

## Viewpoint

# A proposed protocol for identifying native-alien populations

Takalani Nelufule<sup>1,2</sup>, Mark P. Robertson<sup>1</sup>, John R.U. Wilson<sup>2,3</sup> and Katelyn T. Faulkner<sup>1,2</sup>

<sup>1</sup>Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

<sup>2</sup>South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa

<sup>3</sup>Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

ORCIDs: [0000-0001-9823-075X](https://orcid.org/0000-0001-9823-075X) (TN), [0000-0003-3225-6302](https://orcid.org/0000-0003-3225-6302) (MR), [0000-0003-0174-3239](https://orcid.org/0000-0003-0174-3239) (JW), [0000-0002-3955-353X](https://orcid.org/0000-0002-3955-353X) (KF)

Corresponding author: Takalani Nelufule ([takalani.nelu@gmail.com](mailto:takalani.nelu@gmail.com))

**Citation:** Nelufule T, Robertson MP, Wilson JRU, Faulkner KT (2023) A proposed protocol for identifying native-alien populations. *Management of Biological Invasions* 14(4): 579–594, <https://doi.org/10.3391/mbi.2023.14.4.01>

**Received:** 17 November 2022

**Accepted:** 8 June 2023

**Published:** 2 August 2023

**Handling editor:** Vanessa Lozano

**Thematic editor:** Ana Novoa

**Copyright:** © Nelufule et al.

This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

## OPEN ACCESS

### Abstract

It is important for regulators and managers to effectively distinguish native from alien taxa. However, a taxon can have both native and alien populations within the same country as biogeographic and administrative boundaries do not always align. Here we propose a protocol for classifying populations as native, alien, cryptogenic, or native-alien, and describe the evidence required. This protocol comprises of three questions: (1) is the population outside the historic native range of the taxon, (2) is/was natural dispersal from the native range unlikely, and (3) is the taxon native to a part of the administrative region where the population is found. If information on introduction pathways, genetics, and biogeographical barriers is available, we propose an alternative process to answer question 2. The protocol was applied to 176 suspected native-alien populations in South Africa. A total of 132 populations from 77 native taxa were classified as native-alien, 13 as cryptogenic, 13 as alien (native-alien status uncertain), and 18 as native. We believe the protocol provides a transparent and standardised method for categorising native-alien populations and thereby facilitates the appropriate regulation and management of this type of biological invasion.

**Key words:** biological invasions, conservation, dispersal, framework, native taxa

### Introduction

Conserving biodiversity and maintaining the uniqueness of place depends on understanding the nativity of taxa (Vilà et al. 2011). Therefore, it is important for regulators and managers to effectively distinguish native from alien taxa (Pauchard et al. 2018). However, management and regulation often operate based on administrative or political units, which generally do not correspond with biogeographic units (IPBES 2019). This has consequences for understanding the nativity of taxa (Nelufule et al. 2022).

An alien population is a population whose presence in a region is due to human actions that facilitated the movement of individuals over a biogeographic barrier (Richardson et al. 2011). These biogeographical barriers (see Box 1 for a glossary) can be biotic (e.g., the absence of key interacting species, such as dispersal vectors) or abiotic (such as unsuitable

**Box 1: Glossary**

**Biogeographic barrier** — a barrier that prevents the migration of species (Allaby 2010) or natural barriers (oceans, mountain ranges, catchment divides and waterfalls) that prevent the exchange of species among regions (Rahel 2007).

**Population** — a group of organisms of one species that interbreed and live in the same place at the same time (Marczewski et al. 2016).

**Native range** (incl. current or recent historical) — the originating environment of the species, including climate, and extent of the geographic range (Richardson 2000).

**Natural dispersal** (incl. dispersal that became possible due to human modification of the environment) — a process whereby a living organism's presence in a region is due to natural mechanisms of dispersal (Essl et al. 2018).

**Human-mediated dispersal** — it includes the human-mediated physical movement of propagules or individuals, both intentional and unintentional, of any life-cycle stage beyond the native range of the species (Essl et al. 2018).

**Alien population** — a population whose presence in a region is due to human-mediated dispersal (i.e. direct human agency or substantial indirect human agency) across a biogeographic barrier to a site where the species has not recently naturally occurred (Essl et al. 2018).

**Native-alien population** — a population that results from human-mediated dispersal of individuals of a taxon over a biogeographical boundary to a point beyond the taxon's native range that is still within the same political entity as some parts of the taxon's native range (Nelufule et al. 2022).

climatic conditions, oceans, and river valleys). Since biogeographical barriers do not always coincide with political boundaries, the processes that lead to the introduction of alien taxa can act within a single political entity. Therefore, a taxon can have both alien and native populations within a political entity (e.g., a country). This results from the movement of individuals by human agency and subsequent establishment of a population beyond the taxon's native range, but within the political entity to which the taxon is native (Vitule et al. 2009; Guo and Ricklefs 2010; Lockwood et al. 2013; Ellender and Weyl 2014; Skóra et al. 2015), a phenomenon for which the term “native-alien populations” has been proposed (Nelufule et al. 2022). These native-alien populations are a subset of alien populations, but their properties are likely to differ from alien populations introduced from other countries, and these differences will likely have consequences for invasion success, impacts, management, and regulation (Nelufule et al. 2022).

Globally, a wide variety of frameworks have been developed for use in invasion science (Wilson et al. 2020), but there is no standardised protocol for classifying native-alien populations. Native-alien populations have recently been defined (Nelufule et al. 2022), however implementing this definition in practice is challenging. For example, native-alien populations could be misidentified as examples of local range expansion by native taxa (Essl et al. 2019). A further complication is that scientists have used different terms to refer to these populations, for example, “extralimital species” and “domestic exotics” (Guo and Ricklefs 2010; Ellender and Weyl

