PERSPECTIVE ARTICLE

# Invasive neo-species and how to name them

**Daniel Montesinos**[1,2]

1 *Australian Tropical Herbarium, James Cook University, Cairns, Queensland, Australia*
2 *Centre for Functional Ecology, University of Coimbra, Coimbra, Portugal*
Address for correspondence: *daniel.montesinos@jcu.edu.au*

**DOI** https://doi.org/10.1002/tax.12884

**Abstract** Range-expansion and speciation are not new to life on Earth, but they have been scarcely observed contemporarily and, likely, never over several continents simultaneously. Evidence of incipient reproductive isolation between native and non-native regions of some invasive alien species indicates that invasive speciation is closer than we expected. Some neo-allopatric populations are likely to qualify as distinguishable subspecies already. Given their trajectory, whether they will become new species is not an *if*, but a *when*. I present two decision tables to help to (1) assess the coining of new invasive species or subspecies with the current taxonomical approach or (2), introduce the term "neo" to name invasive neo-species resulting from synchronous allopatric speciation from a single, known, living ancestor. This latter case can be exemplified with the hypothetical names: "Ginkgo biloba neo americana", "G. biloba neo europea", etc.

**Keywords** alien species; allopatry; IAS; nomenclature; speciation; taxonomy

## ■ WHY INVASIVE NEO-SPECIES?

Anthropogenic global transport routes have resulted in synchronous global dispersal events which are possibly unique to the history of the planet (Chapman & al., 2017; Turbelin & al., 2017). Contemporary biological invasions are exceptional in that we have no other records of rapid (<200 years) geographic spread of any single species in such a synchronous manner across every landmass on Earth – although we have paleontological evidence for oceans (Vermeij, 2005; Stigall, 2019). This provides us with an exceptional opportunity to assess adaptive processes unfolding simultaneously over several continents (Callaway & Maron, 2006). This process has the potential to result, for any single invasive alien species, into synchronous parallel speciation over several world regions. Indeed, all the data we have points in that direction.

According to the classic model of allopatric speciation, the accumulation of divergent changes, pleiotropy, and genetic drift in the absence of gene flow, is expected to eventually result in reproductive isolation and speciation (Mayr, 1942). We have abundant evidence of such allopatric speciation processes, but these historical "neo-taxa" can be as old as 40,000 years to 2 million years, time during which they have had plenty of time to integrate into their recipient habitats (Levin, 2003). Invasive alien species ("invasives" or "invasive species" hereafter) meet the theoretical conditions for classic allopatric speciation almost perfectly. Different native and non-native populations are frequently exposed to quite distinct climatic niches (Atwater & al., 2018), resulting in rapid local adaptation to the environments of each of the different regions to which they are introduced (Callaway & Ridenour, 2004; Maron & al., 2004; Hierro & al., 2009, 2020; Colautti & Lau, 2015). Adaptive trait divergence commonly involves differences in physiology, size, growth rates, and fitness, which result in significant differences among allopatric populations (Van Kleunen & al., 2010; García & al., 2013; Irimia & al., 2019). The accumulation of local adaptations is expected to lead to reproductive isolation via several potential mechanisms including: pleiotropy, genetic hitchhiking, chromosomal inversions, Bateson-Dobzhansky-Muller interactions, genetic bottlenecks that occurred during the process of geographic isolation, and changes in ploidy (Barton, 2010; Rieseberg & Blackman, 2010; Schemske, 2010; Wolf & al., 2010). Unsurprisingly, we are starting to find evidence of incipient reproductive isolation between native and non-native populations of some invasive species (Montesinos & al., 2012b; Irimia & al., 2021), and of reduced fitness for their hybrid offspring (Montesinos & Callaway, 2017), in a reinforcing process that should result in the emergence of neo-species (Thomas, 2013). Synchronous speciation of invasive organisms across at least some of their invaded regions is therefore not an *if*, but a *when*.

