA-based phylogeny ever assembled for both native and alien woody flora of Southern Africa in one of our recent papers [21]. In summary, this phylogeny was based on a matrix of the two DNA barcode regions *matK* (942 bp) and *rbcLa* (552 bp) generated in two recent studies (ref. [34] for native flora and ref. [21] for alien flora; sequences available since 2015 on www.boldsystems.org;). Although four markers are proposed as plant barcodes, the two regions *matK* and *rbcLa* have been shown to be efficient in several ecological studies, e.g., [21,34]. The phylogeny includes 1400 native and alien taxa representing 117 families and 562 genera. The reconstruction of the phylogeny follows the classical widely established Bayesian method (see details in [21]). Importantly, four independent runs of MCMC were performed, each for 100 million generations, sampling every 1000 generations. The MCMC log files for convergence using the effective sample size (ESS) statistics in Tracer v.1.5 [39] were evaluated, and all ESS values >100. Finally, the resulting tree files from the four runs were combined in LogCombiner v.1.7.5 [39], down sampling 1 in 20,000 trees, and discarding the first 25% trees as burn-in. The maximum clade consensus (MCC) phylogeny was generated with TreeAnnotator v.1.7.5 [39]. This MCC phylogeny is used for all phylogenetic analyses in the present study.

2.5. Data Analysis

- Test of phylogenetic signal in services provided by alien woody species

Prior to the analysis, the phylogeny was pruned off the native species. To test whether species used by humans are randomly selected with respect to the services they provide, a matrix of species and service categories was first created for each plant invasion status (alien non-invasive and alien invasive). In this matrix, the 12 categories of services (Table S1) were transformed into binary data, as follows: 1 (if a species provides a given service), and 0 (if not). Then, using the phylogenetic tree of Southern Africa's flora pruned to have only alien species to South Africa, we applied the D statistic [40] on this binary data to assess whether species used for a particular service are phylogenetically more closely related than expected at random (test of phylogenetic signal). D statistic has the advantage of measuring both a phylogenetic signal and its strength. The strength of the signal was interpreted as follows: $D < 0$ means strong signal; $D = 0$ means presence of signal under Brownian Motion model; D between 0 and 0.5 means moderate signal; D between 0.5 and 1 means weak signal; $D = 1$ means no signal; $D > 1$ means over-dispersion. The statistical significance of the observed D value was tested by comparing the observed D value to 0 (expected value for a phylogenetically conserved pattern under a Brownian Motion model) and 1 (random expectation). The p values for significance tests were reported as P_{BM} (giving the result of testing whether D was significantly different from 0) and P_{rand} (giving the result of testing whether D was significantly different from 1). In the scenario of a D value falling between 0 and 1 but being statistically different from 1, this implies that the observed D value shows moderate/weak signal but is non-random. If D value is between 0 and 1 but not statistically different from 1, then the observed value is moderate/weak and not different from random.

- Tests of link between services provided by alien plants and their invasion status

To test if services can be linked to invasion status, we tested whether the diversity of services provided by alien plants (i.e., total number of services for each alien species) correlates with their invasion status. This analysis was carried out by fitting two types of GLM models on "number of services" (response variable) versus "invasion status" (predictor). On one hand, we fitted a Poisson GLM (given the response variable is count data and on the other, we fitted a phyloGLM as implemented in the R library *Phylolm* [41]. The difference between both tests is that the latter corrects for phylogenetic nonindependence of species, allowing us to assess the potential influence of phylogeny on the result reported in the former test.

Finally, we tested whether there was a direct potential link between each service and the invasion status. The test was run by fitting a binomial GLM since invasion status (response variable) was measured as a binary variable (invasive vs. non-invasive following NEMBA).

3. Results

Firstly, we found evidence for non-random selection of alien species intentionally introduced to South Africa for the services they provide, although most phylogenetic signals were weak to moderate (Table 1). Specifically, we found support for phylogenetically non-random selection of alien species for 75% of services, i.e., 9 services out of 12.

Secondly, we found a correlation between the number of services and invasion status, such that alien non-invasive species tend to have more services than the invasive species (Figure 1; $\beta = -0.28 \pm 0.09$, $p = 0.003$). When we corrected for the phylogeny, our finding still confirms this pattern ($\beta = -0.38 \pm 0.39$, $p = 0.04$).

Table 1. Results of phylogenetic signal test in the services provided by alien plant species using D statistic. The *p* values for tests of significance were reported as P_{BM} (giving the result of testing whether D was significantly different from 0) and Prand (giving the result of testing whether D was significantly different from 1). A weak-to-moderate significant signal was detected in 9 out of 12 services.