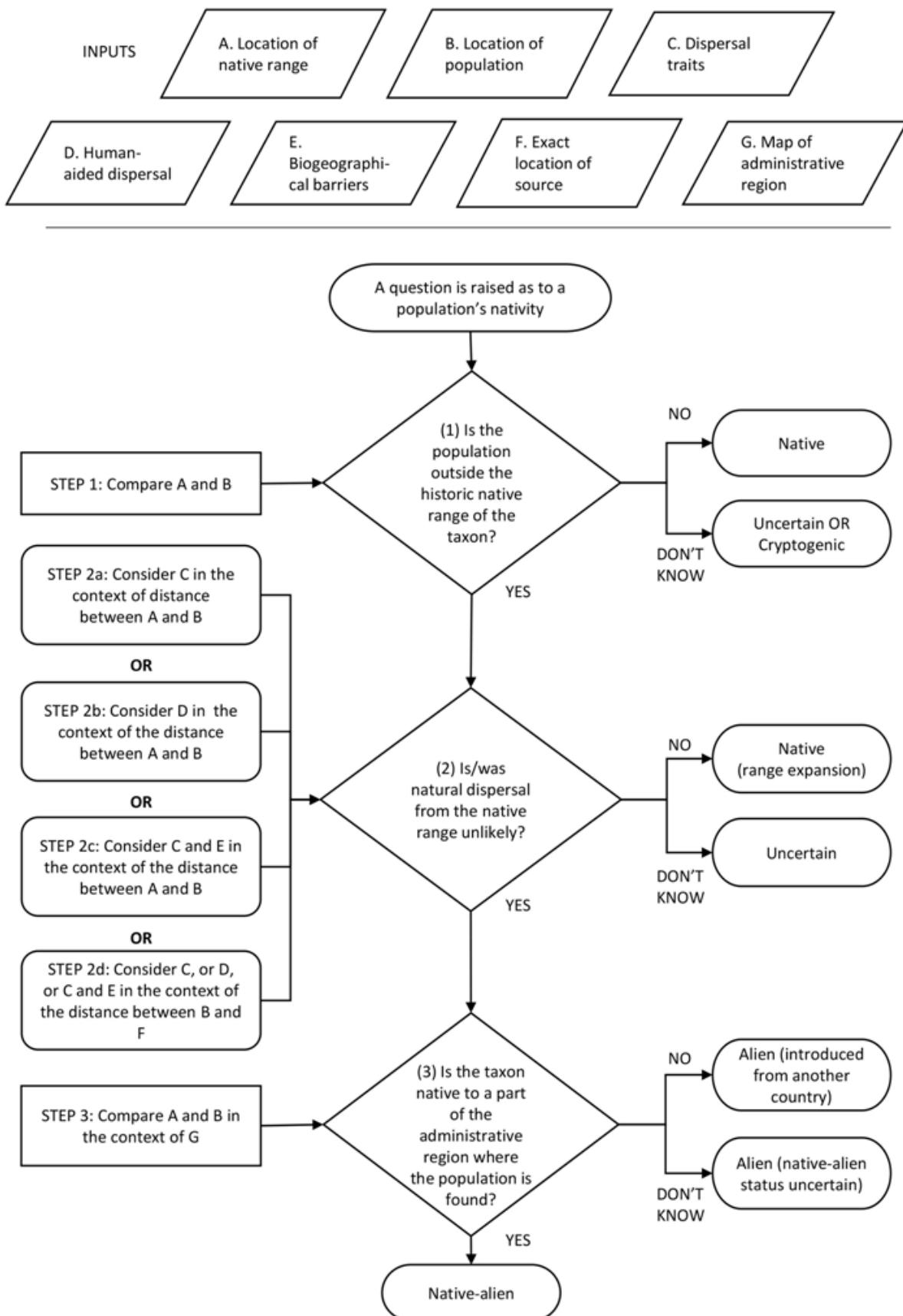
**Box 2: Proposed classification of populations based on Nelufule et al. 2022**

1. Native — the population is within the historic native range of the taxon.
2. Uncertain or Cryptogenic — there is substantial uncertainty as to whether the population is within or outside the historic native range of the taxon.
3. Native (range expansion) — the population is beyond the historic native range but there has been natural dispersal to the new site (even if that was due to human modification of the environment).
4. Alien — the population is outside the native range of the taxon and it was introduced there through human-mediated dispersal either directly or indirectly (i.e. there was human-mediated dispersal followed by natural dispersal). Three additional sub-categories are included based on the administrative region of interest.
  - 4.1. Native-alien — the population is present in an administrative region of which a part includes its native range.
  - 4.2. Alien (native-alien status uncertain) — the population is alien, but there is some uncertainty as to whether the native range also overlaps with the administrative region.
  - 4.3. Alien population introduced from another country — the population is present in an administrative region to which it is entirely alien. Throughout we recommend noting this as simply alien.

2014; Measey et al. 2017). Under the Global Register of Introduced and Invasive Species (GRIIS), these populations are classified as “Native|Alien” (Pagad et al. 2022), and so are distinct from alien populations introduced from other countries. However, under the global biodiversity standard, Darwin Core, each record is classified as either native or introduced to a site (Groom et al. 2019). This means that native-alien populations will not be separated from other types of alien populations, and additional information linked to status at a national scale is needed to do so. Therefore, a protocol that can distinguish native-alien populations from other related phenomena—such as local-scale range expansions or contractions at range margins, and range changes driven by human induced environmental changes—can help solve this problem. Here we propose a standardised protocol for classifying native-alien populations that can be integrated with existing alien species lists and global biodiversity standards, and test it by assessing populations of interest that were reported to be outside their historic native range as a result of human agency in South Africa.

### **Standardised protocol for assessing the status of a population of interest**

We developed a set of scenarios that describe the status of populations (see Box 2). Based on these scenarios we developed questions that need to be answered to determine the status of a population of interest (Figure 1), specifically: (1) is the population outside of the historic native range of the taxon, (2) is/was natural dispersal from the native range unlikely, and (3) is the taxon native to a part of the administrative region where the population is found. Evidence is needed to answer the questions and demonstrate that one scenario is more likely to be true than another, and below we describe the type of evidence required. A minimum standard for



**Figure 1.** A protocol to classify populations as cryptogenic, native, or alien and, within alien, as native-alien or not. The diagram shows the questions that are posed for classification, the inputs and processes required to answer the questions, and the answers and outputs of the protocol. Each output is based on the scenarios that describe the status of populations (see Box 2). A confidence level of high, medium or low can be applied to deal with uncertainties during classification (see Table 1).