The typically disjunct distributions of invasives mean that native and non-native populations can experience little genetic exchange after one or several initial introductions (Irimia & al., 2021; Mounger & al., 2021). Invasive species can benefit from repeated introductions, which are important (but not always necessary) to accumulate enough genetic diversity for selection to act upon. However, reintroductions tend to provide

**Article history:** Received: 31 Aug 2022 | returned for (first) revision: 20 Oct 2022 | (last) revision received: 25 Oct 2022 | accepted: 3 Nov 2022
**Associate Editor:** Dirk C. Albach | © 2023 The Author.
TAXON published by John Wiley & Sons Ltd on behalf of International Association for Plant Taxonomy.

maximal benefits during recent invasion, but usually have diminishing benefits as genetic divergence increases over time as a result of divergent selection (Vellend & al., 2007; Rius & Darling, 2014; Barker & al., 2019). Experimental backcrosses between individuals from allopatric regions of invasive species support this, with world regions with smaller, less successful populations benefiting from admixture, whereas populations from world regions where they are highly invasive and present in large numbers, with high degree of local adaptation, can present reduced fitness – and fertility – when backcrossed with individuals from other regions (Montesinos & Callaway, 2017; Barker & al., 2019; Irimia & al., 2021). These processes do not exclusively apply to highly successful invasive species: all exotic species – for definitions see Colautti & MacIsaac (2004) – and indeed all species, are constantly subject to natural selection by their local environment (Oduor & al., 2016). However, the proven ability of successful invasives to rapidly adapt to contrasting environmental conditions over several distant continents makes them uniquely suited for synchronous allopatric speciation to unfold.

Evidence for invaded communities adapting to invasive species is also mounting, displaying the increased integration of invasives into native communities (Lankau & al., 2009; Lankau, 2012). Invasive species are able to integrate into native seed dispersal communities (Gosper & al., 2005; Montesinos & al., 2012a) and pollinator communities (Correia & al., 2016; Montesinos & al., 2016), where they can increase the reproductive success of some native plants (Ferrero & al., 2013). Soil communities are also responsive to plant invasions, and the presence of native congeners of invasive species speeds up the accumulation of antagonistic soil biota that are able to limit their fitness advantage (Callaway & al., 2013). We also have evidence of coevolution between invasive and native plants, in which native plant communities become increasingly tolerant to allelochemicals produced by the invasive, which in turn reduce allelochemical production in populations where abundant invasives have selected for tolerant natives (Lankau & al., 2009; Lankau, 2012). These numerous but disparate results are still far from portraying complete integration of invasives into recipient communities, but do exemplify the processes by which they will, and for which speciation would be the logical outcome. The integration of invasives into recipient habitats and communities does not revert their impact in terms of biodiversity loss, extinctions, behavioural changes, disruption of interaction networks, changes in ecosystem functioning and ecosystem services – including changes in nutrient cycling, hydrology, habitat structure, and disturbances (Essl & al., 2010; Pyšek & al., 2020). These impacts are real and lasting, but so is the naturalisation of numerous non-native species.

## HOW TO DETERMINE WHAT IS A NEW SPECIES

Determining what constitutes a new species is controversial itself, and might differ depending on the taxonomy of the organisms in question. There is an ongoing debate about what constitutes a distinct species (Stuessy & al., 2014; Aldhebiani, 2018). The evolutionary or lineage species concept states that a species is “a single lineage of ancestral-descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley, 1978: 18). The evolutionary or lineage species concept is prevalent, but its application can be subjective and, thus, inconsistent (de Queiroz, 2005; Freudenstein & al., 2017). Nevertheless, numerous invasive species would be strong neo-species candidates under this paradigm.

The biological species concept is still one of the best-known species concepts, and it is broadly accepted as an unquestionable, if restrictive, proof of speciation. It poses that two organisms are considered to belong to different species if they are unable to breed fertile offspring (Mayr, 1942). There is room for debate on how much isolation is necessary for groups of organisms with incomplete reproductive barriers to be considered distinct biological species. However, there is little debate that if full reproductive isolation is present between two groups of organisms, then they can be confidently considered different species. This is particularly true for zoology, where reproductive barriers tend to be more binary. However, the biological species concept tends to be considered as too conservative for other taxonomic groups. In plants, it is commonly assumed that incomplete reproductive barriers are common within the genus level (Rieseberg & Willis, 2007; Widmer & al., 2009). Hybrid species are a good example of this, when hybridisation between two taxa is so frequent that the hybrid group gains the range of species, with two known ancestral species with whom they might still continue to hybridise when in sympatry. Hybridisation is frequently an important factor for invasive success, often with an invasive hybridising with a local congeneric (Abbott, 1992). The current taxonomical system is likely well suited to accommodate these cases of invasive hybrid speciation just as well as it does for natives.

