Tansley review

Senecio as a model system for integrating studies of genotype, phenotype and fitness

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Received: *19 July 2019*
Accepted: *17 December 2019*

Contents

New Phytologist (2020) **226:** 326–344
doi: 10.1111/nph.16434

Key words: adaptive radiation, Asteraceae, genomics, hybrid speciation, model system, quantitative genetics, self-incompatibility, *Senecio*.

Summary

Two major developments have made it possible to use examples of ecological radiations as model systems to understand evolution and ecology. First, the integration of quantitative genetics with ecological experiments allows detailed connections to be made between genotype, phenotype, and fitness in the field. Second, dramatic advances in molecular genetics have created new possibilities for integrating field and laboratory experiments with detailed genetic sequencing. Combining these approaches allows evolutionary biologists to better study the interplay between genotype, phenotype, and fitness to explore a wide range of evolutionary processes. Here, we present the genus *Senecio* (Asteraceae) as an excellent system to integrate these developments, and to address fundamental questions in ecology and evolution. *Senecio* is one of the largest and most phenotypically diverse genera of flowering plants, containing species ranging from woody perennials to herbaceous annuals. These *Senecio* species exhibit many growth habits, life histories, and morphologies, and they occupy a multitude of environments. Common within the genus are species that have hybridized naturally, undergone polyploidization, and colonized diverse environments, often through rapid phenotypic divergence and adaptive radiation. These diverse experimental attributes make *Senecio* an attractive model system in which to address a broad range of questions in evolution and ecology.

I. Model systems for experimental ecology and evolution

Recent technological advances in genomic and computational technologies have allowed genetic analyses of many nonmodel organisms, providing important insights into genome evolution, the structure of developmental pathways, and the control of gene expression. However, to answer fundamental questions in ecology and evolutionary biology we need to develop model systems that integrate these novel genetic resources with experimentally flexible systems that are also ecologically diverse. Using ecologically divergent systems is critical for understanding how genotypes relate to phenotypes across different environments, and to test the processes driving adaptation, speciation, and biogeographical patterns. Nevertheless, many model systems used in evolutionary biology are only studied in laboratory settings because, despite possessing key experimental attributes (e.g. short life cycles, self-fertility), they show limited variation in life history, mating system, or habitat. The utility of such systems for detailed laboratory or glasshouse experiments therefore limits their value in field experiments testing hypotheses relating to evolution and ecology, such as the interaction between phenotypic plasticity and natural selection, and how and when populations specialize to particular environments. This limitation has become increasingly relevant given the urgent need to predict how, where, and how quickly populations and ecological communities will respond to ongoing environmental change. Research needs to focus on model systems with populations and species that inhabit different environments and ecosystems, but which remain amenable to large field experiments and quantitative genetic crossing designs. Specifically, we need model systems that can connect genotype, phenotype, and fitness under a range of environmental conditions. In this review, we argue that *Senecio* is one of very few model systems that can fill this role.

II. *Senecio* as an experimental model system

Senecio (Linnaeus, 1753) is a large genus of flowering plants within the tribe Senecioneae of the daisy family, Asteraceae. Containing in excess of 1200 species distributed across the globe, *Senecio* radiated rapidly during the Miocene *c.* 10.7 Ma to become one of the largest genera of flowering plants (Kandziora *et al.*, 2017). Species of *Senecio*, commonly known as ragworts and groundsels, are generally herbaceous, but also occur as vines, shrubs, succulents, epiphytes, and small trees (Fig. 1). The genus is aptly named after the tendency for species to produce senescent flower heads resembling tufts of white hair (Latin ‘senex’ = ‘old man’) formed by the pappus, which facilitate airborne seed dispersal.

Many species of *Senecio* have useful attributes of a model system, including small to medium-sized genomes (mean *c.* 5 Gbp; range 1.13–51.25 Gbp; Leitch *et al.*, 2019), a rapid sexual cycle (3–5 months from seed to seed), and ease of crossing because of widespread self-incompatibility (SI). Species are also often perennial or short-lived perennials, and so can be regenerated from cuttings to create genetically identical clones, are genetically transformable (Kim *et al.*, 2008), and are easily grown in glasshouses and field plots. The fact that many species show these attributes, combined with their recent radiation and occupation of a diverse array of habitats, makes *Senecio* species more amenable than many other systems for quantitative genetic designs. Such designs allow researchers to combine genetic and phenotypic studies in both the field and under controlled conditions. The genus *Mimulus* shares some of these experimental characteristics (e.g. short generation times, easy to grow, clonal propagation) and has a widespread distribution across different environments (Wu *et al.*, 2008), but *Senecio* has the added benefit of a world-wide distribution, and a greater diversity of species that include a range of mating systems and a multitude of growth forms (Fig. 1). Such diversity in morphology and habitat makes *Senecio* attractive to a similar diversity of scientists, from ecologists to phylogeneticists, molecular geneticists, and quantitative geneticists. We therefore propose *Senecio* as an attractive model system for answering fundamental questions in ecology and evolution, joining the ranks of *Antirrhinum*, *Arabidopsis* (including *Boechera* and other relatives), *Helianthus*, *Mimulus*, *Silene*, and *Solanum*.

1. What questions can we answer using *Senecio*?

Future work will benefit from the imminent completion of high coverage and highly contiguous annotated genomes for *Senecio squalidus* and *Senecio lautus* (B. Nevado *et al.*, unpublished; Wilkinson *et al.*, 2019). These will be used as references for further genomic analyses of other *Senecio* species, including whole-genome resequencing, DNA methylation, and RNA sequencing (RNA-seq) approaches. These new resources will make *Senecio* a powerful system to study the genomic architecture of selection, adaptation, and divergence across environments. Combining such genetic association techniques with quantitative genetic crossing designs is a powerful way to explore how the relationship between genotype, phenotype, and fitness changes across environments. Of special importance is the ease and speed at which species of *Senecio* can be propagated from cuttings. This ability to generate clones allows researchers to control for genotype and transplant large numbers of clones across multiple environments, setting *Senecio* apart from other model systems. Such approaches can address an array of questions in ecology, evolution, and evolutionary genomics (see Box 1).

2. Origins and diversity of *Senecio*

The presence of repeated radiations in the Americas, Australasia, and across northern Africa into Europe highlights the ability of *Senecio* to colonize and rapidly adapt to multiple environments (Comes & Abbott, 2001; Roda *et al.*, 2013b; Liew *et al.*, 2018). This broad geographical distribution is reflected in species' occupation of contrasting environments, from harsh coastlines to rainforests, deserts, mountains, and alpine areas. Associated with this diversity of habitats is an array of different phenotypes (Fig. 1) typified by the Australian *S. lautus* species complex, which provides a fascinating example where recent radiation into more than 10 contrasting environments across much of the continent has resulted in the evolution of ecotypes with a broad diversity of plant architecture and leaf form (Fig. 2). Among the numerous recorded radiations within *Senecio* there is evidence of local adaptation (Walter *et al.*, 2016), parallel evolution (Roda *et al.*, 2013b; Comes *et al.*, 1997, 2017), polyploidy (Alexander, 1979; Chapman & Abbott, 2010), introgressive hybridization (Kim *et al.*, 2008; Osborne *et al.*, 2016), hybrid speciation (James & Abbott, 2005; Hegarty *et al.*, 2012), and apparently stable hybrid zones (Brennan *et al.*, 2009; Abbott *et al.*, 2018).