**Table 1.** Guidelines for assigning confidence levels when classifying populations as native-alien (c.f. Figure 1).

Question to be answered	Confidence description	Confidence levels
1. Is the population outside the historic native range of the taxon?	There is neither a clear unambiguous geographical separation NOR a clear unambiguous overlap between the putative native range and the population of interest. This can be because the location of the native range and/or the population of interest is not clearly documented or is based on assumptions from the grey literature.	Low
	There is some geographical separation between the putative native range and the population of interest OR they likely overlap. This is usually due to a combination of the precision with which the location of the native range or population of interest are described (e.g., coordinates of the edge of the population are not available, and locations are based on text descriptions or distribution maps without a clear underlying methodology).	Medium
	There is a clear unambiguous geographical separation between the putative native range and the population of interest OR a clear unambiguous overlap between the putative native range and the population of interest.	High
2. Is /was natural dispersal from the native range unlikely?	The distance between the population of interest and its native range is similar to the maximum natural dispersal distance of the organism. Confidence is marked as low particularly in cases when information is not clearly documented or is based on assumptions (information here refers to that concerning the role that humans or natural dispersal likely played in dispersal; the location of the population of interest; or the presence of biogeographical barriers).	Low
	Natural dispersal is improbable and a biogeographical barrier is assigned using the proposed protocol for identifying biogeographical barriers OR natural dispersal is probable and no biogeographic barriers are clearly identified. The difference from high confidence is either that the evidence that humans played a role in dispersal is weak (e.g., based on indirect evidence of pathways) OR human agency is highly likely to have also occurred.	Medium
3. Is the taxon native to a part of the administrative region where the population is found?	It is extremely unlikely that natural dispersal happened (e.g., biogeographical barriers are present and well understood, and there is direct evidence of human-mediated pathways) OR there are no substantive current biogeographic barriers (e.g., they were demonstrably eroded by human activities) and changes in ranges are consistent with range expansion through natural dispersal.	High
	The native range might extend into the administrative region where the population of interest is recorded, but this is not known with high certainty. This can be because the location of the native range (or the population of interest) is not clearly documented (e.g., is based on assumptions from the grey literature or from experts).	Low
	It is highly likely OR unlikely that the native range extends into the administrative region where the population of interest is recorded. This might be because the location of the native range is from the published literature, but the precise location of the native range (or population of interest) is not available (e.g., coordinates of the locations are not available, and locations are based on text descriptions or distribution maps without a clear underlying methodology).	Medium
	There is substantive evidence that the native range includes OR does not include a part of the administrative region where the population of interest is recorded. This might be because the location of the native range (or the population of interest) is precisely known and published OR that the native range is far removed from the administrative region where the population of interest is found.	High

the evidence required to answer the three questions has been identified. We also propose alternative processes that can be used to answer question 2, based on information on human-mediated dispersal, genetics, and biogeographical barriers. We have proposed guidelines to assign a level of confidence (high, medium, or low) when answering each question (Table 1).

(1). *Is the population outside the historic native range of the taxon?*

To answer this question sufficient evidence should be provided to rule out that the population of interest is within its historic native range. Reliable and scientifically accurate information on the location of the native range of the taxon (e.g., a text description or a map) and information on the location of the population of interest are needed (see step 1 in Figure 1). As the distance between the native range and the population of interest will have implications when classifying populations, higher quality information can be used to increase confidence in the classification or when the minimum required evidence does not suffice to rule out that the taxon of interest is within its historic native range. These data would include the precise location of the historic native range and population of interest (e.g., the coordinates of the edge of the population), possibly with pictures of the population of interest obtained from published articles, national databases, or from experts; or grey literature taking into account the Wallacean shortfall (Lomolino 2004).

A temporal threshold is required to determine the historic native range of taxa, but this will be context-specific both to the region and to the taxon of interest. This is because the timing and cause of historic human movements differ for different countries or administrative regions across the world. In particular, European colonisation occurred at different times in different parts of the World, making the date when many taxa were introduced through these movements context specific. For example, following European colonisation in the 1600s, many alien taxa were introduced to South Africa from other countries (Faulkner et al. 2020) and many native taxa were introduced to areas outside their native range within South Africa [e.g., the introduction of nyala (*Tragelaphus angasii*) into the Western Cape province]. However, there is strong evidence that other species were introduced by intra-African human migrations that occurred around 2000 years ago, (e.g., taxa like the plant *Ricinus communis*) and so the 1600s is not a clear threshold (Faulkner et al. 2020).

When the historic native range of the taxon of interest is not well defined or is unknown, the population of interest should be classified as uncertain or cryptogenic, and further research done to determine the native range.

When the answer to the question is no, the population should be classified as a native population, but when the answer is yes, the next question should be addressed (Figure 1).

(2). *Is/was natural dispersal from the native range unlikely?*

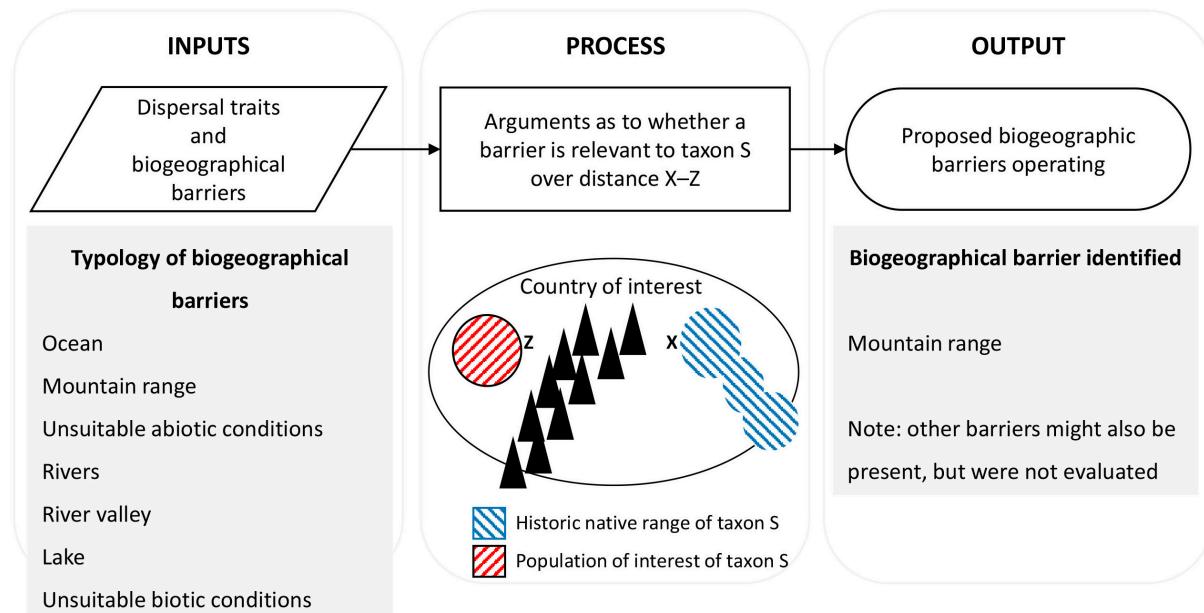
For a population to be considered as alien it should not have arisen due to natural dispersal from the native range. The purpose of this question is to evaluate that possibility. Two lines of evidence can help answer this