Categories of Services of Woody Species (*n* = 1400)	Counts of States	Estimated D	P_{rand}	P_{BM}	Interpretation
Service 1 Human Food (edible fruits, edible starchy roots, edible nuts, beverages)	0 = 169 1 = 39	0.5145573	<0.001	0.002	Weak signal, but non-random
Service 2 Livestock (Fodder and forage)	0 = 193 1 = 15	0.6435349	0.006	0.01	Weak signal, but non-random
Service 3 Medicinal (Human and animal treatment-medicinal oils, purgatives, skin infections, ringworms and other ailments)	0 = 178 1 = 30	0.6578688	<0.001	<0.001	Weak signal, but non-random
Service 4 Body and house care (perfume, essential oils for hair and skin, face and Skin Mask, Exfoliants and Wash, Polishes, Soaps, detergents, Shampoos)	0 = 196 1 = 12	0.5787294	0.001	0.047	Weak signal, but non-random
Service 5 Coloring Substances (Tanbarks, Dyes and Inks)	0 = 200 1 = 8	1.022189	0.508	<0.001	No signal, random
Service 6 Insect Attractants Repellents (Butterflies, Bees, Ants, Bugs, Mosquitoes and Worms)	0 = 172 1 = 36	0.5870513	<0.001	0.001	Weak signal, but non-random
Service 7 Hunting Fishing (Fish and Arrow Poison)	0 = 207 1 = 1	−2.105872	0.093	0.766	NA (there is only one state for 1)
Service 8 Soil Management (Soil Stabilization, Sand-binding, Dune Stabilization and Dune Reclamation)	0 = 191 1 = 17	0.2478724	<0.001	0.0217	Moderate signal, but non-random
Service 9 Fuels Biofuels (Firewood, Woodchips, Biofuel and Charcoal)	0 = 179 1 = 29	0.7891897	0.02	<0.001	Weak signal, but non-random
Service 10 Construction and Manufacturing Materials (Poles, Fence Posts, Timber, Shelter, Fibers, Ropes, Fish Nets, Carving, Windbreak, Hedging and Screening)	0 = 97 1 = 111	0.6462119	<0.001	<0.001	Weak signal, but non-random
Service 11 Ornamental (Indoor and Outdoor Ornament, Street Trees and Shade)	0 = 32 1 = 176	0.4971587	<0.001	0.001	Moderate signal, but non-random
Service 12 Cultural Religious (Traditional, Magical, Religious/Spiritual Values)	0 = 204 1 = 4	0.9566721	0.352	0.046	No signal