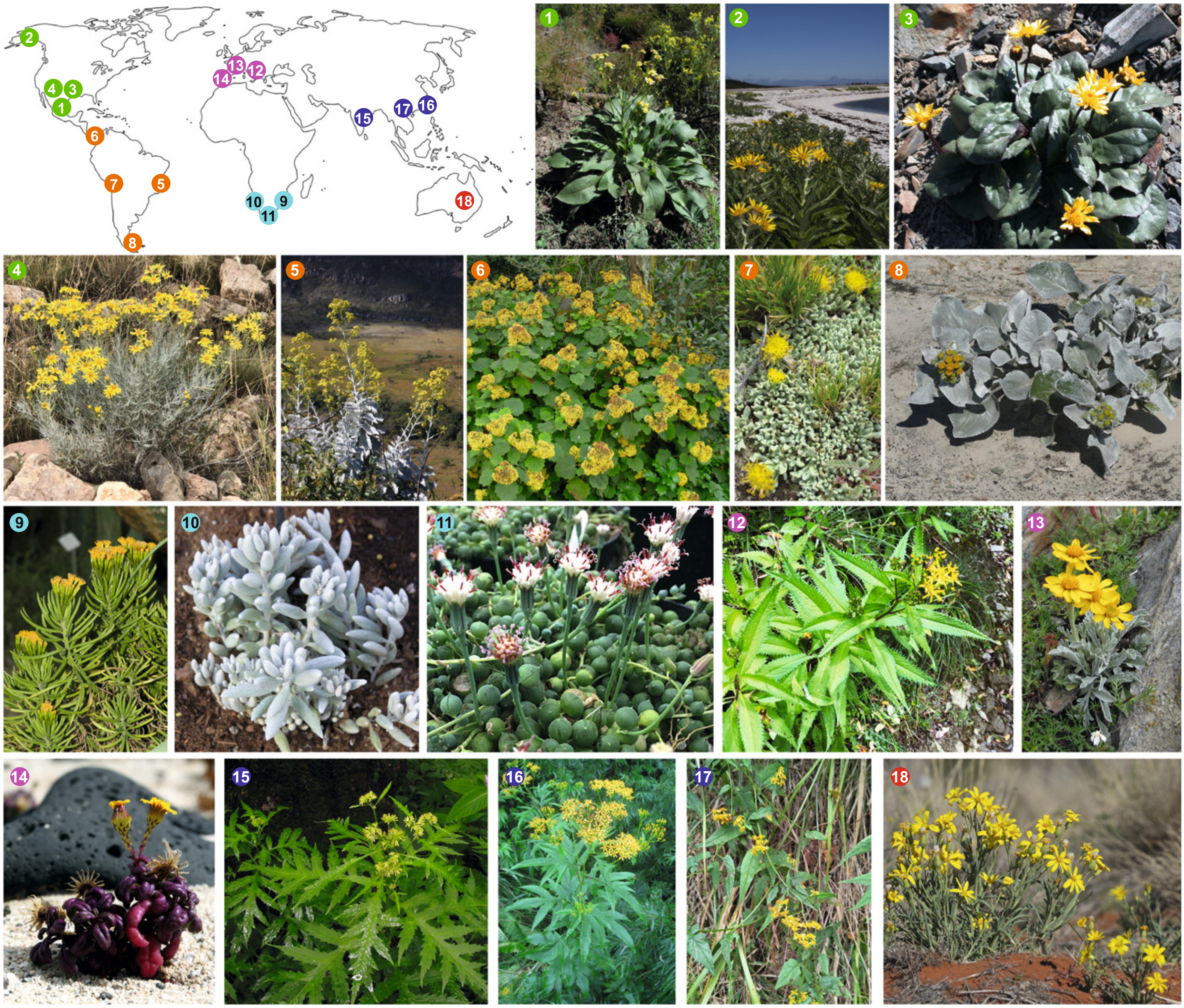

Fig. 1 With a world-wide distribution, species of *Senecio* show dramatic diversity in morphology and the habitats they occupy. Images are protected by copyright; this information is provided in parentheses and Supporting Information Notes S1. (1) *Senecio wootonii* (CC BY-NC-SA 3.0 W. Anderson); (2) *Senecio pseudoarnica* (CC BY-NC 2.0 K. McFarland); (3) *Senecio soldanella* (CC BY-NC 3.0 M.E. Harte); (4) *Senecio flaccidus* (CC BY C.K. Kelly); (5) *Senecio claussenii* (CC BY N. Taylor & D. Zappi); (6) *Senecio petasitis* (© J. Moura); (7) *Senecio moqueguensis* (CC BY D.B. Montesinos-Tubée); (8) *Senecio candidans* (CC BY S.J. Tonge); (9) *Senecio barbertonicus* (CC BY-SA O. Leillinger); (10) *Senecio haworthii* (CC BY D. Avery); (11) *Senecio rowleyanus* (© Surreal Succulents, UK); (12) *Senecio nemorensis* (CC BY-NC C.T. Lin); (13) *Senecio halleri* (© I. Rey); (14) *Senecio leucanthemifolius* (CC BY-SA Petr Brož); (15) *Senecio graciliflorus* (CC BY Prashant Awale); (16) *Senecio cannabifolius* (CC BY Wikimedia); (17) *Senecio scandens* (CC BY-NC S. Duan); (18) *Senecio gregorii* (© P. Campbell).

3. Historical use of *Senecio* for research

With its wealth of morphological, ecological, and reproductive diversity, *Senecio* has attracted studies addressing many different questions in ecology and evolution. Experimental research using *Senecio* began in the late 19th century (Table 1) when Anna Bateson, sister of the geneticist, William Bateson, showed that progeny generated by crossing *Senecio vulgaris* plants were taller and produced more seed per capitulum than those generated by self-fertilization, suggesting an heterotic effect (Bateson, 1888). Because *S. vulgaris* has a short generation time and is self-compatible (SC) but easy to cross, Trow recognized its value for genetic research and used it to establish the genetic basis of several discontinuous and semi-continuous traits within the species in the early 20th century (Trow, 1912, 1916a,b). Approximately 40 yr then passed before Harland emphasized the value of *Senecio* in both genetic and evolutionary research by using interspecific crosses to show that *Senecio cambrensis* was the recent allohexaploid of *S. vulgaris* and *S. squalidus* (Harland, 1954a,b). Through this early work, Bateson, Trow and Harland laid the foundation for more extensive works that followed (Table 1).

Box 1 Future research using *Senecio* as a model system

In this box we detail research directions we consider likely to be particularly productive using *Senecio* as a model system.

(1) **Responses to climate change**. Owing to its widespread distribution and occupation of numerous habitats, *Senecio* allows the response of populations and communities to climate change to be tested across a range of biotic and abiotic interactions. Such tests could include: (a) responses in ecologically similar but phylogenetically different *Senecio* (e.g. across Mediterranean or Alpine habitats in Europe, Africa, and Australasia); (b) comparisons of ecologically different but phylogenetically similar species (e.g. Alpine species can be compared with closely related taxa at lower elevations, as on Mount Etna); (c) field transplants across elevational gradients to simulate future climate scenarios. These transplants can also assess how transitions in plant, mycorrhizal, microbial, and insect communities across elevational gradients interact with changes in the fitness and phenotypes of different *Senecio* species.

(2) **Factors determining patterns of adaptive radiation**. Adaptive radiation appears rapid and common in *Senecio*. A major challenge is to identify the factors that have driven adaptive diversification, leading to its broad distribution across environments and geography. Potential approaches could be: (a) Bringing phylogenetic and morphological data together to test whether innovation in key traits created species radiations in the Asteraceae. This could include traits associated with long-distance dispersal (i.e. the pappus), variation in leaf morphology, or the production of toxic alkaloids that deter herbivores. (b) Studying the genetics and evolution of barriers to gene flow in *Senecio* using examples of ecotypic divergence, recent hybrid speciation, and stable hybrid zones. (c) Using the many self-incompatible and self-compatible species of *Senecio* to study the evolution of diverse mating systems, especially within a broad phylogenetic context. (d) Using the repeated examples of morphological convergence and divergence in *Senecio* to test for genomic convergence in the evolution of complex traits within a single plant genus; for example, the evolution of growth habit in ecotypes of *Senecio lautus* could be expanded by studying how dramatic variation in growth habit has evolved in varied, but closely related, *Senecio* species.

(3) **Ecological and evolutionary importance of phenotypic plasticity.** Many species of *Senecio* show considerable variation in phenotypic plasticity in response to environmental heterogeneity (e.g. in *Senecio vulgaris*) and can be used in experiments to determine the relative importance of phenotypic plasticity versus adaptation in responding to such heterogeneity. The utility of *Senecio* in glasshouse and field experiments, especially when combined with quantitative genetic breeding designs, makes it possible to combine large experimental studies with emerging genetic approaches: (a) Using genetic transformation based on existing *Agrobacterium*-mediated methods or the development of CRISPR/Cas9 gene editing, it will be possible to conduct functional analyses of genes associated with specific traits, as well as characterize the function of loci identified through field and omics studies. (b) Transplanting a breeding design across environmental variation allows us to study changes in relative fitness, which can then be related to transcriptomic data to identify how differential gene expression contributes to fitness variation. Quantitative PCR could then be used to study the specific regions of the genome underlying differential expression, and the role of small RNAs (small interfering RNA and microRNA) in determining patterns of differential expression to identify the regulatory basis of local adaptation and phenotypic plasticity.

(4) **Developmental genetics of trait adaptations.** The diverse array of traits and habitats of *Senecio* species provides a rich resource for understanding the developmental and genetic pathways of many traits; for example, leaf shape variation. Studying the ecological variation underlying already identified pathways could complement work on *Arabidopsis* and relatives.

(5) **Life history evolution.** With a diverse array of life history strategies in closely related species, *Senecio* can be used to study the ecological genetics of developmental plasticity and the evolution of life history and resource allocation trade-offs, particularly where some species have overlapping generations and others do not. For example, *Senecio* species with diverse growth habits could be used to study transgenerational effects on adaptive phenotypes and how the nature of such transgenerational effects is shaped by environmental predictability and variability.

(6) **The ecology and evolution of invasive species.** Notable examples of invasive species within *Senecio* are prime models for detailed analysis, especially where they are invading habitat already dominated by other *Senecio*: (a) In Australia, *Senecio madagascariensis* is colonizing ecosystems occupied by a closely related native *Senecio* species. (b) In the UK, the recently formed hybrid species *Senecio squalidus* has colonized much of the British Isles in the last 200 yr, providing an important model system to study how invasive species form, spread, and adapt rapidly to their new geographic range. (c) South African *Senecio inaequidens* has spread rapidly across Europe, the Americas, and Australia and shows differences in chromosome number across its range, allowing detailed investigation of how ploidy level correlates with invasiveness.

(7) **Ecological and evolutionary importance of hybridization.** *Senecio* contains many species that have been formed by recent hybridization, with associated effects on chromosome number, genome size, and gene regulation. These include multiple examples of homoploid hybrid and allopolyploid species and provide excellent opportunities to test how introgression changes the architecture of genetic variation across geography and promotes hybrid speciation.

(8) **How biotic and abiotic factors shape the distribution of widespread versus more specialized species.** In *S. lautus*, populations of ecotypes often exhibit very narrow distributions despite a wide distribution of their habitat, allowing studies to investigate what determines the distribution of populations, and their fundamental versus realized niches. For example, to test how abiotic stress tolerances and biotic interactions together determine range limits, and whether this changes across habitats.