question: i) evidence of dispersal facilitated by human agency; and ii) evidence which shows that natural dispersal is very unlikely to have taken place. As a minimum, information on the dispersal traits of the taxon and data on the location of the native range and population of interest are required to answer this question (see step 2a on Figure 1). This should include information on how the taxon disperses naturally and an estimate of how far it can disperse, or biological trait data that could be used as a proxy for information on dispersal processes. For example, edible seeds can be dispersed long distances by birds (Howe and Smallwood 1982), while seeds with hooked appendages dispersed when attached to animals tend to be dispersed over shorter distances (Tamme et al. 2014). Information on dispersal traits and the distance between populations is used to estimate the likelihood that the population was the result of a natural dispersal event from the native range (Wilson et al. 2009; Richardson et al. 2011). It is likely that introduction events, whether intentional or accidental, will not be observed or documented in most cases. However, if natural dispersal from the native range seems unlikely, then it is reasonable to argue that the population should be classified as an alien population, rather than a native population. For example, if a taxon is a poor disperser, and the distance between the native range and the location of the population of interest is relatively far (and especially if there is unoccupied suitable habitat in between), then natural dispersal most likely did not occur. In such cases, it can be concluded that the population of interest was moved by human-agency, albeit with low confidence. Higher quality evidence, such as documented events of natural or human-mediated dispersal can be used to increase certainty in classification (see section below on alternative inputs and processes). It is also important to assess whether range disjunctions might have been due to historical biogeographic processes (e.g., relictual fragmented populations post-glaciation).

If the answer to this question is no, the population of interest is assumed to be within its native range and the result of natural range expansion, which in some cases may be facilitated by human-driven environmental change (Essl et al. 2019). No further assessment is required for these populations (Figure 1). When the population of interest is found outside the historic native range, but it is not clear from the evidence obtained how this population of interest could have arrived at the site, then the population should be classified as uncertain, and further research is needed to improve the classification. When the answer is yes, the next question should be addressed (Figure 1).

#### *Alternative inputs and processes to answer question 2*

There are alternative inputs and processes that can be used to answer question 2. These involve using evidence of human-mediated dispersal, genetics, and/or presence of biogeographical barriers between the native range and the population of interest (Figure 1).



**Figure 2.** Proposed steps to be followed when classifying biogeographical barriers that separate different parts of a taxon's range.

Genetic evidence, which can be used to estimate the source of the population (e.g., Thomson et al. 2014), and evidence of how the individuals dispersed (e.g., from other native-alien populations) or were introduced through human agency [direct or substantial indirect human agency (see Essl et al. 2018)] can also be used to conclude that the population did not or need not have resulted from a natural dispersal event from the native range (see step 2b of Figure 1). This would include direct evidence such as records of interceptions with imported goods, documented events of introductions or release or escape; and indirect evidence such as the existence of pathways associated with a taxon, and first records in transport hubs (e.g., ports) (Pyšek et al. 2004; Hulme et al. 2008; Blackburn et al. 2011). Indirect evidence includes putative pathways by which a population or propagules of a specific taxon could have recently been introduced to the area of interest (e.g., via trade), and evidence that the pathway is in operation in that area. Notably, of course, evidence of human-mediated dispersal is evidence that natural dispersal need not have occurred, rather than that natural dispersal did not occur.

Evidence that there is a biogeographical barrier that separates the population of interest from the native range and prevents natural dispersal between these two locations provides a more mechanistic reason to rule out a natural dispersal event (step 2c, Figure 1). This includes evidence of biogeographic barriers that cannot be surpassed by the taxon, taking its dispersal abilities into account, such as mountain ranges, unsuitable habitat, and river catchments between the population of interest and the native range (Essl et al. 2018). However, it is likely that the relevant biogeographical barriers between the population and its native range will not be documented in most cases. In such cases, the topology of the biogeographical barriers presented in Figure 2 could be used to determine

if there is a biogeographic barrier between the native range and the population of interest. This topology comprises seven types of biogeographical barrier, ranked from the most likely to prevent dispersal to the least likely to prevent dispersal (Figure 2). Information on life-history traits (with reference to dispersal) of the organism that are likely to facilitate the crossing of biogeographical barriers should be collected by searching for information on the biology of the taxon in the literature. For example, strong swimming ability for marine taxa, ability to fly at high altitude for birds, and passive or active dispersal for plants. This information is then used to determine whether a biogeographic barrier would likely prevent the dispersal of the taxon of interest from its native range to the location of the population of interest (Figure 2).

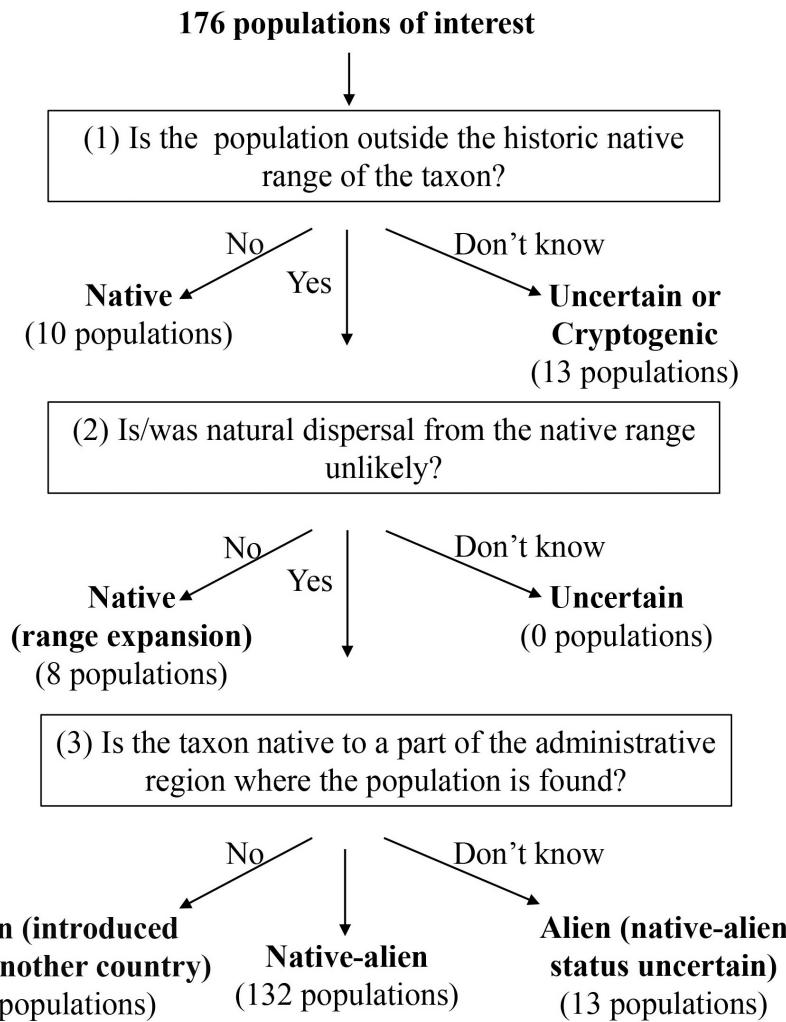
*(3). Is the taxon native to a part of the administrative region where the population is found?*

The purpose of this question is to rule out that the population is alien to all parts of the administrative region in which the population of interest is located (in which case it would simply be an alien population introduced from another country and not a native-alien population).