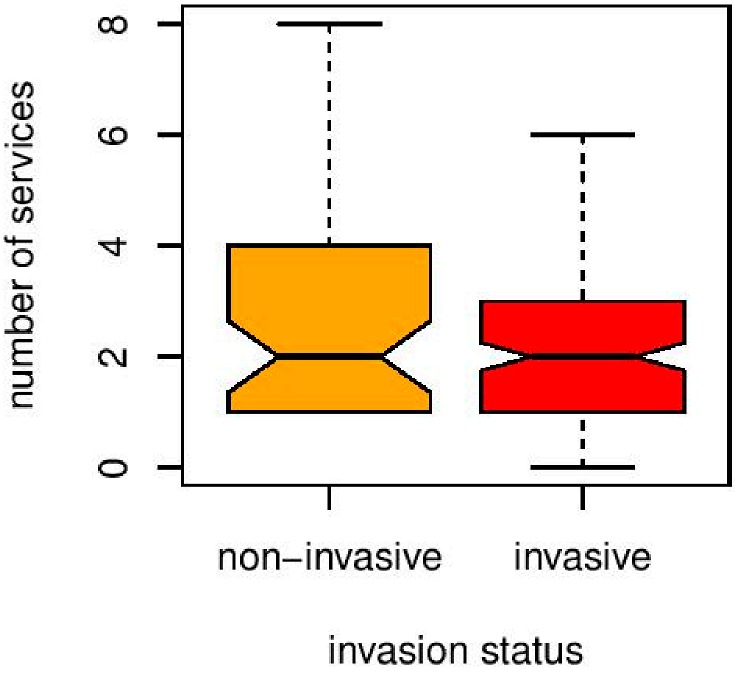
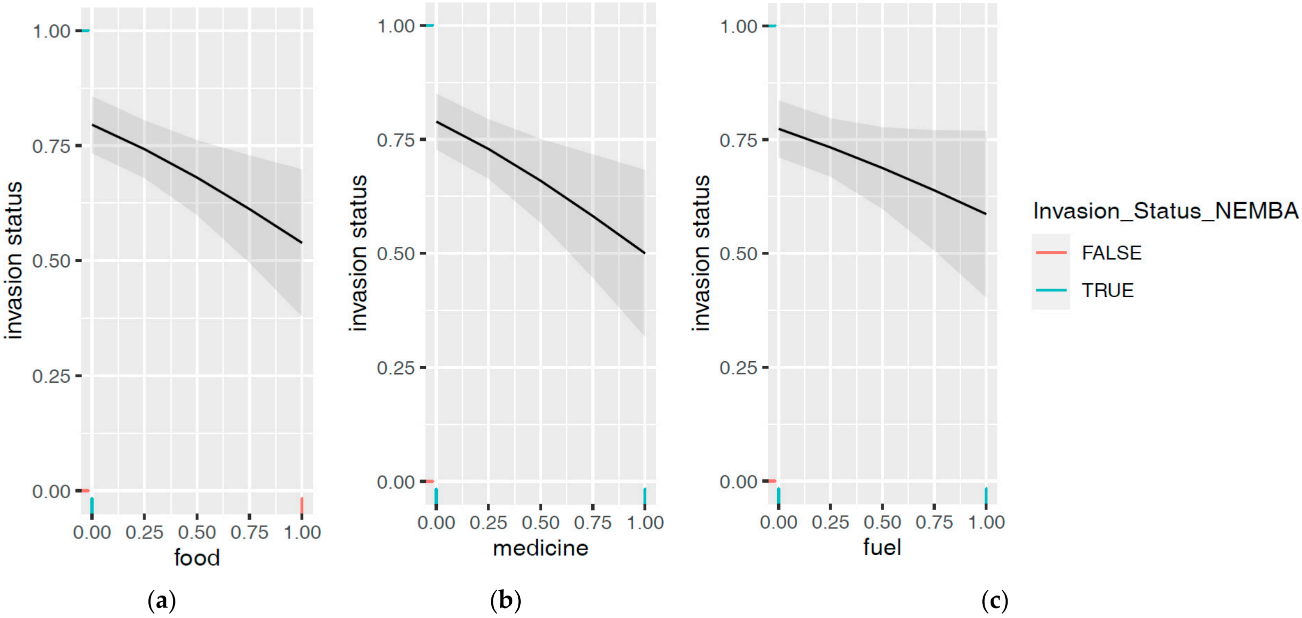


Figure 1. Relationships between the number of known services provided by alien species and their invasion status.

Finally, when we tested for the link between each of the 12 services and invasion status, we found that, among the 12 services recorded, only three services (food, medicine, and fuel) show significant correlations with invasion status, but this correlation is negative (Figure 2), as follows: food (β = −1.20 ± 0.37, p = 0.001); medicine (β = −1.31 ± 0.41, p = 0.00124); fuel (β = −0.88 ± 0.42, p = 0.03), implying that these services tend to be provided by non-invasive species.



(**a**) (**b**) (**c**)

Figure 2. Relationships between invasion status and each service category. Only the three services that show significant correlation with invasion status are presented, which are as follows: (**a**) food, (**b**) medicine, (**c**) fuel. Invasion status is coded as follows: 0 (non-invasive) and 1 (invasive). The following are for service 'food': 0 (a species is not used as food) and 1 (the species is used as food). Same for medicine and fuel.

4. Discussion

The phylogeny used in the present study, and reconstructed using two markers of DNA barcodes for plants (rbcLa + matK), has been used in several studies to test various ecological hypotheses [21,34]. Using this DNA barcode phylogeny, our study indicates that there is a phylogenetic signal in the services provided by intentionally introduced alien woody plant species used by humans in South Africa. From a phylogenetic perspective, this is an indication of non-random selection of alien plants. However, taxonomic non-random plant selection was initially suggested almost four decades ago to explain human–plant interactions, particularly for native plants used in traditional medicine [6,41,42]. This was later supported in several other studies, but mostly for native plants used in traditional medicine [8,43–45]. Nonetheless, only a few studies have tested whether this taxonomic signal translates into a phylogenetic signal (e.g., [46,47]). In addition, the question of whether alien species introduced into a new environment follow the general pattern of non-random selection is not yet widely explored (but see [48]). The present study contributes to filling such a gap, showing that alien woody species in South Africa are not randomly selected; phylogenetically closely related alien species, intentionally introduced into the region, tend to provide similar services. Can services then be used to predict the invasion status of these alien species?