III. Mating system diversity and evolution in *Senecio*

1. Outcrossing and self-incompatibility

As a member of the Asteraceae, *Senecio* inflorescences are capitula ('flower heads'), comprising multiple uni-ovulate flowers (florets) tightly gathered across a disc-shaped receptacle. Florets are frequently differentiated into two types dependent on their position within the capitulum ('disc'). Centrally located disc florets are usually radially symmetrical, whereas outermost ray florets are bilaterally symmetrical with petals fused into a single large 'ray' (Abbott & Schmitt, 1985; Gillies *et al.*, 2002; Kim *et al.*, 2008; Garcês *et al.*, 2016), which facilitates outcrossing by attracting generalist insect pollinators (Abbott & Irwin, 1988; Andersson & Widén, 1993).

The genetic control of flower development has been studied in *S. vulgaris* (ssp. *vulgaris*), which is mostly rayless throughout its range but has a rayed variant in the UK (*S. vulgaris* var. *hibernicus*) that originated via introgressive hybridization with *S. squalidus* (Abbott *et al.*, 1992; Kim *et al.*, 2008). The emergence of a rayed

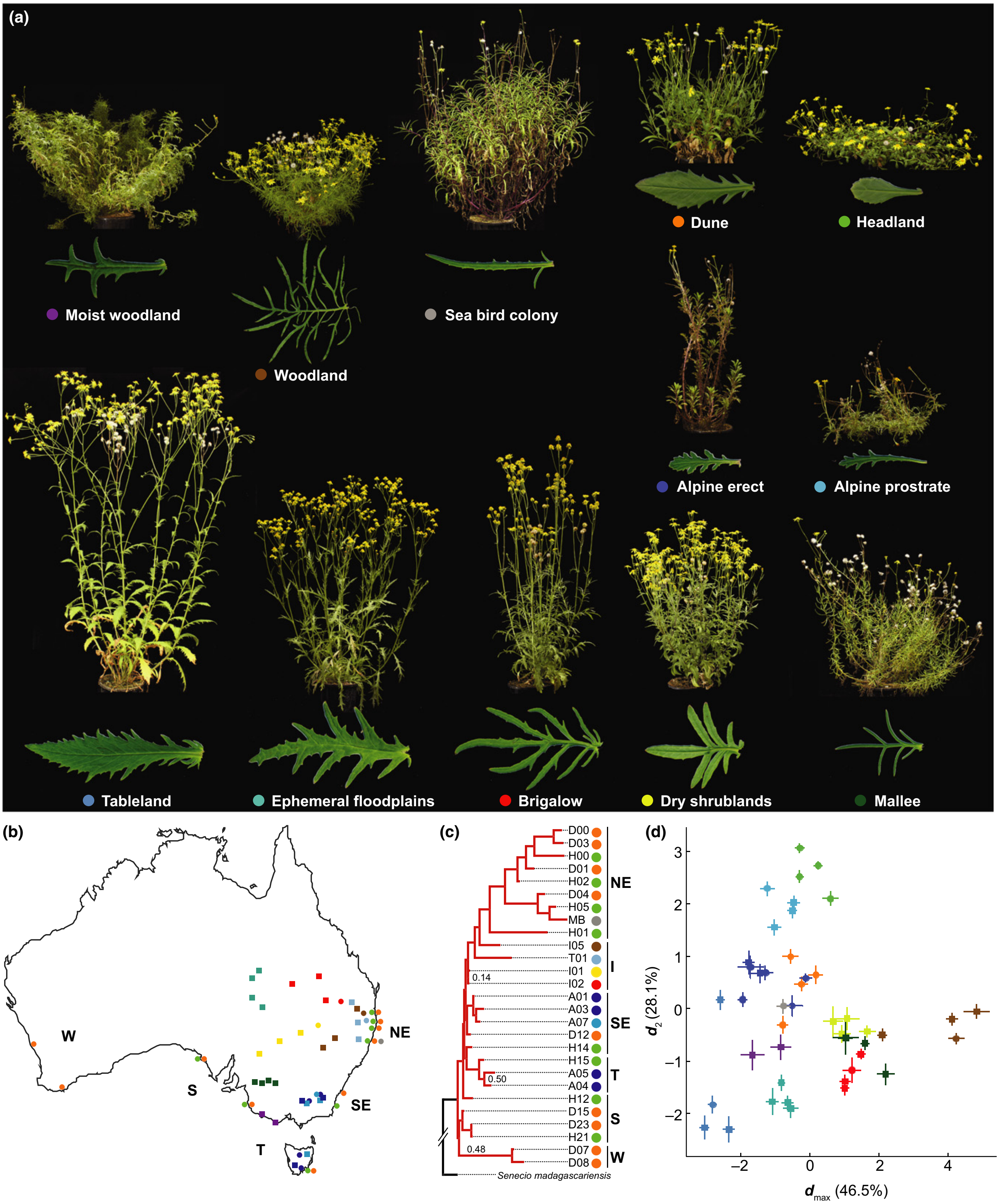

Fig. 2 Australian *Senecio lautus* complex contains 12 ecotypes that have diverged rapidly from each other. (a) Ecotypes vary dramatically in leaf morphology and growth form, reflecting the diversity of habitats they occupy. (b, c) Ecotypes are distributed widely across Australia. Clades (represented by uppercase letters) group by geography, rather than ecology. (b, c) Reproduced from Roda *et al.* (2013b), with permission. (d) Morphological divergence of the ecotypes. Points and confidence intervals represent the mean and one standard error for each population measured. Colours represent ecotypes from (c). See Supporting Information Notes S2 for details of the data analysis.

Table 1 Use of *Senecio* in genetic, evolutionary, systematic and ecological research.

Topic	Taxa	References
Genetics, cytology, development		
Heterosis	*S. vulgaris*	Bateson (1888)
Genetics of traits	*S. vulgaris* *S. lautus*	Trow (1912, 1916a,b); Skinner (1952); Basford (1961a,b); Comes (1998); Brennan *et al.* (2016)
	S. squalidus	Roda *et al.* (2017)
		Ingram & Taylor (1982); Hiscock (2000a); Hiscock *et al.* (2003); Tabah *et al.* (2004); McInnis *et al.* (2005)
Genome size variation	Diverse *Senecio*	Ornduff *et al.* (1963); Lawrence (1980, 1985); Lafuma & Maurice (2007); Lopez *et al.* (2013)
Maternal effects	*S. vulgaris*	Aarssen & Burton (1990)
Heteroplasmy	*S. vulgaris*	Frey (1998); Frey *et al.* (2005)
Evolution		
Hybridization and introgression	*S. vulgaris* × *S. squalidus* *S. vulgaris* × *S. viscosus*	Harland (1954a); Ingram (1977, 1978); Ingram *et al.* (1980); Marshall & Abbott (1980); Abbott *et al.* (1992); Kim *et al.* (2008); Lowe & Abbott (2015)
	S. viscosus × *S. squalidus*	Gibbs (1971)
	S. vulgaris × *S. vernalis*	Crisp & Jones (1978)
	S. pinnatifolius × *S. madagascariensis*	Comes & Kadereit (1990); Comes (1994a)
		Prentis *et al.* (2007)
Hybrid speciation – Allopolyploidy	*S. cambrensis* *S. mohavensis* *S. hoggariensis*	Harland (1954b); Rosser (1955); Weir & Ingram (1980); Ingram & Noltie (1984, 1986, 1987, 1995); Ashton & Abbott (1992); Lowe & Abbott (1996); Abbott & Forbes (2002); Hegarty *et al.* (2006, 2008, 2011, 2012)
		Coleman *et al.* (2001); Kadereit *et al.* (2006); Alexander-Webber *et al.* (2016)
		Kadereit *et al.* (2006)
Hybrid speciation – Homoploidy	*S. eboracensis*	Irwin & Abbott (1992); Lowe & Abbott (2000, 2003, 2004)
	S. squalidus	James & Abbott (2005); Brennan *et al.* (2012, 2019); Hegarty *et al.* (2009)
Hybrid zone structure and maintenance	*S. aethnensis* × *S. chysanthemifolius*	James & Abbott (2005); Chapman *et al.* (2005); Brennan *et al.* (2009); Ross *et al.* (2012)
	S. vernalis × *S. glaucus*	Abbott *et al.* (2018)
	S. hercynicus × *S. ovatus*	Raudnitscka *et al.* (2007); Bog *et al.* (2017a)
Floral polymorphism	*S. vulgaris*	Richards (1975); Oxford & Andrews (1977); Marshall & Abbott (1982, 1984a,b, 1987); Abbott (1985, 1986); Ross & Abbott (1987); Abbott & Irwin (1988); Oxford *et al.* (1996); Abbott *et al.* (1998); Kim *et al.* (2008); Garcês *et al.* (2016)
Breeding/Mating system variation	Diverse *Senecio*	Gibbs *et al.* (1975)
	S. vulgaris *S. vernalis* *S. squalidus*	Haskell (1953); Hull (1974); Campbell & Abbott (1976); Marshall & Abbott (1982, 1984a, b, 1987); Ross & Abbott (1987); Warren (1988); Damgaard & Abbott (1995); Irwin *et al.* (2016); Love *et al.* (2016); Comes (1994b)
	S. inaequidens *S. cambrensis*	Abbott & Forbes (1993); Hiscock (2000a,b); Hiscock *et al.* (2003); Brennan *et al.* (2002, 2003a,b, 2005, 2006); Tabah *et al.* (2004); McInnis *et al.* (2006); Allen *et al.* (2010, 2011)
		Lafuma & Maurice (2007)
		Brennan & Hiscock (2010)
Ecotypic divergence and speciation	*S. vulgaris* *S. sylvaticus*	Crawford (1966); Abbott (1976a,b); Briggs (1976, 1978); Ren & Abbott (1991); Theaker & Briggs (1993); Müller-Schärer & Fischer (2001)
	S. viscosus	Kumler (1969)
	S. lautus	Akeroyd *et al.* (1978)
	S. squalidus	Radford & Cousens (2004); Melo *et al.* (2014); Richards *et al.* (2016, 2019); Richards & Ortiz-Barrientos (2016); Walter *et al.* (2016, 2018a,b, 2019)
		Allan & Pannell (2009)
	S. aethnensis – *S. chrysanthemifolius*	Chapman *et al.* (2013); Muir *et al.* (2013); Osborne *et al.* (2013); Brennan *et al.* (2014, 2016)
Parallel divergence and speciation	*S. lautus* complex	Roda *et al.* (2013a,b, 2017)
	Mediterranean *Senecio*	Comes *et al.* (2017)
Herbicide resistance	*S. vulgaris*	Ryan (1970); Holliday & Putwain (1977); Scott & Putwain (1981); Holt (1988)
Systematics		
Biosystematics	European and African *Senecio*	Crisp (1972); Alexander (1979); Kadereit (1984a,b); Gilmer & Kadereit (1989); Emig & Kadereit (1993); Comes (1995a); Hodálová & Marhold (1996)
Molecular systematics	British *Senecio*	Harris & Ingram (1992a,b)
Phylogeography and speciation	European & African *Senecio*	Kadereit *et al.* (1995); Comes (1995); Comes *et al.* (1997); Comes & Abbott (1998, 1999, 2000, 2001); Purps & Kadereit (1998); Coleman & Abbott (2003); Chapman & Abbott (2005)