The minimum information required to answer this question is information on the location of the native range and the boundaries of the relevant administrative regions although it is also important to confirm that the population of interest is within the relevant administrative region (see step 3 on Figure 1). Higher quality information (see details under the section for question 1), can be used to increase certainty in the classification. If the evidence is unclear or contradictory, the classification should be classified as “alien (native-alien status uncertain)” and further research is needed. If the answer to the question is no, the population is an “alien population introduced from another country”. If the answer is yes, then the population of interest is a native-alien population, and no further assessment is required (Figure 1). Even if the native range is uncertain it can often still be stated with high confidence that the population is alien to the whole of a country, e.g., the native range of Afro-Eurasian taxa with a long-history of association with humans (domesticated taxa in particular) is often unclear, but it is often clear that such taxa are alien to Australasia and the Americas (Canavan et al. 2022).

### **Confidence estimates**

We have proposed broad guidelines to assign a level of confidence (high, medium, or low) when classifying native-alien populations. This was based on approaches used by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) to classify the degree of confidence when assessing biodiversity and ecosystem services (IPBES 2016), and by Wilson and colleagues (2018) to classify the uncertainty in indicators for monitoring biological invasions at a national level. For each

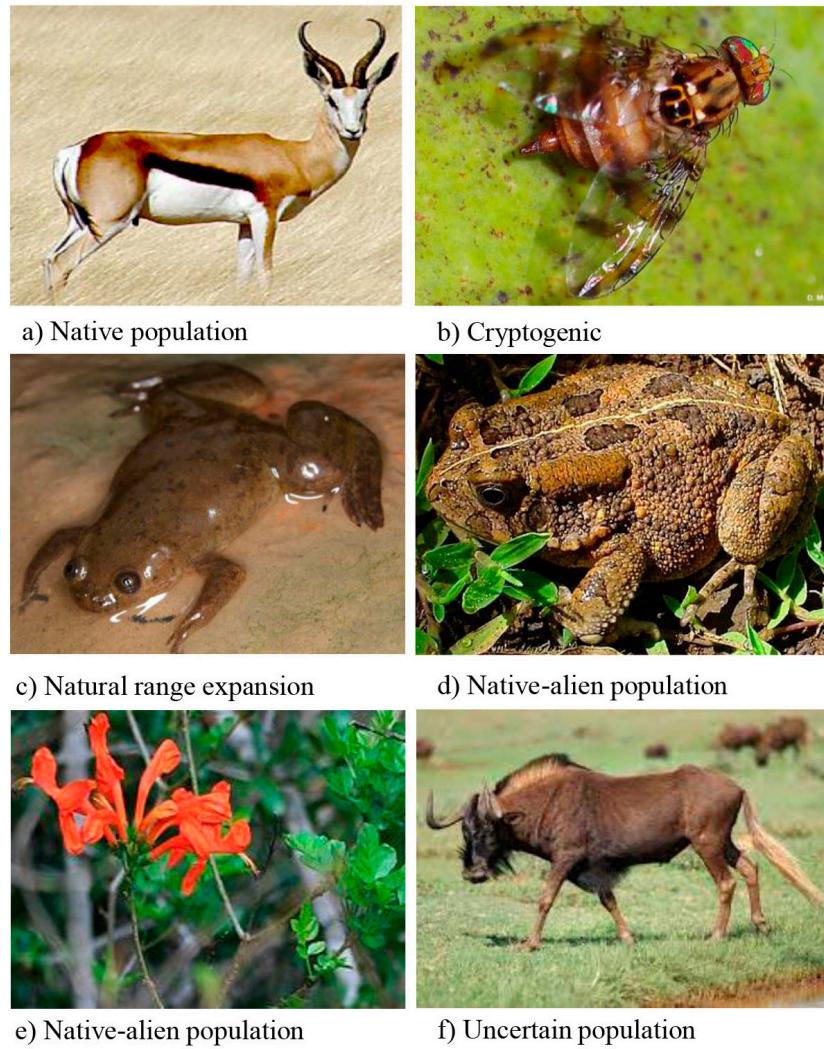


**Figure 3.** The classification of 176 suspected native-alien populations in South Africa according to the protocol presented in Figure 1 (Nelufule et al. 2023a).

population, confidence levels should be estimated based on the quality of the evidence. The criteria for the different levels of confidence varies between the questions (see Table 1). As new data become available, confidence levels can also change over time.

### Application of the protocol in South Africa

We applied this protocol to 176 recorded populations of interest from nine classes in South Africa (Figure 3; Nelufule et al. 2023a, b; Supplementary material Table S1). Populations of interest are those populations that were suspected to be outside their historic native range as a result of human agency and are regarded as pests or weeds. These populations were reported as potential native-alien populations, but had not been formally assessed using a standardised protocol. These populations were identified through online searches, an online survey, and by directly consulting experts that had responded to the survey. Details of the process used, and the full dataset, are outlined in Nelufule et al. (2023a). In brief, the ISI Web of Knowledge and Google Scholar search engines were used to search for