The aim of this article is to focus on the specific case of synchronous allopatric speciation, since delving into other pathways to speciation – for which invasives can also be interesting study cases – like hybridisation, apomixis, or others, would deserve their own independent and extensive reviews. This article also does not intend to change the definitions or criteria by which we define species, but to acknowledge some unique aspects associated with the rapid and synchronous spread of many invasive species across the world, and to reflect on whether some nomenclatural fine tuning might be necessary. The novelty posed by invasive systems is not that they might be diverging fast, but that some might be diverging fast and synchronously across several continents. One ancestral invasive species introduced into several world regions is likely to result not in one but in several derived neo-species in each of the invaded regions (Irimia & al., 2021). When this happens, we will potentially encounter several species in different parts of the world, all with the same known ancestor. This opens interesting and unprecedented nomenclatural possibilities.

## ■ THE CURRENT TAXONOMICAL SYSTEM

Our current taxonomical system is based on a two-word naming system accounting for the genus (first word) and the species epithet (second word). For instance, and to use an emblematic tree species that is highly unlikely to ever become invasive or to speciate: the relictual Asian tree *Ginkgo biloba*. In the unlikely case that the charismatic relictual tree *G. biloba* speciated in allopatry – it certainly is cultivated in many botanical gardens around the world as an exotic species – we would need to coin a new specific epithet for it within the genus *Ginkgo*. For instance, "Ginkgo nova".

Our taxonomical system also includes a category for subspecies ("subsp."), which introduces a third word after the genus and the species epithet. This is used for distinct varieties of a species that are not considered to be sufficiently different to be distinct species. Subspecies are often described in the context of a strong geographical pattern, and it is common to find different subspecies in different sub-regions, or with distinct phenotypes along an environmental cline. Subspecies commonly present minor or no reproductive barriers with other subspecies within the same species. Following up on our prior example, using this nomenclature we could name a new neo-allopatric subspecies as "Ginkgo biloba subsp. nova".

## ■ POSSIBLE TAXONOMICAL HACKS FOR INVASIVE NEO-SPECIES

Invasive species have already proven to be able to develop significant morphological and genetic divergence, and important reproductive barriers, between native and non-native regions (Montesinos & al., 2012b; Irimia & al., 2021). These certainly are enough to grant, at least, the rank of subspecies for some current neo-allopatric populations. Darwin recognised the importance of divergent selection when he explained in *On the origin of species* how "the dominant species […] oftenest produce well-marked varieties, or, as I consider them, incipient species" (Darwin, 1859: 54). Notice that the definition of "varieties" and "subspecies" is fuzzy even today, and they were commonly considered synonyms at the time (Stuessy & al., 2014). In any case, invasives pose an interesting case for contemporary taxonomy and, so far, we had not documented or even envisaged a situation in which one known ancestral species would speciate into several derived allopatric species as a result of human introductions and rapid evolution. Taxonomically, there could be more than one valid approach to deal with this novel situation:

(1) Naming invasive neo-species as subspecies. This fits nicely with the intuition of many taxonomists, as it recognises well the common ancestor, and allows to include as many subspecies as necessary. We should be already able to define some neo-subspecies based on these criteria. However, if reproductive isolation is significant among the neo-species, making them subspecies would not be an option as, at least for plants, subspecies are usually fully inter-breedable, and only rarely present mild reproductive isolation among them. Contrarily, incomplete reproductive barriers among species of a given genus are common. Given current levels of phenotypic and genotypic differentiation, and even some rare cases of incipient reproductive isolation, we could certainly coin some invasive neo-subspecies already.

(2) Naming neo-species as new species within the genus of the ancestral species (see Table 1). The advantage of this approach is that this would fit the tried-and-true current naming system, and it is unlikely to raise controversy. The disadvantage is that it will not acknowledge the close proximity of the neo-taxa with the ancestral species from which we know it originates. If more than one neo-species stems from the same ancestral species, it risks resulting in a cluster of very similar species with a taxonomical relatedness that is not proportional to the relative taxonomic distance of other species within the same genus. This might result in a genus that contains species with markedly different phenotypic, genotypic, and phylogenetic distances, opening the door to the creation of new subgenus, or even new genus, which could put more strain on the coherence of higher taxonomical levels. Either way, this might not be an exclusive issue of invasive species, but the options and solutions resulting from this debate might also benefit other similarly unique taxonomical conundrums involving young species (e.g., young selfing apomictic lineages, ecological speciation).