Table 1 (Continued).

Topic	Taxa	References
Phylogeny	Representatives of genus	Pelser *et al.* (2002, 2007, 2010, 2012); Coleman *et al.* (2003); Calvo *et al.* (2013); Osborne *et al.* (2016); Kandziora *et al.* (2016a,b)
	South American *Senecio*	Montesinos-Tubée (2014); Dušková *et al.* (2017)
	Australasian *Senecio*	Liew *et al.* (2018)
Ecology		
Plant invasions	*S. squalidus*	Kent (1956, 1960); Harris (2002); Abbott *et al.* (2009); Allan & Pannell (2009)
	S. vernalis	Kadereit (1983)
	S. inaequidens	Ernst (1998); Lafuma *et al.* (2003); Heger & Böhmer (2005); Bossdorf *et al.* (2008); Monty & Mahy (2009)
	S. madagascariensis	Scott *et al.* (1998); Kinoshita *et al.* (1999); López-García & Maillet (2005); Le Roux *et al.* (2006, 2010); Prentis *et al.* (2007); Dormontt *et al.* (2014)
	S. pterophorus	Scott & Delfosse (1992); Pino *et al.* (2000); Caño *et al.* (2008)
	S. vulgaris	Zhu *et al.* (2017)
Physiological variation	*Senecio* species adapted to dry and wet habitats	Crawford (1966)
Life history	*S. sylvaticus, S. viscosus*	Palmblad (1968)
	S. vulgaris	Harper & Ogden (1970); Popay & Roberts (1970a,b); Kadereit (1984c); Abbott (1986); Fenner (1986a,b); Ren & Abbott (1991); Leiss & Müller-Schärer (2001)
	S. vernalis	Comes (1995)
	S. lautus	Walter *et al.* (2018b)
Chemical defence by pyrrolzidine alkaloids	*S. vulgaris*	Aplin *et al.* (1968); Hartmann *et al.* (1989); Frischknecht *et al.* (2001); Cheng *et al.* (2017)
	S. vulgaris, S. vernalis	Hartmann & Zimmer (1986)
	S. pterophorus	Castells *et al.* (2014)
	S. nemorensis complex	Bog *et al.* (2017b)
	Diverse *Senecio*	Langel *et al.* (2011)
Disease susceptibility to:	*S. vulgaris*	Ben-Kalio & Clarke (1979); Harry & Clarke (1986)
- *Erysiphe fischeri*	*S. vulgaris*	Paul & Ayres (1984)
- *Puccinia lagenophorae*	Diverse *Senecio*	Alber *et al.* (1986)
- *Puccinia expansa*		
Plant-pollinator interactions	Diverse *Senecio*	Schmitt (1980, 1983); Abbott & Irwin (1988)
Interspecific competition	*S. vulgaris*	Aarrsen (1989); Bergelson & Perry (1989); Bergelson (1990a,b); Bergelson *et al.* (1993)
Long distance dispersal	*S. flavus, S. mohavensis*	Liston *et al.* (1989); Liston & Kadereit (1995); Coleman *et al.* (2003)
	S. inaequidens	Pelser *et al.* (2012)

Within each section of the table, studies are listed in approximate historical sequence. Full references of citations are listed in Supporting Information Notes S3. Research on taxa formerly within *Senecio* but now placed within the genus *Jacobaea* is not cited in the table.

form increased the attractiveness of *S. vulgaris* to insect pollinators (Abbott & Irwin, 1988) and increased maternal outcrossing in the newly formed radiate variant (Marshall & Abbott, 1982, 1984a). This provides a rare example of a shift towards outcrossing in a selfing species (Abbott *et al.*, 1998), in contrast to the more typical trend for selfing to evolve from outcrossing (Barrett, 2013). Floret development in this rayed variant is controlled by localized expression of, and interactions between, at least three *cycloidea* (*CYC*)-like genes (Kim *et al.*, 2008; Garcês *et al.*, 2016). There is evidence for selection on a duplicated cluster of these genes, collectively known as *Ray*, in the form of gene transfer between species and clinal patterns of variation across ecotones, reflecting the adaptive importance of ray florets as a modulator of outcrossing (Kim *et al.*, 2008; Chapman & Abbott, 2010).

Outcrossing in many *Senecio* species is maintained by the presence of SI, a molecular mechanism of self-pollen recognition and rejection (Hiscock, 2000a,b) that is common among species within the Asteraceae (Ferrer & Good-Avila, 2007). SI in *Senecio* is controlled sporophytically with a single genetic locus, *S*, determining both the pollen and stigma recognition phenotypes (Hiscock, 2000a,b; Brennan *et al.*, 2002, 2006, 2011). Interestingly, the expression of sporophytic SI (SSI) in *Senecio* appears to be affected by additional unlinked modifier loci (Hiscock, 2000a,b; Brennan *et al.*, 2011), which raises intriguing questions about its underlying molecular mechanism. To date, however, unravelling the molecular basis of SSI in *Senecio* has proved challenging (Allen *et al.*, 2011). Those studies that have been undertaken provide clear evidence that this molecular mechanism is distinct from the well-characterized SSI system of the Brassicaceae (Tabah *et al.*, 2004; McInnis *et al.*, 2006; Allen *et al.*, 2011), indicating the evolution of a different mechanism of SSI in the Asteraceae and further supporting phylogenetic analyses that have shown that SI has evolved multiple times during the radiation of flowering plants (Allen & Hiscock, 2008). Encouraging progress towards characterizing the *S*-locus in members of the Asteraceae is being made through mapping genomic regions linked to SI in sunflower (Gandhi *et al.*, 2005; Gonthier *et al.*, 2013), which are also proving useful in identifying syntenic regions in the *Senecio* genome (B. Nevado *et al.*, unpublished). Nevertheless, it remains a possibility that the Asteraceae harbours more than one SI system, especially as elements of an underlying gametophytic SI system have been described in certain crosses between SSI species of *Parthenium* (Lewis, 1994) and also in *Senecio* (Hiscock, 2000a,b; Tabah, 2004). This important area of mating system evolution will benefit from further research as more genomic tools emerge for *Senecio*.

2. Implications of self-incompatibility for genomic structure and regulation

Suppressed recombination around the *S* locus Since both pollen and pistil *S* determinants are required for functional SI, all *S* loci characterized to date have a haplotypic structure containing at least two tightly linked polyallelic genes, one of which is responsible for male SI function and the other for female SI function (Iwano & Takayama, 2012). Recombination between haplotypes is necessarily minimized through extensive structural differences between haplotypes and/or high sequence divergence (Boyes *et al.*, 1997; Shiba *et al.*, 2003; Goubet *et al.*, 2012). This extensive sequence divergence is created by balancing selection that maintains many functionally distinct *S* haplotypes to maximize population mate availability (Schierup & Vekemans, 2008; Roux *et al.*, 2013). The availability of sequenced genomes for *Senecio* species will allow testing of predictions about the genomic structure of the *S* locus in this novel SSI system, thereby broadening the taxonomic breadth of studies of the evolution of SI and *S* loci.

Dominance in self-incompatibility systems Sporophytic expression of male determinant *S* alleles in pollen creates dominance interactions between *S* alleles that optimize mate availability in populations while effectively restricting self-pollination, even when allelic diversity is relatively low (Vekemans *et al.*, 1998; Brennan *et al.*, 2003a; Billiard *et al.*, 2007). The presence of *S* allele dominance interactions (both for pollen and stigma *S* determinants) is thought to have contributed to the colonizing success of self-incompatible *S. squalidus* in the UK and *Senecio inaequidens* in continental Europe despite the presence of limited functional *S* haplotype diversity (Brennan *et al.*, 2002; Brennan *et al.*, 2003a, 2006; Lafuma & Maurice, 2007). Moreover, evidence for differences in *S* allele dominance interactions across different UK *S. squalidus* populations suggests that *S* allele dominance is labile and can evolve (Brennan *et al.*, 2006). *Senecio* can be used to determine whether independently evolved systems of SSI have also independently evolved this flexible mechanism of *S* allele dominance regulation. Future research on SSI in *Senecio* could explore the relevance of recent discoveries in the Brassicaceae, such as the control of pollen *S* allele dominance by *S* allele-specific small RNAs (Durand *et al.*, 2014) and the accumulation of inbreeding depression associated with the *S* locus (Billiard *et al.*, 2007; Llaurens *et al.*, 2009), generating an important test of whether such mechanisms apply beyond a single SSI system.