**Figure 4.** Examples of South African populations categorised according to the protocol (Figure 1). a) springbok (*Antidorcas marsupialis*) is native to much of the country. The population in the Eastern Cape province was of interest because it was classified as an extralimital species due to genetic variation (white and black springbok) (Castley et al. 2001). However, springbok are native to most of the eastern and central parts of the Eastern Cape province and so the population was classified as native recognising that such a population might still affect sub-specific genetic diversity and be undesirable. b) The native range of the Natal fruit fly (*Ceratitis rosa*) is uncertain in South Africa (Karsten et al. 2016), and so we were not able to clearly designate populations recorded at 22 localities across the country as native-alien or native (Karsten et al. 2016). c) The African clawed frog (*Xenopus laevis*) has expanded its range through leading edge dispersal (Measey 2004) into areas of the south-western Cape of South Africa that have become suitable due to the development of farm dams, irrigation channels, and other artificial water bodies, and so its populations in the south-western Cape were classified as native populations that have resulted from natural range expansion due to modification of the environment by humans. d) guttural toad (*Sclerophrys gutturalis*), is native to the KwaZulu-Natal province of South Africa, but individuals were transported unintentionally as eggs or tadpoles with consignments of aquatic plants to the Western Cape province and many other places in South Africa, where the taxon is not native (Measey et al. 2017). e) Cape honeysuckle (*Tecoma capensis*) is native to the Eastern Cape, KwaZulu-Natal, Limpopo and Mpumalanga provinces, but has been introduced for horticulture purposes to the Western Cape province where it is not native (Baard and Kraaij 2014). f) Black wildebeest (*Connochaetes gnou*) was recorded as an extralimital species in the Eastern Cape and Northern Cape, however, the exact location of the populations was not specified in the literature. Given black wildebeest is native to parts of the Eastern Cape and Northern Cape it was uncertain as to whether these populations were outside or within the historic native range (Castley et al. 2001). Photographs courtesy of: a) Wikimedia/ C. Coza; b) CABI/D. Martiré; c) Wikimedia/B. Gratwicke; d) Wikimedia/Ijargoud; e) Wikimedia/ D. Keats; and f) Wikimedia/F. Xaver. The images were not taken of individuals from the populations of interest.

**Table 2.** South African native taxa that have formed native-alien populations, classified according to the class, and for each taxon the number of native-alien populations recorded.

Taxa	Class	Number of populations
<i>Chetia brevis</i> Jubb, 1968	Actinopterygii	1
<i>Clarias gariepinus</i> (Burchell, 1822)	Actinopterygii	3
<i>Enteromius anoplus</i> (Weber, 1897)	Actinopterygii	1
<i>Enteromius treurensis</i> (Groenewald, 1958)	Actinopterygii	1
<i>Kneria auriculata</i> (Pellegrin, 1905)	Actinopterygii	1
<i>Labeo capensis</i> (Smith, 1841)	Actinopterygii	5
<i>Labeobarbus capensis</i> (Smith, 1841)	Actinopterygii	2
<i>Labeo umbratus</i> (Smith, 1841)	Actinopterygii	1
<i>Labeobarbus aeneus</i> (Burchell, 1822)	Actinopterygii	5
<i>Nothobranchius rachovii</i> Ahl, 1926	Actinopterygii	1
<i>Oreochromis mossambicus</i> (Peters, 1852)	Actinopterygii	1
<i>Tilapia rendalli</i> (Boulenger, 1897)	Actinopterygii	1
<i>Tilapia sparrmanii</i> Smith, 1840	Actinopterygii	3
<i>Hyperolius marmoratus</i> Rapp, 1842	Amphibia	1
<i>Sclerophrys gutturalis</i> (Power, 1927)	Amphibia	1
<i>Agapornis roseicollis</i> (Vieillot, 1818)	Aves	1
<i>Numida meleagris</i> (Linnaeus, 1758)	Aves	1
<i>Lonchura fringilloides</i> (Lafresnaye, 1835)	Aves	2
<i>Atoxonoides meridionalis</i> (Forcart, 1967)	Gastropoda	1
<i>Cochlitoma zebra</i> (Bruguière, 1792)	Gastropoda	1
<i>Haliotis midae</i> Linnaeus, 1758	Gastropoda	1
<i>Laevicaulis alte</i> (Férussac, 1822)	Gastropoda	1
<i>Nata (Nata) vernicosa</i> (F.Krauss, 1848)	Gastropoda	1
<i>Anisorrhina (Anisorrhina) flavomaculata</i> (Fabricius, 1798)	Insecta	4
<i>Charaxes brutus</i> (Cramer)	Insecta	1
<i>Chlorocala africana</i> subsp. <i>subsuturalis</i> (Kraatz, 1891)	Insecta	1
<i>Cochlochlila bullita</i> (Stål, 1873)	Insecta	1
<i>Coeliades libeon</i> (Druce, 1875)	Insecta	2
<i>Glutophrissa sabina</i> (Felder & Felder, 1865)	Insecta	1
<i>Dicronorhina derbyana</i> Westwood, 1842	Insecta	1
<i>Ellimenistes laesicollis</i> Fähraeus, 1871	Insecta	1
<i>Junonia orithya</i> subsp. <i>madagascariensis</i> Guenée, 1872	Insecta	1
<i>Mausoleopsis amabilis</i> (Schaum, 1844)	Insecta	3
<i>Mylothris agathina</i> (Cramer, 1779)	Insecta	2
<i>Leucocelis rubra</i> (Gory & Percheron, 1833)	Insecta	4
<i>Neuranethes spodopterodes</i> Hampson, 1908	Insecta	2
<i>Pachnoda sinuata</i> subsp. <i>flaviventris</i> (Gory & Percheron, 1833)	Insecta	1
<i>Brachylaena discolor</i> DC.	Magnoliopsida	2
<i>Carissa macrocarpa</i> (Eckl.) A.DC.	Magnoliopsida	1
<i>Crassula multicava</i> Lem.	Magnoliopsida	3
<i>Cyperus papyrus</i> L.	Magnoliopsida	1
<i>Dais cotinifolia</i> L.	Magnoliopsida	1
<i>Ekebergia capensis</i> Sparrm.	Magnoliopsida	1
<i>Erythrina lysistemon</i> Hutch.	Magnoliopsida	1
<i>Euryops virgineus</i> (L.fil.) Less.	Magnoliopsida	1
<i>Gynandropsis gynandra</i> (L.) Briq.	Magnoliopsida	1
<i>Harpephyllum caffrum</i> Bernh.	Magnoliopsida	1
<i>Ipomoea cairica</i> (L.) Sweet	Magnoliopsida	1
<i>Jasminum multipartitum</i> Hochst.	Magnoliopsida	1
<i>Podocarpus henkelii</i> Stapf ex Dallim. & A.B.Jacks.	Magnoliopsida	1
<i>Rauvolfia caffra</i> Sond.	Magnoliopsida	1
<i>Senecio angulatus</i> L.fil.	Magnoliopsida	1
<i>Setaria megaphylla</i> (Steud.) T.Durand & Schinz	Magnoliopsida	2
<i>Syzygium cordatum</i> Hochst.	Magnoliopsida	4
<i>Tecoma capensis</i> (Thunb.) Lindl.	Magnoliopsida	2
<i>Tetradenia riparia</i> (Hochst.) Codd	Magnoliopsida	1
<i>Thunbergia alata</i> Bojer ex Sims	Magnoliopsida	1
<i>Austruca occidentalis</i> (Naderloo, Schubart & H.-T.Shih, 2016)	Malacostraca	1

