Rapid acceleration of plant speciation during the Anthropocene

Chris D. Thomas

Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK

Speciation rates need to be considered when estimating human impacts on the numbers of species on Earth, given that past mass extinctions have been followed by the accelerated origination of new taxa. Here, I suggest that the Anthropocene is already exhibiting a greatly accelerated plant speciation rate due to agriculture, horticulture, and the human-mediated transport of species, followed by hybridisation. For example, more new plant species have come into existence in Europe over the past three centuries than have been documented as becoming extinct over the same period, even though most new hybrid-origin species are likely to remain undetected. Current speciation rates are unusually high and they could be higher than during or after previous mass extinctions.

Gains as well as losses

Considerable attention has been paid to the present-day Anthropocene extinction rate [1–3] but not to speciation, even though mass extinctions in the history of life have typically been followed by increased speciation rates [4–7]. Most speciation estimates are based on genetic divergence data from living species [1] and, thus, reflect 'background' speciation over many millions of years rather than present-day rates [8]. We need to quantify the current speciation rate if we wish to estimate the net effect of humans on the number of other species living on Earth, given that human actions can bring new species into existence as well as eliminate those that existed previously [8,9].

The human-assisted movement of plants, animals, and microbes around the world has increased hugely over recent centuries, breaking down geographic barriers between species that exhibit incomplete genetic barriers to reproduction and, hence, setting the scene for a massive increase in levels of hybridisation [8–12]. Subsequent genetic changes, including duplication of the entire genome (polyploidy) and chromosomal rearrangements, have, in one or a few generations, converted small numbers of these hybrid individuals or their offspring into sexually reproducing species that have limited compatibility with the parental species [9,12–16]. The new hybrids can be at least as genetically distinct (by virtue of genomes derived from two parental species) as congeneric species that have arisen through geographic separation over longer periods of time.

Corresponding author: Thomas, C.D. (chris.thomas@york.ac.uk).

Keywords: evolution; mass extinction; hybridisation; speciation; origination.

0169-5347/

 http://dx.doi.org/10.1016/j.tree.2015.05.009

That hybridisation is an important generator of diversity has long been recognised in the genetics, speciation, and plant biology literatures [9,12–16], but has failed to permeate the more ecologically oriented biodiversity literature, where hybridisation is normally seen as a process that eliminates 'native' genotypes and generates invasive forms that may reduce species-level biodiversity (both of which can be true). Here, I consider the role of humans in bringing new species into existence. I concentrate on hybridisation because of the speed with which this process can generate new species, while recognising that speciation through ecological separation can also be rapid ([17,18]; see [9] for a wider framework). In addition, I focus on new species as opposed to other levels of genetic variation because researchers use species as the primary currency to estimate biodiversity losses, and species often represent the focus of conservation efforts. I suggest that the plant speciation rate has accelerated during the Anthropocene and it is possible that the current rate is higher than at any other time since terrestrial plants evolved (Box 1).

The species we want

Humans are responsible for the formation and maintenance of new hybrid crops: at least two new hybrid wheat species (*Triticum aestivum* and *Triticum zhukovskyi*) ultimately derive their genomes from wild grasses [19], the peanut *Arachis hypogaea* represents a cultivated hybrid species containing full sets of the chromosomes of both *Arachis duranensis* and *Arachis ipaensis* [20], and three new hybrid *Brassica* species (rapeseed, Indian mustard, and Ethiopian mustard) obtained their genomes as a result of hybridisation between cultivated plants of three previously wild brassicas [21]. Many additional interspecific hybrids are cultivated, but most of these new forms are propagated clonally and do not merit full species status (Box 2). Scanning the approximately 95 plant species that produce the 40 most important crop products listed by value by the Food and Agriculture Organisation of the United Nations (http://faostat3.fao.org/; excluding 'beans', for which the number of contributing species is unclear), reveals approximately six to eight new species. This puts us in the ballpark of a speciation rate of 10–20 speciation events per Million Species Years (MSY; the number of new speciation events expected if one species lives for a million years, or a million species live for 1 year; calculated assuming that the average duration that these 95 plant species have been grown is 5000 years). This is exceptionally high (see below).

Box 1. Hypothesis that plant speciation has accelerated during the Anthropocene

The rate of speciation is high and has accelerated during the Anthropocene

- Recent plant speciation rates appear to be unusually high in agriculture and in naturalised plant populations (and potentially in horticulture).
- Most new species will not have been detected because they have only just arisen, remain cryptic, are highly localised, or have already become extinct again.
- The Anthropocene plant speciation rate could be orders of magnitude higher than the background rate of speciation.