3. Implications of self-incompatibility for hybridization and polyploidy

As a mechanism promoting outcrossing, SI also increases opportunities for interspecific hybridization (Brennan *et al.*, 2013; Vallejo-Marin & Hiscock, 2016). Hybridization is recognized as an important evolutionary force that rapidly generates new genetic combinations for selection to act upon, which enhances the spread of adaptive traits across related groups (Abbott *et al.*, 2013; Harrison & Larson, 2014). Strong balancing selection promoting *S* haplotype diversity increases the likelihood of gene flow between taxa at the *S* locus (Castric *et al.*, 2008), as reflected by extensive *S* haplotype sharing between hybridizing *Senecio* species (Brennan *et al.*, 2013).

Senecio provides many examples of allopolyploid hybrid species, created when interspecific hybridization is accompanied by a doubling of a hybrid's chromosome number (Abbott & Lowe, 2004; Kadereit *et al.*, 2006; Hegarty *et al.*, 2012; Pelser *et al.*, 2012). Different ploidy levels between species need not present an insurmountable barrier to gene flow following hybridization, as shown by examples of gene transfer of the *Ray* locus from diploid *S. squalidus* to tetraploid radiate *S. vulgaris* (Fig. 3; Kim *et al.*, 2008; Chapman & Abbott, 2010). Sometimes, ploidy differences can contribute to genetic swamping from the dominant pollen donor as sterile progeny with unbalanced chromosome numbers are produced. This process is thought to be contributing to the invasive success of diploid *Senecio madagascariensis* in encroaching upon the habitat occupied by native tetraploid *Senecio pinnatifolius* in Australia (Prentis *et al.*, 2007).

Hybridization between *S. squalidus* (SI) and SC *S. vulgaris* within the last 100 yr has resulted in the evolution of the allohexaploid hybrid species *S. cambrensis* (SC) on at least two occasions in North Wales and Edinburgh (Fig. 3; Abbott & Lowe, 2004; Brennan & Hiscock, 2010; Hegarty *et al.*, 2012). The process of genome duplication itself might have led to the disruption of the SI system inherited from *S. squalidus*, resulting in the SC condition in *S. cambrensis*. SC might, therefore, be selected for in new polyploids because they are initially rare with limited *S* haplotype diversity soon after origin, which could cause problems with mate availability under obligate outcrossing. However, many polyploid self-incompatible *Senecio* species are known (Andersson, 2001; Lafuma & Maurice, 2007), and in resynthesized *S. cambrensis* allohexaploids it was found that SI reappeared among some offspring in the F_2 generation (Brennan & Hiscock, 2010), suggesting complex control of SSI in neopolyploids. These examples demonstrate that *Senecio* provides a fascinating study system to better understand how breeding system, hybridization, and polyploidy interact to generate and maintain genetic, taxonomic and ecological diversity.

4. Implications of self-incompatibility for invasiveness and colonization

According to Baker's law, self-compatibility is favoured in invasive populations because of enhanced reproductive assurance during colonization (Baker, 1967; Pannell & Barrett, 1998). However, many exceptions exist, and it is clear that the interactions between breeding systems and colonization or invasiveness can be complex. In the UK, investigations of invasive *S. squalidus* populations have revealed individual variation in the strength of SI within and between populations, a phenomenon often referred to as pseudo-

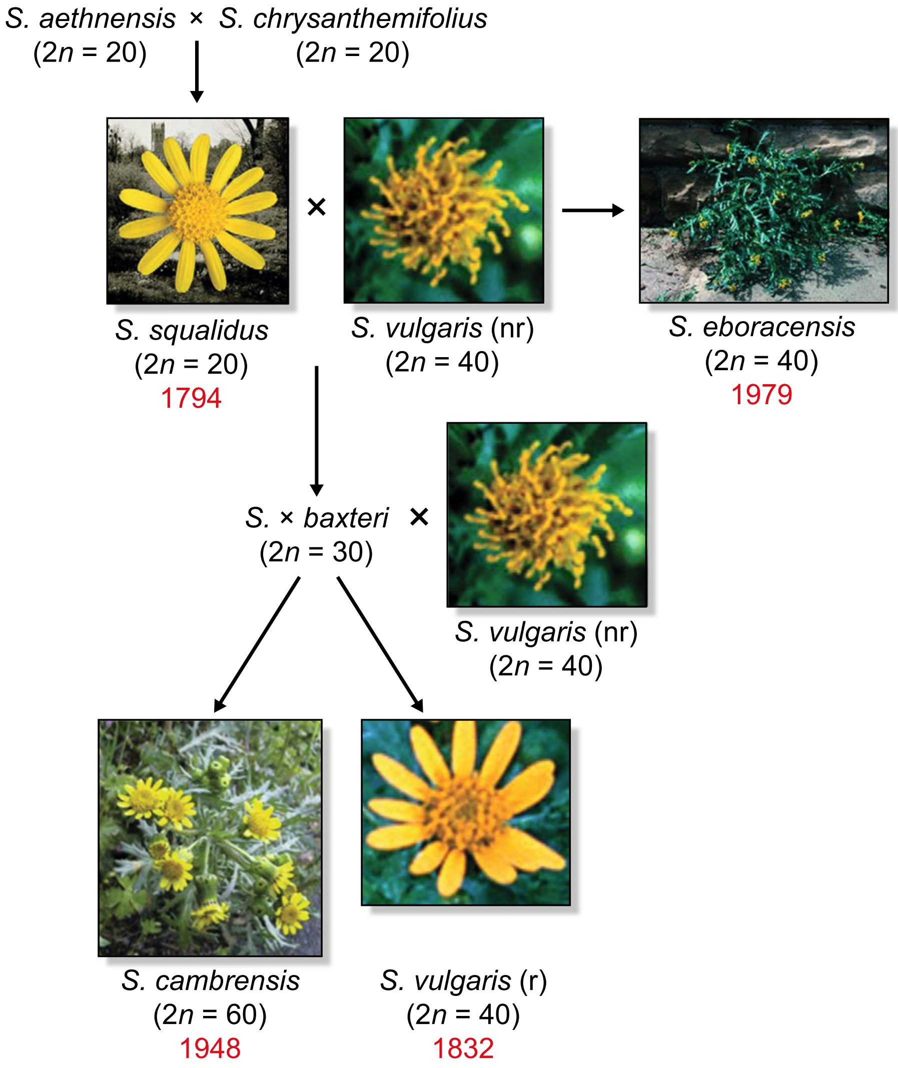

Fig. 3 Hybrid origins of new *Senecio* taxa in the British Isles. Dates of first records are in red. For *Senecio vulgaris*, the nonradiate (nr) and radiate (r) forms are presented.
Figure reproduced from Abbott & Rieseberg (2012) with permission.

self-compatibility (PSC; Brennan *et al.*, 2011). Despite SI being predominant in all populations of *S. squalidus*, a low frequency of PSC (*c.* 6–8%), sometimes higher (40% SC, 13% PSC in an Exeter sample; A. Brennan & S. Hiscock, unpublished), was detected in all UK populations sampled, and may be contributing to mating and colonizing success (Brennan *et al.*, 2005). PSC might be of considerable adaptive importance in conferring reproductive assurance through breeding system 'flexibility', particularly during periods of population disturbance or establishment when the relative advantages of selfing outweigh those of outcrossing (Levin, 1996; Stephenson *et al.*, 2000; Hiscock, 2000a,b).

PSC and SC in *S. squalidus* are heritable and appear regulated by multiple genetic loci that interact with the *S* locus to modify its expression (Hiscock, 2000a,b; Tabah, 2004; Brennan *et al.*, 2011), similar to the control of unilateral interspecific incompatibility, which regulates the compatibility of crosses between closely related SI and SC species (Hancock *et al.*, 2003). Environmental factors, such as salt concentration, also affect the expression of SI and PSC (Hiscock, 2000a,b), potentially providing a mechanism for the environment to have direct effects on recombination rates in natural populations (Stevison *et al.*, 2017). Furthermore, it has been demonstrated experimentally that recombination can 'resurrect' SI to varying levels of penetrance in SC lines of synthetic *Senecio* allopolyploids generated by crossing an SC (*S. vulgaris*: 4n) with an SI species (*S. squalidus*: 2*n*) (Brennan & Hiscock, 2010). Therefore, rather than a qualitative trait (as it has traditionally been viewed), SI *sensu lato* could be viewed as a quantitative trait at the end of a potentially flexible continuum from SI through PSC to SC. These studies highlight the potential of *Senecio* as an informative model system for investigating evolutionary interactions between breeding systems and invasiveness.

IV. Mechanisms and consequences of hybrid speciation

Historical and current interspecific hybridization is common in *Senecio* (e.g. Comes & Abbott, 2001; Pelser *et al.*, 2012; Osborne *et al.*, 2016), occurring both within and across ploidy levels, and between selfing and outcrossing species (e.g. Kadereit *et al.*, 2006; Chapman & Abbott, 2010). Indeed, *Senecio* has been highlighted for its exceptional recent rates of hybrid speciation, particularly as opportunities for new interspecific interactions arise due to humanmediated change (Thomas, 2015). *Senecio* is notable for containing examples of both recent homoploid hybrid speciation (involving no change in chromosome number) and allopolyploid speciation (inheritance of more than two sets of chromosomes), serving as excellent models for investigating hybrid speciation (Fig. 3).