Contradicting evidence has been provided in several studies that investigated the correlates of invasion success, suggesting the context specificity of invasions. Because species' functional roles (ecology and physiology) in ecosystems are linked to the services that they provide to humans [49], and functional traits drive invasion success [21,28], our expectation is that the services should also correlate with invasion success [29]. In addition, if an alien species provides a higher number of services, the chances are greater for that species not only to be sought after, but also to be introduced in a high number and independently multiple times into new environments. This is predicted in the propagule pressure theory [30–32]. Indeed, the propagule pressure theory has been demonstrated in several studies for different taxa in various geographic regions [30,50,51]. In the present study, we found a significant correlation between the number of services (which may indicate propagule pressure) and invasion status, but, contrary to expectation, it is alien non-invasive species that provide more services than invasive species. This pattern is maintained whether we corrected for phylogeny or not, and supports the finding reported in a recent study that naturalized plants provide more services than plants that are not naturalized [29].

This counter-intuitive finding may be expected if our dataset comprises a large proportion of unintentionally introduced alien species (this is not the case). It is also possible that an alien species can be introduced both intentionally and unintentionally into an area. This possibility may a priori complicate the detection of a strong correlation between services and invasion status. However, in our case, we focused only on alien species recorded as intentionally introduced and for which the services these species provide to humans are relatively well documented. As such, even if some of these intentionally introduced species are also transported through unintentional introduction pathways, this would simply increase the propagule pressure of the species and would support our expectations of strong relationships between the number of services (used as proxy for propagule pressure) and invasion status. Furthermore, even if we assume that some of the alien species in our list (Table S1) are unintentionally introduced, the fact that these species are now recorded as providing some services to humans implies that humans may further cultivate these species (for the services they provide), thus contributing to the spread of the species. In such a scenario, our hypothesis of a strong relationship between services and invasion would still hold, since we are not analyzing species' traits, but the services they provide. This scenario would actually make it meaningless to distinguish between intentional and unintentional introduction, since what matters in our approach is the services that species provide (not their ecological traits). In addition, the counter-intuitive finding reported here could possibly be because alien non-invasive species might not yet have enough residence time in their new environment to become invasive. It could also be because the variable "number of services" is not a strong proxy for propagule pressure, as an alien species with a high number of services may not necessarily be introduced multiple times in an area; a species S1 with only one known service may be introduced several times and more often than a species S2 with multiple services if those multiple services are less valuable to communities (i.e., lower use value) than the single service of S1. A further possibility is that the lack of positive relationships between the number of services and invasion status could be because of the differences in species' performances (ecological, physiological) in different environments/habitats in the same country; alien species providing a similar number of services for different human communities may perform differently in different environments or ecosystems. Another possibility is that the NEMBA alien categorization itself may be a source of concern, due to human misjudgment or bias, or decisions that are not ecologically informed, since the NEMBA list was generally criticized for not being science-based (it was allegedly influenced by politics). Potential bias in the list may perhaps lead to the unexpected results that we found. However, the fact that our findings mirror what was recently reported at the global scale (see ref. [29]) means that the NEMBA list may not be a profoundly biased representation of alien invasion status in South Africa. These various scenarios that potentially explain our findings call for future studies that link species' use values to their alien invasion status.

When we tested the link between invasion status and each of the service categories, only three services (food, medicine, and fuel) correlated significantly, in a negative direction, with invasion status, suggesting that these services tend to be provided by non-invasive species. All these findings confirm that alien non-invasive species tend to provide more services to humans than alien invasive species, corroborating a recent finding that naturalized species provide more services to humans at the global scale [29]. These findings prompt the following key question: by harvesting alien plants for human use, do humans limit their ability to invade? Although we did not test this hypothesis, we strongly suspect this possibility, given that alien plants providing more services, or even specific services (food, medicine), tend to be non-invasive (naturalized) or are geographically constrained.

Overall, by aiming to link services to invasion, this study pointed to potential roles played by human choices of specific products (e.g., plants for medicine) in driving species invasion. Our tests reveal unexpected evidence that alien non-invasive species provide more or unique services to humans in comparison to alien invasive species, supporting the recent similar finding reported at the global scale (see ref. [29]). Although a number of scenarios are plausible to explain our finding, we suggest that human utilization/harvest of alien species may constrain their ability to spread and become invasive. This requires further investigations. Other studies in other geographies have shown the following similar finding with that reported in the present study: the uses of alien plants by humans determine their outcome along the introduction–naturalization–invasion continuum [52–54]. Our study also provides additional evidence that DNA barcodes, initially thought of as a taxonomic tool (e.g., [55]), can be used beyond taxonomy and for ecological investigations (see reviews in ref. [56]).

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d13110553/s1: Table S1. The raw data collected for the present study. The definitions of Services 1–12 are in Table 1.

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