Humans are causing the increase in the speciation rate

- Most new species that have been recognised have hybrid origins, where at least one of the parent species has been transported around the world by humans.
- Many of the new forms are arising and establishing in human-created habitats.
- Most new agricultural and horticultural plant species are obligate mutualists of humans and many of the new species that have naturalised are facultative mutualists.
- Humans are in some cases responsible for maintaining the genetic integrity of new species and, hence, humans represent an important new agent of ecological speciation.

The current speciation rate may be higher than at any time since plants colonised the land

- The recent rate of transport of species around the world is unprecedented and, hence, the current rate of hybrid speciation of flowering plants could be generating the highest speciation rate ever.

Most new species only survive for a short period, with a few surviving 'indefinitely'

- Most of the new (hybrid) taxa are 'point origin species', arising at one or a few specific locations. Point origin species face a high initial probability of extinction associated with small population sizes and mismatches between the location of origin and places where demographic growth is possible.
- New species that are mutualists or commensals of humans may thrive but disappear again if human behaviours change (e.g., altered land management, or food preferences change, or they are replaced by more productive crops).

The recent plant speciation rate could be comparable to the Anthropocene extinction rate

- Critical comparisons of Anthropocene extinction and speciation rates are required. The data available suggest that the recent plant speciation rate exceeds the extinction rate.
- Speciation rates are sufficiently high that they cannot be ignored when estimating the impacts of humans on global and regional numbers of species.

Additional species have arisen within horticulture, but there is remarkably little information on how many. *Primula kewensis* was formed in Kew Gardens in London between 1898 and 1905 as a result of hybridisation between two other (previously geographically separate) *Primula* species, followed by chromosome duplication (Table 1). Biologically, it is a 'good' species, but it only exists in cultivation. Naturalised hybrids may also be heading in the direction of becoming distinct species: *Rhododendron x superponticum* arose in Britain through hybridisation between garden *Rhododendron ponticum* from the Mediterranean and *Rhododendron catawbiense* and *Rhododendron maximum* from North America [22]. It has since become a widespread member of the British flora and is genetically and ecologically

Box 2. Criteria used to recognise new species

Most ecologists and evolutionary biologists find the species concept useful to define separate groups of multicellular animals and plants, although there is now widespread recognition that the genetic boundaries between different species may not be complete. Speciation through hybridisation would not exist without this incomplete separation. In this article, I took the view that a new species could be recognised if:

- Genetic research had been undertaken to demonstrate restricted or no gene flow (potential or realised) of the new species with related ancestral forms. New species were recognised if they were expected to sustain their genetic identities despite some continued gene flow (as in many existing plant species);
- Evolutionary biologists, systematists, and plant taxonomists who were consulted, and scientific articles, agreed that the new forms could be regarded as species (i.e., they were as 'good' as many longer-standing plant species that might, for example, be placed on lists of endangered species);
- At least some seed production takes place and involves meiosis (there is potential for gene transfer between individuals, even if selfing is more common); and
- The taxon remains the same 'species' once a new zygote is formed (i.e., completely clonal forms and microspecies whose apomictic seeds are genetic copies of the parent were excluded. I treat these forms as clonal individuals rather than full species)

Any comparisons of speciation and extinction rates should ensure that the same definitions of species are used for both.

distinct, and geographically separated from its parental species.

The majority of these novel plants only exist in heavily modified environments (e.g., gardens or arable fields), and they engage humans to reduce competition (e.g., via tillage, weeding, selective herbicides, or fertiliser addition), evade natural enemies (e.g., via insecticides or fungicides) and disperse their seeds (e.g., via harvesting or sowing). They represent a set of species and other genetically distinct forms that have become mutualists of humans within the past approximately 12 000 years, or 300 years in the case of most horticultural plants. I call on plant geneticists to estimate speciation rates among the approximately 7000 crop plants and 28 000 other plant species that are in cultivation (approximately 14% of all plants) [23]. Rates are likely to have increased during the Anthropocene, and are likely to increase further with the introduction of genetic technologies.

The species we get

New hybrid species have also arisen in naturalised and native floras but without deliberate intent, although still through human action. Examples include the origination in Washington and Idaho states in the USA of two or three new species of *Tragopogon* (*Tragopogon mirus* is a hybrid formed in naturalised populations of the introduced European *Tragopogon dubius* and *Tragopogon porrifolius*; *Tragopogon miscellus* is one or two new species formed by hybridisation between naturalised *T. dubius* and *Tragopogon pratensis* [24]), of *Cardamine schulzii* in human-created habitats in Switzerland [25], and of sexual hybrids between introduced European *Hieracium* species in New Zealand [26], as well as several cases of recent hybrid speciation in animals [9,14,16]. In Great Britain (GB), where the land has been transformed by human activities, six or seven new sexually reproducing vascular plant