The homoploid hybrid species *S. squalidus* (Oxford ragwort) originated from material introduced to the Oxford Botanic Garden (UK) at the end of the 17th century (Harris, 2002) derived from hybridization between two species native to Mount Etna, Sicily, *Senecio aethnensis* and *Senecio chrysanthemifolius* (Fig. 3a,b; James & Abbott, 2005). Following almost a century of cultivation in the Oxford Botanic Garden, the new homoploid hybrid species rapidly spread across Britain and into Ireland over the next 200 yr (Abbott *et al.*, 2009). *Senecio squalidus* is genetically and phenotypically divergent from its parents and their hybrids, which are restricted to Sicily (Brennan *et al.*, 2012), with evidence of extreme divergence in gene expression (Hegarty *et al.*, 2008, 2009). In addition to its ecogeographical isolation, recent genetic mapping studies indicate that *S. squalidus* has inherited a combination of genetic incompatibilities from its parent species, contributing further to its reproductive isolation (Brennan *et al.*, 2019). Together, this genetic, phenotypic, and transcriptomic divergence has likely contributed to its local adaptation to the UK (Allan & Pannell, 2009; Ross, 2010), which is the target of current transcriptomic (RNA-seq) research aimed at identifying candidate genes for local adaptation (Nevado and Hiscock, pers. comm.).

During its spread in Britain, *S. squalidus* has repeatedly hybridized with the native tetraploid, *S. vulgaris*, resulting in the origin of the introgressant *S. vulgaris* var. *hibernicus*, a new tetraploid species, *Senecio eboracensis* (Irwin & Abbott, 1992; Lowe & Abbott, 2003), and multiple origins of the neoallo-hexaploid, *S. cambrensis* (Figs 3, 4; Abbott & Lowe, 2004; Hegarty *et al.*, 2012). These hybridization events were associated with marked changes in gene expression (Hegarty *et al.*, 2012, 2006, 2013) that may have had adaptive consequences by facilitating the establishment of new hybrid taxa through ecological differentiation (see also 'Differential gene expression associated with hybrid speciation and adaptation' in Section VI). Multiple independent hybridization events, as observed in *Senecio*, provide a natural experiment with which to study the consequences of hybridization and polyploidy in populations. Species of *Senecio*, therefore, provide abundant systems for future detailed genomic analyses of mechanisms favouring the origin and establishment of hybrid taxa and introgression in the wild (e.g. Alexander-Webber *et al.*, 2016).

V. Adaptation and speciation in *Senecio*

1. The evolution of reproductive isolation during the formation of ecotypes

Ecotypes originate when adaptation to contrasting habitats leads to a build-up of extrinsic reproductive isolation between populations. Understanding how and when ecotypes become independent species remains a fundamental issue in evolutionary biology (Abbott & Comes, 2007; Lowry, 2012). Of particular importance is how ecological divergence becomes associated with intrinsic barriers to gene flow, created by genetic divergence that produce genetic incompatibilities between ecotypes.

In the *S. lautus* complex, which consists of multiple taxonomic ecotypes and species (see Roda *et al.*, 2013b), a strong correlation is observed between plant morphology and habitat (Fig. 2; Radford *et al.*, 2004; Walter *et al.*, 2018a). Coastal populations grow tall on sand dunes (Dune ecotype), but prostrate on rocky headlands (Headland ecotype) and cliffs along the Australian coastline (Fig. 2; Roda *et al.*, 2013b). Dune and Headland populations often occur in adjacent habitats and are self-incompatible and interfertile. Transplant experiments have revealed that neither Dune nor Headland ecotypes, nor their hybrids, can colonize each other's habitat (Melo *et al.*, 2014; Richards & Ortiz-Barrientos, 2016; Richards *et al.*, 2016; Walter *et al.*, 2016). The probability of surviving in the alternative environment is a function of the proportion of alleles of local origin that a hybrid individual carries

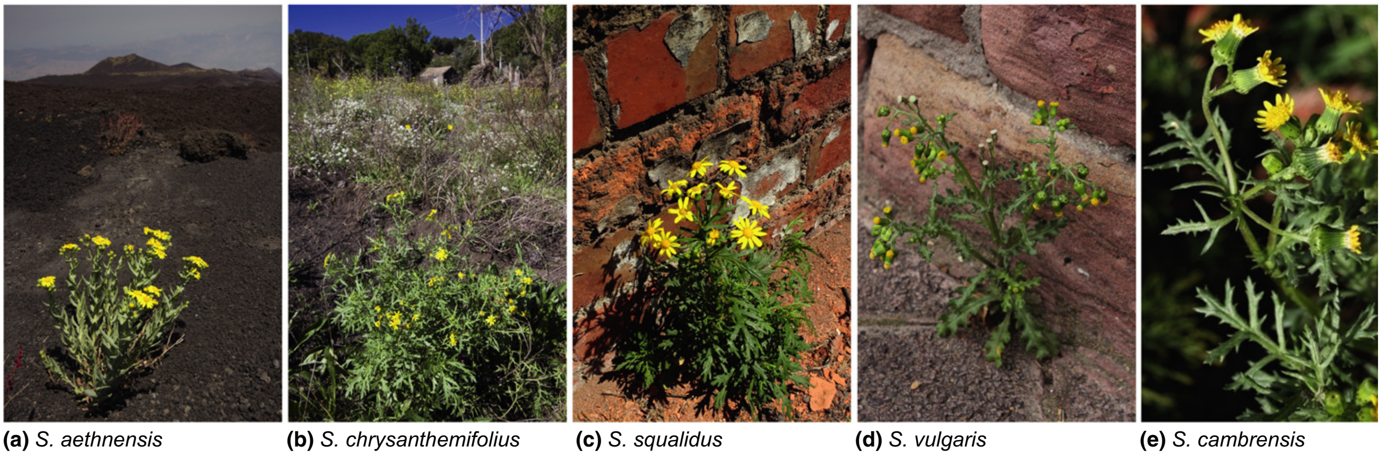
(a) *S. aethnensis* **(b)** *S. chrysanthemifolius* **(c)** *S. squalidus* **(d)** *S. vulgaris* **(e)** *S. cambrensis*

Fig. 4 European *Senecio* species that have been studied extensively. (a) *Senecio aethnensis* and (b) *Senecio chrysanthemifolius* occur on Mount Etna (Sicily, Italy) at different altitudes. Hybrids between these two species were cultivated at the Oxford Botanic Garden (UK), from which they escaped in the late 18th century and spread across the UK, becoming (c) the new species *Senecio squalidus.* Hybridization between *S. squalidus* and (d) *Senecio vulgaris* created (e) the neoallohexaploid *Senecio cambrensis* and the tetraploid *Seneci eboracensis* (Fig. 3). Image of *S. vulgaris* © Botanical Society of Britain & Ireland, *S. cambrensis* © Frau-Doktor.

(Richards *et al.*, 2016). Together, these observations suggest that limited dispersal and natural selection against migrants and hybrids keep populations distinct despite their parapatric distribution, and that selection acting in opposing directions has played a fundamental role in the formation of ecotypes in this system, likely leading to the formation of new plant species.

Barriers to gene flow that act after pollination, such as F_1 hybrid inviability or sterility, are often masked by heterosis (Lowry *et al.*, 2008). This can bias perception as to how intrinsic and extrinsic reproductive barriers evolve in a system that has diverged recently. For instance, in transplant experiments of *S. lautus*, F_1 hybrids show strong hybrid vigour (Walter *et al.*, 2016), suggesting that heterosis masks the deleterious effects of gene flow between populations locally adapted to contrasting habitats. However, a more detailed reciprocal transplant including all combinations of F_1 hybrids amongst four ecotypes (Fig. 2, Woodland ecotype (dry sclerophyll woodland) and Tableland ecotype (subtropical rainforest edges)) showed that field fitness depended on the chromosomal origins in a hybrid (Walter *et al.*, 2016). For each of the four transplant environments, F_1 hybrids with a chromosome native to the transplant environment (e.g. Dune in the dune environment) performed better than F_1 hybrids where both chromosomes were from foreign ecotypes (e.g. $F_{1\text{Headland}\times\text{Tableland}}$ in the dune environment). This suggests that alleles associated with heterosis were also involved in adaptation. F_1 hybrids also show vigour in glasshouses when compared with parents, whereas F_2 hybrids perform poorly. The presence of F_2 hybrid breakdown suggests that intrinsic postzygotic isolation is created by alleles that reduce fitness when recombined into other genetic backgrounds (Walter *et al.*, 2016).

Although reproductive compatibility seems to be high among ecotypes of *S. lautus*, geographical patterns of reproductive isolation suggest that different populations of the same ecotype are becoming reproductively isolated (Melo *et al.*, 2019). Such patterns provide the opportunity to study the evolution of reproductive isolation along a speciation continuum to identify generalizations for speciation in plants (Melo *et al.*, 2014). Recent work has identified molecular links between adaptation and speciation in *S. lautus* (Melo *et al.*, 2019) and found evidence that adaptive divergence also creates genetic incompatibilities between populations inhabiting contrasting habitats (Walter *et al.*, 2019). Overall, current evidence suggests that natural selection plays a fundamental role in creating barriers to gene flow between *S. lautus* populations and that extrinsic barriers seem to have evolved early during divergence, whereas intrinsic barriers were initially weak but have accumulated. This work highlights the potential for using *Senecio* to better understand how adaptation and speciation occur across environments and geographical ranges.