**Table 2.** (Continued).

Taxa	Class	Number of populations
<i>Ocypode ceratophthalmus</i> (Pallas, 1772)	Malacostraca	1
<i>Portunus segnis</i> (Forskål, 1775)	Malacostraca	1
<i>Varuna litterata</i> (Fabricius, 1798)	Malacostraca	1
<i>Acinonyx jubatus</i> (Schreber, 1775)	Mammalia	1
<i>Aepyceros melampus</i> (Lichtenstein, 1812)	Mammalia	2
<i>Ceratotherium simum</i> (Burchell, 1817)	Mammalia	1
<i>Connochaetes gnou</i> (Zimmermann, 1780)	Mammalia	1
<i>Connochaetes taurinus</i> (Burchell, 1823)	Mammalia	2
<i>Damaliscus pygargus</i> subsp. <i>pygargus</i> (Pallas, 1767)	Mammalia	2
<i>Damaliscus pygargus</i> subsp. <i>phillipsi</i> Harper, 1939	Mammalia	2
<i>Equus quagga</i> Boddaert, 1785	Mammalia	1
<i>Giraffa camelopardalis</i> (Linnaeus, 1758)	Mammalia	3
<i>Hippotragus niger</i> (Harris, 1838)	Mammalia	1
<i>Kobus ellipsiprymnus</i> (Ogilby, 1833)	Mammalia	3
<i>Redunca fulvorufula</i> (Afzelius, 1815)	Mammalia	1
<i>Tragelaphus angasii</i> Angas, 1849	Mammalia	5
<i>Bradypodion ventrale</i> (Gray, 1845)	Reptilia	5
<i>Hemidactylus mabouia</i> (Moreau De Jonnés, 1818)	Reptilia	3
<i>Lygodactylus capensis</i> (Smith, 1849)	Reptilia	5

scientific publications and grey literature on potential native-alien populations in South Africa using terms such as “extralimital species”, “native alien species”, “within-country aliens”, “within-country movement of native species in South Africa”, “Intracontinental exotics”, “Intra-country established alien species”, “native-alien populations”, “alien natives”, and “domestic exotics”. Papers with information on possible native-alien populations in South Africa were selected based on the content of their titles and abstracts. The results of each question in the protocol are summarised in Figure 3. Of the 176 populations of interest recorded, 18 populations were classified as native populations, 13 populations as cryptogenic, 132 as native-alien populations, 13 as alien (native-alien status uncertain), and none as alien introduced from other countries (Figure 4; Table S1). The native-alien populations were from 77 taxa, 49 families and nine classes (Table 2; Nelufule et al. 2023b).

### Conclusion and recommendations

We hope that the development of this protocol will increase the recording of native-alien populations and stimulate further discussion and research on this understudied phenomenon globally. We recommend that these types of populations are classified as native-alien populations in the global biodiversity standard, Darwin Core, because classifying them as introduced to a site will not distinguish them from alien populations introduced from another country and might lead to the assumption that the taxon is alien to the whole country. We believe the protocol provides a transparent and standardised method for categorising native-alien populations and thereby facilitates the appropriate regulation and management of this type of biological invasion.

## Acknowledgements

We thank Arne Witt, Brett Hurley, Charles Griffiths, David Herbert, George Branch, Ian Little, Ian Rushworth, Jan Giliomee, Johan Baard, John Donaldson, John Measey, Llewellyn Foxcroft, Michael Cheek, Mike Picker, Nanna Joubert, Mbali Mkhize, Pieter Winter, Riaan Stals, Tammy Robinson, Thulisile Jaca, Tony Rebelo and Olaf Weyl (may his soul continue to rest in peace) for contributing data on native-alien populations. Sabrina Kumschick, Michael Cheek, Sven Bacher, Andrew Turner, Jean Vitule, and two anonymous reviewers are thanked for comments on earlier drafts.

## Funding declaration

The South African Department of Forestry, Fisheries and the Environment (DFFE) are thanked for funding, noting that this publication does not necessarily represent the views or opinions of DFFE or its employees.

## Author's contribution

TN, KTF, MPR and JRUW research conceptualization; TN, KTF, MPR, and JRUW sample design and methodology; TN investigation and data collection; TN, KTF, MPR and JRUW writing – review and editing. TN writing – original draft.

## References

- Allaby M (2010) A dictionary of ecology. Oxford university press, United States of America, 432 pp
- Baard J, Kraaij T (2014) Alien flora of the Garden Route National Park, South Africa. *South African Journal of Botany* 94: 51–63, <https://doi.org/10.1016/j.sajb.2014.05.010>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, <https://doi.org/10.1016/j.tree.2011.03.023>
- Castley JG, Boshoff AF, Kerley GIH (2001) Compromising South Africa's natural biodiversity – Inappropriate herbivore introductions. *South African Journal Science* 97: 344–348
- Canavan S, Brym Z, Brundu G, Dehnen-Schmutz K, Lieurance D, Petri T, Wadlington W, Wilson J, Flory S (2022) Cannabis de-domestication and invasion risk. *Biological Conservation* 274: 1–9, <https://doi.org/10.1016/j.biocon.2022.109709>
- Ellender BR, Weyl OLF (2014) A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. *Aquatic Invasions* 9: 117–132, <https://doi.org/10.3391/ai.2014.9.2.01>
- Essl F, Bacher S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kowarik I, Kühn I, Pyšek P, Rabitsch W, Schindler S, van Kleunen M, Vilà M, Wilson JRU, Richardson DM (2018) Which taxa are alien? Criteria, applications, and uncertainties. *BioScience* 68: 496–509, <https://doi.org/10.1093/biosci/biy057>
- Essl F, Dullinger S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kühn I, Lenzer B, Pauchard A, Pyšek P, Rabitsch W, Richardson DM, Seebens H, van Kleunen M, van der Putten WH, Vilà M, Bacher S (2019) A Conceptual framework for range-expanding species that track human-induced environmental change. *BioScience* 69: 908–919, <https://doi.org/10.1093/biosci/biz101>
- Faulkner KT, Burness A, Byrne MJ, Kumschick S, Peters K, Robertson MP, Saccaggi DL, Weyl OLF, Williams VL (2020) South Africa's pathways of introduction and dispersal and how they have changed over time. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA (eds), *Biological invasions in South Africa*. Springer, Berlin, pp 311–352, [https://doi.org/10.1007/978-3-030-32394-3\\_12](https://doi.org/10.1007/978-3-030-32394-3_12)
- Groom Q, Desmet P, Reyersehoeve L, Adriaens T, Oldoni D, Vanderhoeven S, Baskauf SJ, Chapman A, McGeoch M, Walls R, Wieczorek J, Wilson JRU, Zermoglio PFF, Simpson A (2019) Improving Darwin Core for research and management of alien species. *Biodiversity Information Science and Standards* 3: e38084, <https://doi.org/10.3897/biss.3.38084>
- Guo Q, Ricklefs RE (2010) Domestic exotics and the perception of invasibility. *Diversity and Distributions* 16: 1034–1039, <https://doi.org/10.1111/j.1472-4642.2010.00708.x>
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecological Systematics* 13: 201–228, <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414, <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- IPBES (2016) The methodological assessment report on scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Science-Policy Platform on

- Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, 348 pp, <https://ipbes.net/document-library-catalogue/methodological-assessment-report-scenarios-models-biodiversity-ecosystem>
- IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Advance unedited edition). IPBES secretariat, Bonn, 45 pp, <https://doi.org/10.1111/padr.12283>
- Karsten M, Addison P, Van Vuuren BJ, Terblanche JS (2016) Investigating population differentiation in a major African agricultural pest: Evidence from geometric morphometrics and connectivity suggests high invasion potential. *Molecular Ecology* 25: 3019–3032, <https://doi.org/10.1111/mec.13646>
- Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology, 2<sup>nd</sup> edn. Wiley, Chichester, UK, 325 pp
- Lomolino MV (2004) Conservation biogeography. In: Lomolino MV, Heaney LR (eds), *Frontiers of Biogeography: new directions in the geography of nature*. Sinauer Associates, Sunderland, Massachusetts, pp 293–296
- Marczewski T, Ma Y-P, Zhang X-M, Sun W-B, Marczewski AJ (2016) Why is population information crucial for taxonomy? A case study involving a hybrid swarm and related varieties. *AoB PLANTS* 8: plw070, <https://doi.org/10.1093/aobpla/plw070>
- Measey GJ (2004) *Xenopus laevis*. In: Minter LR, Burger M, Harrison JA, Braack HH, Bishop PJ, Knoepfer D (eds), *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland. SI/MAB Series No 9*, Smithsonian Institution Press, Washington, DC, pp 264–266
- Measey J, Davies SJ, Vimercati G, Rebelo T, Schmidt W, Turner A (2017) Invasive amphibians in southern Africa: A review of invasion pathways. *Bothalia - African Biodiversity and Conservation* 47: 1–12, <https://doi.org/10.4102/abc.v47i2.2117>
- Nelufule T, Robertson MP, Wilson JRU, Faulkner KT (2022) Native-alien populations - an apparent oxymoron that requires specific conservation attention. *NeoBiota* 74: 57–74, <https://doi.org/10.3897/neobiota.74.81671>
- Nelufule T, Robertson MP, Wilson JRU, Faulkner KT (2023a) An inventory of native-alien populations in South Africa. *Scientific Data* 10: 213, <https://doi.org/10.1038/s41597-023-02119-w>
- Pagad S, Bisset S, Genovesi P, Groom Q, Hirsch T, Jetz W, Ranipeta A, Schigel D, Sica YV, McGeoch MA (2022) The Global Register of Introduced and Invasive Species: country compendium. *Scientific Data* 9: 391, <https://doi.org/10.1038/s41597-022-01514-z>
- Pauchard A, Meyerson LA, Bacher S, Blackburn TM, Brundu G, Cadotte MW, Courchamp F, Essl F, Genovesi P, Haider S, Holmes ND, Hulme P, Jeschke JM, Lockwood JL, Novoa A, Nuñez MA, Peltzer DA, Pyšek P, Richardson DM, Simberloff D, Smith K, van Wilgen BW, Vilà M, Wilson JRU, Winter M, Zenni RD (2018) Biodiversity assessments: origin matters. *PLoS Biology* 16: e2006686, <https://doi.org/10.1371/journal.pbio.2006686>
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143, <https://doi.org/10.2307/4135498>
- Rahel FJ (2007) Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology* 52: 696–710, <https://doi.org/10.1111/j.1365-2427.2006.01708.x>
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107, <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU (2011) Human-mediated introductions of Australian acacias - a global experiment in biogeography. *Diversity and Distributions* 17: 771–787, <https://doi.org/10.1111/j.1472-4642.2011.00824.x>
- Skóra F, Abilhoa V, Padial AA, Vitule JRS (2015) Darwin's hypotheses to explain colonization trends: evidence from a quasinatural experiment and a new conceptual model. *Diversity and Distributions* 21: 583–594, <https://doi.org/10.1111/ddi.12308>
- Tamme R, Götzemberger L, Zobel M, Bullock JM, Hooftman DAP, Kaasik A, Partel M (2014) Predicting species' maximum dispersal distances from simple plant traits. *Ecology* 95: 505–513, <https://doi.org/10.1890/13-1000.1>
- Thomson V, Aplin KP, Cooper A, Hisheh S, Suzuki H, Maryanto I, Yap G, Donnellan SC (2014) Molecular genetic evidence for the place of origin of the Pacific Rat, *Rattus exulans*. *PLoS ONE* 9: e91356, <https://doi.org/10.1371/journal.pone.0091356>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecological Letters* 14: 702–708, <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vitule JRS, Freire CA, Simberloff D (2009) Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10: 98–08, <https://doi.org/10.1111/j.1467-2979.2008.00312.x>
- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution* 24: 136–144, <https://doi.org/10.1016/j.tree.2008.10.007>

- Wilson JRU, Faulkner KT, Rahlao SJ, Richardson DM, Zengeya TA, van Wilgen BW (2018) Indicators for monitoring biological invasions at a national level. *Journal of Applied Ecology* 55: 2612–2620, <https://doi.org/10.1111/1365-2664.13251>
- Wilson JRU, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (2020) Frameworks used in invasion science: progress and prospects. *NeoBiota* 62: 1–30, <https://doi.org/10.3897/neobiota.62.58738>

## Web sites and online databases

Nelufule T, Robertson MP, Wilson JRU, Faulkner KT (2023b) List of native-alien populations in South Africa. *Figshare*, <https://doi.org/10.6084/m9.figshare.21084829.v19>

## Supplementary material

The following supplementary material is available for this article:

**Table S1.** A total of 44 populations of interest that were not classified as native-alien populations. These taxonomic groups are arranged per class. Classification is per the protocol (Figure 1).

This material is available as part of online article from:

[http://www.reabic.net/journals/mbi/2023/Supplements/MBI\\_2023\\_Nelufule\\_etal\\_SupplementaryMaterial.pdf](http://www.reabic.net/journals/mbi/2023/Supplements/MBI_2023_Nelufule_etal_SupplementaryMaterial.pdf)