(3) Alternatively, we could use an approach similar to that used for subspecies, but acknowledging the uniqueness of these neo-species, which for all other regards would be considered at the same taxonomical level of species since, functionally, they will present similar levels of phenotypic, genotypic, and reproductive differentiation to any other species (see Table 2). This could be done by using "neo" instead of "subsp." in the naming system. Following the example above: "G. biloba neo americana", "G. biloba neo australis", etc. This approach has the advantage of clearly acknowledging the common ancestor of all neo-species, while recognising their distinct idiosyncrasy. Being the most different from the current naming system, it could perhaps be also the more informative, useful, and easy to adopt.

**Table 1.** Decision table based on the presence of reproductive barriers and phenotypic differentiation using the current nomenclature.

| | | Substantial reproductive isolation | |
|---|---|---|---|
| | | Yes | No |
| Substantial phenotypic differentiation | Yes | New species within genus | New subspecies (subsp.) |
| | No | New species within genus | No changes |

It is obvious that this latter approach also introduces some awkwardness. Biologically, ecologically, and functionally, neo-species should behave as distinct species in their natural communities due to substantial differentiation – including, at least under the biological species concept, some reproductive isolation protecting them against backcrosses or reintroductions. However, by recognising a closer relationship among them than among other congeneric species we create a taxonomic level that, in practice, puts these neo-species somewhere between species and subspecies. This should be a non-issue for several reasons. Firstly, it accurately represents the idiosyncrasy of invasive neo-species, solving the inadequacy of either of the other two categories. Secondly, the goal of this approach is precisely to keep fine-tuning our taxonomical procedures so that we strike the right balance between usability and phylogenetic accuracy. Like in many other complex choices in life, the imperfection inherent to each potential option should not prevent us from choosing the one that is less imperfect, since inaction is nearly always an imperfect choice itself.

## ■ CASE STUDIES

Yellow star-thistle (*Centaurea solstitialis* L.; Asteraceae) is a species native to the Mediterranean which has spread to North and South America and to Australia, where it is widely considered a problematic invader. The species has been found to present significant phenotypical divergence, which is putatively adaptive. Genetic analyses show markedly differentiated genetic signatures across its world distribution. It is also, for now, the only plant species for which significant levels of reproductive isolation between some native and non-native populations has been described (Montesinos & al., 2012b; Irimia & al., 2021). Current data should grant the coining of new taxa at least at the subspecies level. Given the combined data on trait and genetic divergence, and the levels of reproductive isolation detected via experimental crosses, I believe that, at the very least, the following subspecies could be coined: "*C. solstitialis* subsp. *eurasiatica*" (for populations from Europe, the Mediterranean, and Australia) showing smaller size, lower fertility, and heterosis when crossed with non-native populations (except Australia); "*C. solstitialis* subsp. *americana*" (for populations from the Americas, including the western U.S.A., Chile, and Argentina) presenting significantly larger size, larger spine size, higher fertility, higher growth rates, and important levels of reproductive isolation when backcrossed with individuals from Eurasia or Australia. Further subspecies might be considered if additional data allows to distinguish within each of the two large regions initially proposed, as there is some evidence of variation between populations (e.g.) west and east of the Andes (i.e., Chile and Argentina), or between North and South America.

The Italian wall lizard (*Podarcis sicula*; Reptilia) has been introduced from its native range in Italy and the North Adriatic coast to other Mediterranean areas, central Europe, and North America, where it has established as an alien invasive that can displace local native lizard species (Nevo & al., 1972). We have evidence of rapid adaptive processes in some of its introduced areas, including increased tolerance to freezing and supercooling activity of populations in non-native New York, something that native *P. sicula* cannot do without dying or experiencing severe injuries (Burke & al., 2002). The most striking example of rapid adaptation, though, comes from the Mediterranean itself, where five pairs of *P. sicula* were introduced to Pod Mrcaru island, where it had no previous presence, and where in the course of only 30 generations (36 years) the introduced lizards developed dramatic changes in their digestive system that had allowed them to shift from a primarily insectivore diet to a primarily herbivore one. These changes included larger jaws, an overall increase in body size, and the presence of cecal valves, which are common in other reptiles, but had never before been found on *P. sicula* (Herrel & al., 2008). Neither the populations of New York or Pod Mrcaru have been described as subspecies yet, but there is no reason why they could not. Given time and geographic isolation – something more likely for the New York populations than for the Pod Mrcaru ones – we can expect them to develop at least some level of reproductive isolation, or at least outbreeding depression, as hybrids with native genotypes should experience lower fitness on the cold of New York, or hunger, under the predominantly herbivore diet of Pod Mrcaru island.