2. Ecological speciation on Mount Etna

Genomic analyses have made it clear that, in the presence of divergent selection, evolutionary divergence can occur despite populations continuing to exchange alleles (whether in sympatry or parapatry), with intrinsic reproductive isolation arising as a consequence later (Rundle & Nosil, 2005). This 'divergence with gene flow' scenario is of interest to evolutionary biologists because the relative roles of major mechanisms of evolution (ecology, selection, genetic drift, and gene flow) can be studied together to understand how phenotypes, genotypes, and alleles of diverging populations interact during speciation.

On Mount Etna, Sicily, two sister *Senecio* species inhabit ecologically distinct, high and low-elevation environments. *Senecio aethnensis* (Fig. 4a) is found above *c.* 2000 m asl on old lava flows, and is covered by snow each winter, and *S. chrysanthemifolius* (Fig4b) occurs in disturbed habitats and along roadsides below *c.* 1000 m asl and endures intense summer heat. At intermediate elevations the species form a hybrid zone (James & Abbott, 2005; Brennan *et al.*, 2009). The parental species show divergence in leaf and capitulum shape and size, with plants in the hybrid zone exhibiting a range of intermediate phenotypes, with clines for different traits varying significantly in width, suggesting selection against at least some intermediate traits (Brennan *et al.*, 2009). The two species are almost completely interfertile, with hybrids generally fit and fertile, even in later generations. It is therefore likely that selection is responsible for maintaining the distinctness of the two parental species (Chapman *et al.*, 2005; but see Brennan *et al.*, (2014) and Chapman *et al.* (2016) for evidence of incompatibility due to hybrid breakdown).

Using transcriptome sequences from one individual from each of *S. aethnensis* and *S. chrysanthemifolius* (and *S. vernalis* as an outgroup), Osborne *et al.* (2013) found evidence that speciation occurred with gene flow (i.e. in parapatry versus allopatry). Supported by Chapman *et al.* (2013), both studies found similar estimates in mean divergence time between the two species of *c.* 108 000 yr ago (bootstrap range: 53 000–187 000 yr), which coincides with the uplift of Mount Etna that likely produced a novel high-altitude habitat in which *S. aethnensis* could have originated (Chapman *et al.*, 2013; Osborne *et al.*, 2013). The well-characterized demographic history of the Mount Etna hybrid zone provides an intriguing system and an ideal basis for future work to study the genetic architecture of traits underlying adaptation, speciation, and hybrid breakdown, especially in combination with fully annotated genomes for these species.

3. Introgression and clinal analysis in the formation of a hybrid zone during adaptive divergence

The hybrid zone between populations of *S. aethnensis* and *S. chrysanthemifolius* on Mount Etna has been studied by quantifying how traits (associated with reproduction, growth form, and leaf shape) and neutral microsatellite markers change across a hybrid zone (Brennan *et al.*, 2009). This analysis provides evidence for strong selection on leaf traits (relative to neutral markers), which have narrower cline widths (strong selection) than genetic markers (1.49 km compared with 3.24 km), and for selection against hybrids associated with the elevational gradient (1515–1795 m), which determines the position of the cline centre. There were also significant increases of covariances and variances of genotypes and ecological variation at the cline centre, suggesting a high frequency of relatively recent hybrids at the centre. A significant displacement of the cline centre of floral traits compared with genetic markers of

0.41 km suggests that alleles associated with variation in some traits may be moving to higher elevations. Reciprocal transplants throughout the hybrid zone on Mount Etna (or other *Senecio* hybrid zones), at different spatial scales, and in combination with high-throughput sequencing, can provide an important way to explore the genetic and genomic architecture of traits affecting fitness in *Senecio* in contrasting environments.

VI. Genomics of adaptation and speciation

1. Genomics of adaptation and parallel evolution

The genetic basis of adaptation in plants remains largely unexplored outside model and crop systems. Notable exceptions are wild sunflowers (*Helianthus* spp.), rockcress (*Boechera stricta*), and monkeyflowers (*Mimulus* spp.), where studies have revealed the genetic architecture and molecular basis of adaptive traits, including flowering time (Blackman *et al.*, 2011), flowering phenology (Anderson *et al.*, 2013), physiological adaptations to contrasting environments (Rieseberg *et al.*, 2003) and drought resistance (Lowry & Willis, 2010; VanWallendael *et al.*, 2019). In *S. lautus*, where multiple pairs of dune and headland populations have evolved repeatedly and independently along the Australian coast, genomic approaches are providing important insights into the genetic changes associated with rapid adaptive divergence.

Using single nucleotide polymorphisms (SNPs) distributed across the genome, Roda *et al.* (2013b) showed that different pairs of parapatric dune and headland populations had unique patterns of genetic differentiation, suggesting independent adaptive differentiation. Although patterns of population pair differentiation were unique at the SNP level, they were similar at the level of predicted function, notably for development and growth via auxin. This suggests that paths towards adaptation and patterns of repeated speciation (between ecotypes for multiple population pairs) are often different but lead to similar end results in terms of phenotypes. Current research using *S. lautus* is exploring the molecular basis of auxin and gravity responses (Wilkinson *et al.*, 2019). Within *Senecio*, the parallel evolution of traits across populations occurs in many other species; for example, nickel (Ni) accumulation in *Senecio coronatus* (Meier *et al.*, 2018) and ecotype formation in Mediterranean *Senecio* (Comes *et al.*, 2017). The existence of multiple adaptive radiations in *Senecio*, each involving adaptation to similar or contrasting environmental stresses, highlights the potential of the genus to understand the ecological genetics of adaptation and speciation.

2. Population genomics of ecological speciation

The interaction between recombination, gene flow, and selection during speciation is still poorly understood but actively researched, both theoretically (e.g. Schilling *et al.*, 2018) and empirically (e.g. Chapman *et al.*, 2016; Safran *et al.*, 2016; Doellman *et al.*, 2018; Stankowski *et al.*, 2019). *Senecio* contains multiple systems where these evolutionary dynamics can be studied. For example, despite differing profoundly in phenotypes, life history, and ecology, *S. aethnensis* and *S. chrysanthemifolius* on Mount Etna show surprisingly little genomic divergence (Chapman *et al.*, 2013, 2016; Filatov *et al.*, 2016). Osborne *et al.* (2016) demonstrated extensive contemporary gene flow between the two species, supported by a demographic analysis of the species (Chapman *et al.*, 2013), with more gene flow from *S. aethnensis* to *S. chrysanthemifolius* than in the opposite direction. Genomic comparisons between *S. aethnensis* and *S. chrysanthemifolius* revealed the clustering of highly differentiated genetic markers (identified by outlier scan; Chapman *et al.*, 2013) in a handful of small regions of the genome (Chapman *et al.*, 2016). However, their clustering appeared to be associated with low recombination regions and not islands of divergence. Quantitative trait locus (QTL) mapping demonstrated that outlier genetic markers tended to underlie morphological QTLs, suggesting a link between genomic divergence, morphological divergence, and adaptation to altitude (Chapman *et al.*, 2016). In *S. lautus*, Roda *et al.* (2017) found evidence for clustering of adaptive alleles associated with variation in both architectural and reproductive traits. This suggests that pre and post-pollination reproductive barriers can evolve concomitantly and facilitate speciation.

3. Differential gene expression associated with hybrid speciation and adaptation

The extent and role of changed patterns of gene expression in local adaptation or the formation of new species via hybridization is not well understood (Vallejo-Marin & Hiscock, 2016). However, there is considerable interest in the idea that the regions of the genome that show environmental (or trans-generational) mediation of gene expression may be disproportionally involved in local adaptation (West-Eberhard, 2005). Gene expression can also be altered dramatically during the rapid changes in gene number associated with speciation by hybridization. To investigate how gene expression changes during homoploid and allopolyploid hybrid speciation, Hegarty *et al.* (2005) performed microarray experiments and sequenced genes that showed over or underexpression in *Senecio* hybrids, relative to one or both parents. Gene expression was explored in natural and resynthesized allopolyploid hybrids between *S. vulgaris* and *S. squalidus* (Fig. 3), their primary triploid hybrid *Senecio* × *baxteri* ($3n = 3\times = 30$) and their allohexaploid hybrid *S. cambrensis* ($2n = 6\times = 60$) (Hegarty *et al.*, 2006, 2005). Early generation hybrids exhibited massive changes in gene expression affecting hundreds of genes, a phenomenon described as 'transcriptome shock' (Hegarty *et al.*, 2006, 2005). Interestingly, changes in levels of gene expression were greater in triploid *S.* × *baxteri* than in the allohexaploid *S. cambrensis*, suggesting that genome duplication, leading to the formation of the allohexaploid, has an 'ameliorating' effect on hybridization-induced 'transcriptome shock' (Hegarty *et al.*, 2006).

Transcriptome shock was also observed in the homoploid hybrid *S. squalidus* and in artificial '*S. squalidus*' hybrids (propagated for five generations) produced by crossing its parental taxa (Hegarty *et al.*, 2009). The effect of transcriptome shock was more extreme in the artificial homoploid hybrids. In a subset of genes, transgressive expression (up or downregulation with respect to both parents) was maintained in subsequent generations, whereas other affected genes tended to move towards a pattern of expression consistent with wild *S. squalidus*. These transgressive genes were involved in photosynthesis, catalytic activity, lipid binding, protein biosynthesis, and protein folding (Hegarty *et al.*, 2009). The finding of transgressive expression was consistent with similar microarray analysis in hybrid sunflowers (Lai *et al.*, 2006), which identified transgressive levels of gene expression in wild hybrids adapted to environmental conditions not tolerated by their parent species. Both studies suggest that new patterns of transgressive gene expression arising from hybridization could provide genetic novelty for selection to facilitate adaptive divergence.