Threespine stickleback fishes (*Gasterosteus aculeatus*; Gasterosteidae) are a key model group for the study of animal speciation. In Switzerland they are native to only a small number of freshwater habitats, from where they have colonised lakes across the country during the last 150 years, where they are considered invasive (Rösch & al., 2018). There is comprehensive evidence of genetic and adaptative divergence among several different "forms", each adapted to the different food sources available at the different habitats they occupy: from freshwater streams, lake surfaces, lake depths, and marine. Obvious morphological differences include loss of pelvic spines, pelvic girdle, differences in the number of armour plates, capacity to produce fatty acids, etc. Currently they are called "forms" within the so-called "*G. aculeatus* species complex". However, at least

**Table 2.** Decision table based on the presence of reproductive barriers and phenotypic differentiation using the term "neo".

| | | Substantial reproductive isolation | |
|---|---|---|---|
| | | Yes | No |
| Substantial phenotypic differentiation | Yes | New neo-species (neo) | New subspecies (subsp.) |
| | No | New neo-species (neo) | No changes |

some of these forms are reproductively isolated from each other (Hudson & al., 2021). For any native fish species, such marked genotypical, phenotypical, and reproductive differences would have resulted in the coining of different species. And yet, while evolutionary ecologists thoroughly describe these adaptive changes, taxonomists have to cope with imperfect nomenclatural means to properly classify these forms.

## ■ WHO CAN MAKE IT HAPPEN?

There is no single international organisation deciding on nomenclatural rules. For algae, plants and fungi, the International Association of Botanical and Mycological Societies (IABMS) and the International Mycological Association organize, respectively, the International Botanical Congress (IBC) and the International Mycological Congress, where changes to the *International Code of Nomenclature for algae, fungi, and plants* (*ICN*) (Turland & al., 2018) must be approved. For animals, the International Society of Zoological Sciences (ISZS) organises the International Congress of Zoology. Other groups of organisms might not have such a pressing need to consider neo-species, and for some organisms it might not make too much sense to worry about invasive neo-taxa (e.g., viruses). Regardless, they have similar procedures or events to approve the taxonomical changes necessary to accommodate invasive neo-species, need be.

Eventually, the scientific community will need to pragmatically embrace the solution most commonly adopted, and hopefully it would be a coherent solution across taxonomic groups. Prominently, between zoology and botany, perhaps the best outcome would be to adopt whichever change is decided by the first large group of taxonomists to adopt a coherent solution openly and explicitly. Whether the current "subsp." plus regular species system is adopted by inaction, or "neo" is proactively adopted, is still up for discussion. Potential arguments against the adoption of the term "neo" will likely overlap with discussions about what constitutes a species and a subspecies, and thus must be enriched by voices informing of their suitability to different taxonomic groups and individual cases. Regardless of what nomenclatural option ends up being adopted, I hope that this contribution can help to set the bases for a fruitful debate.

## ■ CONCLUDING REMARKS

For at least some invasive alien species we have enough evidence of incipient, but significant, levels of synchronous allopatric divergence at the phenotypic, genotypic, and reproductive levels. Given the predictable dynamics of divergent allopatric selection, there will clearly be a need to taxonomically recognise invasive neo-species at some point in the not-so-distant future. Candidate species would be those with non-native populations that are well-established, successful, and adapted to their local habitat. In some cases, the current taxonomical categories will be suitable to accommodate them (e.g., hybridisation), in some others, not so much (e.g., synchronous allopatric radiation). It would be for the common good to agree on a consensual position in advance, before the next discovery requires to rush a suboptimal taxonomical solution.

## ■ AUTHOR INFORMATION

DM, https://orcid.org/0000-0003-2893-0878

## ■ ACKNOWLEDGEMENT

Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

## ■ LITERATURE CITED

**Abbott, R.** 1992. Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends Ecol.* 7: 401–405. https://doi.org/10.1016/0169-5347(92)90020-C

**Aldhebiani, A.Y.** 2018. Species concept and speciation. *Saudi J. Biol. Sci.* 25: 437–440. https://doi.org/10.1016/j.sjbs.2017.04.013

**Atwater, D.Z., Ervine, C. & Barney, J.N.** 2018. Climatic niche shifts are common in introduced plants. *Nat. Ecol. Evol.* 2: 34–43. https://doi.org/10/cgx3

**Barker, B.S., Cocio, J.E., Anderson, S.R., Braasch, J.E., Cang, F.A., Gillette, H.D. & Dlugosch, K.M.** 2019. Potential limits to the benefits of admixture during biological invasion. *Molec. Ecol.* 28: 100–113. https://doi.org/10.1111/mec.14958

**Barton, N.H.** 2010. What role does natural selection play in speciation? *Philos. Trans., Ser. B* 365: 1825–1840. https://doi.org/10.1098/rstb.2010.0001

**Burke, R.L., Hussain, A.A., Storey, J.M. & Storey, K.B.** 2002. Freeze tolerance and supercooling ability in the Italian wall lizard, *Podarcis sicula*, introduced to Long Island, New York. *Copeia* 2002: 836–842. https://doi.org/10.1643/0045-8511(2002)002[0836:FTASAI]2.0.CO;2

**Callaway, R.M. & Maron, J.L.** 2006. What have exotic plant invasions taught us over the past 20 years? *Trends Ecol. Evol.* 21: 369–374. https://doi.org/10.1016/j.tree.2006.04.008

**Callaway, R.M. & Ridenour, W.M.** 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers Ecol. Environm.* 2: 436–443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

**Callaway, R.M., Montesinos, D., Williams, K. & Maron, J.L.** 2013. Native congeners provide biotic resistance to invasive *Potentilla* through soil biota. *Ecology* 94: 1223–1229. https://doi.org/10.1890/12-1875.1

**Chapman, D., Purse, B.V., Roy, H.E. & Bullock, J.M.** 2017. Global trade networks determine the distribution of invasive non-native species. *Global Ecol. Biogeogr.* 26: 907–917. https://doi.org/10.1111/geb.12599

**Colautti, R.I. & Lau, J.A.** 2015. Contemporary evolution during invasion: Evidence for differentiation, natural selection, and local adaptation. *Molec. Ecol.* 24: 1999–2017. https://doi.org/10.1111/mec.13162

**Colautti, R.I. & MacIsaac, H.I.** 2004. A neutral terminology to define "invasive" species. *Diversity & Distrib.* 10: 135–141. https://doi.org/10.1111/j.1366-9516.2004.00061.x

**Correia, M., Montesinos, D., French, K. & Rodríguez-Echeverría, S.** 2016. Evidence for enemy release and increased seed production and size for two invasive Australian acacias. *J. Ecol.* 104: 1391–1399. https://doi.org/10.1111/1365-2745.12612

**Darwin, C.R.** 1859. *On the origin of species by means of natural selection; or The preservation of favoured races in the struggle for life*. London: John Murray. https://doi.org/10.5962/bhl.title.82303

**De Queiroz, K.** 2005. Ernst Mayr and the modern concept of species. *Proc. Natl. Acad. Sci. U.S.A.* 102: 6600–6607. https://doi.org/10.1073/pnas.0502030102

**Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A. & Pyšek, P.** 2010. Socioeconomic legacy yields an invasion debt. *Proc. Natl. Acad. Sci. U.S.A.* 108: 203–207. https://doi.org/10.1073/pnas.1011728108

**Ferrero, V., Castro, S., Costa, J., Acuña, P., Navarro, L. & Loureiro, J.** 2013. Effect of invader removal: Pollinators stay but some native plants miss their new friend. *Biol. Invas.* 15: 2347–2358. https://doi.org/10.1007/s10530-013-0457-4

**Freudenstein, J.V., Broe, M.B., Folk, R.A. & Sinn, B.T.** 2017. Biodiversity and the species concept—Lineages are not enough. *Syst. Biol.* 66: 644–656. https://doi.org/10.1093/sysbio/syw098

**García, Y., Callaway, R.M., Diaconu, A. & Montesinos, D.** 2013. Invasive and non-invasive congeners show similar trait shifts between their same native and non-native ranges. *PLOS ONE* 8: e82281. https://doi.org/10.1371/journal.pone.0082281

**Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G.** 2005. Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. *Diversity & Distrib.* 11: 549–558. https://doi.org/10.1111/j.1366-9516.2005.00195.x

**Herrel, A., Huyghe, K., Vanhooydonck, B., Backeljau, T., Breugelmans, K., Grbac, I., Van Damme, R. & Irschick, D.J.** 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proc. Natl. Acad. Sci. U.S.A.* 105: 4792–4795. https://doi.org/10.1073/pnas.0711998105

**Hierro, J.L., Eren, Ö., Khetsuriani, L., Diaconu, A., Török, K., Montesinos, D., Andonian, K., Kikodze, D., Janoian, L., Villarreal, D., Estanga-Mollica, M.E. & Callaway, R.M.** 2009. Germination responses of an invasive species in native and non-native ranges. *Oikos* 118: 529–538. https://doi.org/10.1111/j.1600-0706.2009.17283.x

**Hierro, J.L., Eren, Ö., Montesinos, D., Andonian, K., Kethsuriani, L., Özcan, R., Diaconu, A., Török, K., Cavieres, L. & French, K.** 2020. Increments in weed seed size track global range expansion and contribute to colonization in a non-native region. *Biol. Invas.* 22: 969–982. https://doi.org/10.1007/s10530-019-02137-z

**Hudson, C.M., Lucek, K., Marques, D.A., Alexander, T.J., Moosmann, M., Spaak, P., Seehausen, O. & Matthews, B.** 2021. Threespine stickleback in Lake Constance: The ecology and genomic substrate of a recent invasion. *Frontiers Ecol. Evol.* 8: 611672. https://doi.org/10.3389/fevo.2020.611672

**Irimia, R.E., Lopes, S.M.M., Sotes, G., Cavieres, L.A., Eren, Ö., Lortie, C.J., French, K., Hierro, J.L., Rosche, C., Callaway, R.M., Pinho e Melo, T.M.V.D. & Montesinos, D.** 2019. Biogeographic differences in the allelopathy of leaf surface extracts of an invasive weed. *Biol. Invas.* 21: 3151–3168. https://doi.org/10.1007/s10530-019-02038-1

**Irimia, R.E., Hierro, J.L., Branco, S., Sotes, G., Cavieres, L.A., Eren, Ö., Lortie, C.J., French, K., Callaway, R.M. & Montesinos, D.** 2021. Experimental admixture among geographically disjunct populations of an invasive plant yields a global mosaic of reproductive incompatibility and heterosis. *J. Ecol.* 109: 2152–2162. https://doi.org/10/gh6jtb

**Lankau, R.A.** 2012. Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proc. Natl. Acad. Sci. U.S.A.* 109: 11240–11245. https://doi.org/10.1073/pnas.1201343109

**Lankau, R.A., Nuzzo, V., Spyreas, G. & Davis, A.S.** 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. *Proc. Natl. Acad. Sci. U.S.A.* 106: 15362–15367. https://doi.org/10.1073/pnas.0905446106

**Levin, D.A.** 2003. Ecological speciation: Lessons from invasive species. *Syst. Bot.* 28: 643–650.

**Maron, J.L., Vilà, M., Bommarco, R., Elmendorf, S. & Beardsley, P.** 2004. Rapid evolution of an invasive plant. *Ecol. Monogr.* 74: 261–280. https://doi.org/10.1890/03-4027

**Mayr, E.** 1942. *Systematics and the origin of species*. New York: Columbia University Press.

**Montesinos, D. & Callaway, R.M.** 2017. Inter-regional hybrids of native and invasive *Centaurea solstitialis* display intermediate competitive ability. *Ecography* 40: 801–802. https://doi.org/10.1111/ecog.02653

**Montesinos, D., Castro, S. & Rodríguez-Echeverría, S.** 2012a. Invasive acacias experience higher ant seed removal rates at the invasion edges. *Web Ecol.* 12: 33–37. https://doi.org/10.5194/we-12-33-2012

**Montesinos, D., Santiago, G. & Callaway, R.M.** 2012b. Neo-allopatry and rapid reproductive isolation. *Amer. Naturalist* 180: 529–533. https://doi.org/10.1086/667585

**Montesinos, D., Castro, S. & Rodríguez-Echeverría, S.** 2016. Two invasive acacia species secure generalist pollinators in invaded communities. *Acta Oecol.* 74: 46–55. https://doi.org/10.1016/j.actao.2016.06.002

**Mounger, J., Ainouche, M.L., Bossdorf, O., Cavé-Radet, A., Li, B., Parepa, M., Salmon, A., Yang, J. & Richards, C.L.** 2021. Epigenetics and the success of invasive plants. *Philos. Trans., Ser. B* 376: 20200117. https://doi.org/10.1098/rstb.2020.0117

**Nevo, E., Gorman, G., Soulé, M., Yang, S.Y., Clover, R. & Jovanović, V.** 1972. Competitive exclusion between insular *Lacerta* species (Sauria, Lacertidae). *Oecologia* 10: 183–190. https://doi.org/10.1007/BF00347990

**Oduor, A.M.O., Leimu, R., Van Kleunen, M. & Mack, R.** 2016. Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *J. Ecol.* 104: 957–968. https://doi.org/10.1111/1365-2745.12578

**Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., Kleunen, M., Vilà, M., Wingfield, M.J. & Richardson, D.M.** 2020. Scientists' warning on invasive alien species. *Biol. Rev. (Cambridge)* 95: 1511–1534. https://doi.org/10.1111/brv.12627

**Rieseberg, L.H. & Blackman, B.K.** 2010. Speciation genes in plants. *Ann. Bot. (Oxford)* 106: 439–455. https://doi.org/10.1093/aob/mcq126

**Rieseberg, L.H. & Willis, J.H.** 2007. Plant speciation. *Science* 317: 910–914. https://doi.org/10.1126/science.1137729

**Rius, M. & Darling, J.A.** 2014. How important is intraspecific genetic admixture to the success of colonising populations? *Trends Ecol. Evol.* 29: 233–242. https://doi.org/10.1016/j.tree.2014.02.003

**Rösch, R., Baer, J. & Brinker, A.** 2018. Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. *Hydrobiologia* 824: 243–254. https://doi.org/10.1007/s10750-017-3479-6

**Schemske, D.W.** 2010. Adaptation and *The Origin of Species*. *Amer. Naturalist* 176: S4–S25. https://doi.org/10.1086/657060

**Stigall, A.L.** 2019. The invasion hierarchy: Ecological and evolutionary consequences of invasions in the fossil record. *Annual Rev.*

*Ecol. Evol. Syst.* 50: 355–380. https://doi.org/10.1146/annurev-ecolsys-110617-062638

**Stuessy, T.F., Crawford, D.J., Soltis, D.J. & Soltis, P.L.** 2014. *Plant systematics: The origin, interpretation and ordering of plant biodiversity.* Regnum Vegetabile 156. Königstein: Koeltz Scientific Books.

**Thomas, C.D.** 2013. The Anthropocene could raise biological diversity. *Nature* 502: 7. https://doi.org/10.1038/502007a

**Turbelin, A.J., Malamud, B.D. & Francis, R.A.** 2017. Mapping the global state of invasive alien species: Patterns of invasion and policy responses. *Global Ecol. Biogeogr.* 26: 78–92. https://doi.org/10.1111/geb.12517

**Turland, N., Wiersema, J., Barrie, F., Greuter, W., Hawksworth, D., Herendeen, P., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T., McNeill, J., Monro, A., Prado, J., Price, M. & Smith, G. (eds.)** 2018. *International Code of Nomenclature for algae, fungi, and plants*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

**Van Kleunen, M., Weber, E. & Fischer, M.** 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Letters* 13: 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

**Vellend, M., Harmon, L.J., Lockwood, J.L., Mayfield, M.M., Hughes, A.R., Wares, J.P., Sax, D.F. & Thomas, C.D.** 2007. Effects of exotic species on evolutionary diversification. *Trends Ecol. Evol.* 22: 481–488. https://doi.org/10.1016/j.tree.2007.02.017

**Vermeij, G.J.** 2005. One-way traffic in the Western Atlantic: Causes and consequences of Miocene to Early Pleistocene molluscan invasions in Florida and the Caribbean. *Paleobiology* 31: 624–642.

**Widmer, A., Lexer, C. & Cozzolino, S.** 2009. Evolution of reproductive isolation in plants. *Heredity* 102: 31–38. https://doi.org/10.1038/hdy.2008.69

**Wiley, E.O.** 1978. The evolutionary species concept reconsidered. *Syst. Biol.* 27: 17–26. https://doi.org/10.2307/2412809

**Wolf, J.B.W., Lindell, J. & Backström, N.** 2010. Speciation genetics: Current status and evolving approaches. *Philos. Trans.*, *Ser. B* 365: 1717–1733. https://doi.org/10.1098/rstb.2010.0023