Comparisons of gene expression and transcriptome sequences between *S. aethnensis* and *S. chrysanthemifolius* identified genes potentially involved in adaptation to high and low altitudes, and the relative roles of expression and sequence divergence in the genomic basis of adaptive divergence (Chapman *et al.*, 2013). However, in sequence comparisons, alleles that showed high interspecific divergence (*c.* 200) were just a small fraction of the loci that were analysed (*c.* 18 000), suggesting that species boundaries due to morphological differences and ecological adaptations might be maintained by just a small portion of the genome (Chapman *et al.*, 2013), a pattern consistent with recently diverged species as part of the 'genic view' of speciation (Wu, 2001). Future work should exploit the ability to clone and transplant individuals across environments. Combining such field experiments with recent advances in next-generation sequencing and transcriptomic analyses can explore the adaptive potential of changes in gene expression among *Senecio* taxa (e.g. Alexander-Webber *et al.*, 2016), as well identify as the loci underlying plastic responses to environmental variation within species.

VII. Integrating studies of genotype, phenotype and fitness

1. The challenge of integrating genotype, phenotype, and fitness information in the field

Quantifying genetic variation in fitness, and its relationship with quantitative traits, allows the responses of groups of traits to natural selection to be predicted. This information is central to understanding how populations and ecological communities will respond to the reductions in fitness predicted by ongoing global change, as well to explore how selection varies in strength and form among populations, species, and in different ecological contexts (Shaw & Etterson, 2012). Knowledge on genetic and ecological correlations among traits will also help us to understand what drives populations to specialize, forming new species with narrow ecological tolerances, rather than creating ecologically widespread species that show local adaptation across their range.

Quantitative genetic analyses of traits and fitness across ecological context demand large sample sizes and large experiments that integrate genetic, phenotypic, and fitness information, ideally across a range of natural environments. To estimate genetic variation in fitness, selection should be measured on individuals of known relatedness (pedigrees or crossing designs) by quantifying phenotypic traits and fitness under field conditions, and estimating the additive genetic covariance between traits and fitness (Morrissey *et al.*, 2012; Pujol *et al.*, 2018; Shaw, 2019). The combination of appealing experimental attributes (short generation times, recent genetic developments, and the ease to which they can be propagated) and the range of ecologies in which the fitness of phenotypes can be assessed means that such integrative experiments are more tractable (and powerful) in *Senecio* than in many other model systems, especially when incorporated with five powerful experimental approaches outlined below.

Full-sibling families Controlled crosses can be carried out easily in most *Senecio* species. In most cases they can also produce sufficient seed/genetic resources to conduct the large-scale field experiments with sufficient power to quantify evolutionary parameters (e.g. Wilkinson *et al.*, 2019). Crossing designs containing both full and half-sibling families (i.e. individuals sharing only a father) allow partitioning of the phenotypic information to estimate the additive genetic covariation between traits, or between traits and fitness (Lynch & Walsh, 1998). The benefit of using families within a breeding design is two-fold. First, transplanting multiple individuals (siblings) from the same family in different environments allows them to be tested in different environments to identify how fitness varies across environments. Second, with sufficient seed, the same families can be propagated in separate glasshouse and field experiments. In this scenario, we can connect the mean of each family across separate experiments, making it possible to estimate the mean phenotype in the glasshouse and the mean fitness in the field. Connecting phenotype with fitness using family means is logistically simpler than measuring phenotypes in the field where selection may have removed variation, and plasticity may mask genotypic effects. In addition, because phenotypes are measured under controlled conditions, the number of phenotypes that can be measured can be maximized and each trait measured more precisely by minimizing environmental variation. Traits that are difficult to measure in the field, such as physiological traits, can then be included more easily in large-scale experiments. Fieldwork can then focus on quantifying different and more comprehensive measures of fitness to characterize how these performance measures change with ecological, geographic, or temporal variation.

Clones Ideally, the phenotype and fitness of a given individual within a pedigreed population (or crossing design) should be assessed across different environments, controlling for genetic variation. However, this is only possible where genotypes can be replicated (i.e. cloned) and transplanted into multiple environments, an approach that assesses the reaction of the same genotype to environmental variation. Such an approach can be implemented in very few other model systems (e.g. *Mimulus*). However, many *Senecio* species produce roots readily from cuttings, allowing the use of clones of known genotypes in field and molecular experiments at sufficiently high replication to allow useful estimates of genetic variation in fitness to be made under field conditions, as well as exploration of the genomic bases of such variation.

Artificial hybridization Detecting ongoing natural selection, and genetic variation in fitness, is difficult if populations are already close to their optimal phenotype and stabilizing selection is strong, or genetic variation low (Walsh & Lynch, 2018). The benefit of using *Senecio* as a model system to overcome such difficulties is twofold. First, many *Senecio* species show evidence of recent rapid adaptive radiation, providing the opportunity to characterize the strength and direction of selection during the early stages of adaptive diversification using transplant experiments (Walter *et al.*, 2016; Richards *et al.*, 2019). Second, *Senecio* species often display high levels of intraspecific variation, often with a well-defined structure among populations (i.e. ecotypes). In many cases, species also produce viable hybrids (unlike highly divergent taxa), allowing their use in multigeneration artificial hybridization experiments (e.g. Richards *et al.*, 2019; Walter *et al.*, 2019; Wilkinson *et al.*, 2019). These crosses can be used to recreate genetic and phenotypic variation that is currently absent in natural populations and may reflect earlier stages of divergence among sister species. If transplanted into the field, the fitness of these alleles and genotypes can be used to explore the ecological consequences of such variation, as has also been conducted with great success to study hybrid speciation in *Helianthus* sunflowers (Lexer *et al.*, 2003a,b).

Molecular methods for relating genotype to phenotype The transcriptome is a critical intermediary between genetic and phenotypic variation. Appropriately designed experiments can answer fundamental questions about the genomic architecture underlying phenotypic responses to the environment. *Senecio* can be used in experiments that propagate large numbers of clones of a single genotype, which are then transplanted across environmental conditions to produce powerful analyses of differential gene expression. Changes in levels of gene expression across the genome can then quantify the effects of the environment, tissue-type, sex, or developmental stage. RNA-seq has been used to study differential expression between divergent species on Mount Etna (Hegarty *et al.*, 2008; Chapman *et al.*, 2013), between polyploids and their diploid progenitors (Alexander-Webber *et al.*, 2016), and also intraspecific variation of specific traits, such as Ni hyperaccumulation in *S. coronatus* (Meier *et al.*, 2018). Differential expression analyses tend to yield lists of tens to hundreds of genes that differ in the number of transcripts produced between conditions. However, functional annotation of genes provides a means of deriving meaningful results from such lists. For example, Meier and colleagues found significant enrichment for transporter proteins, and quantitative reverse transcription PCR confirmed elevated expression of two known Ni transporters (IRT1 and IREG2), which were associated with intraspecific variation in Ni accumulation.

Genetic transformation and gene editing More explicit tests of function are possible in *Senecio* using *Agrobacterium*-mediated transformation (Kim *et al.*, 2008; Garcês *et al.*, 2016). By combining gene expression and functional analyses with phylogenetic analyses, Chen *et al.* (2018) showed that ray florets in *S. vulgaris* are regulated by three CYC2-like paralogues. The phylogenetic history of this gene family across *Senecio*, and Asteraceae more broadly, can identify how gene duplication and introgression can give rise to greater floral complexity. Finally, the development of the CRISPR/Cas9 gene editing technology for nonmodel organisms (Shan *et al.*, 2018) will allow fast targeted mutagenesis in *Senecio* to test the function of loci identified from comparative genomic studies and field experiments. Such technologies will provide an excellent opportunity to relate gene function to evolutionary ecology and the gain and loss of key traits across a diverse plant genus.

2. Exploring the evolution of environmental sensitivity

The ability of a single genotype to produce different phenotypes in response to environmental variation (phenotypic plasticity) allows complex organisms to survive in a variable world. Across environments where this plasticity is adaptive, it reduces the exposure of alleles to selection (Ghalambor *et al.*, 2007), acting against the formation of clines (local adaptation) at many loci. Such responses of genotypes to environmental variation in time and space determine the distribution of populations, their range limits, and how they will respond to future environmental disturbances (Chevin *et al.*, 2010). The relatively recent radiation of *Senecio* (10.7 Ma), their occupation of contrasting environments, and their ability to hybridize make *Senecio* a powerful system to study how environmental sensitivity evolves in different environmental contexts.

Local adaptation in many plant systems (Hereford, 2009), including *Senecio* species (e.g. Walter *et al.*, 2016), confirms that plasticity within a given species can only be adaptive across the limited range of environments that typically define their ecological niche (DeWitt *et al.*, 1998). Studies have also identified heritable variation in plasticity for several important traits (Nussey *et al.*, 2005), suggesting that genetic variation for plasticity persists that may permit future evolution of different forms of environmental sensitivity. However, such studies are rare in plants and require the development of model systems that can integrate the approaches described herein (especially clonal propagation).

In other systems, reciprocal transplants of clones, seeds, or seedlings within and outside existing habitats have been used to explore genetic variation in phenological traits at range margins (e.g. Sheth & Angert, 2016). Ongoing *Senecio* research on Mount Etna is complementing these studies by testing how adaptation to contrasting environments affects their capacity for phenotypic plasticity when exposed to environmental variation (G. Walter *et al.*, unpublished). Therefore, *Senecio* can be used to understand how local adaptation (i.e. specialization) may reduce the forms and magnitude of plasticity possible within a species, with concomitant consequences for fitness and resilience to future environmental change.

3. Understanding trade-offs in life history and among environments

Understanding life history trade-offs is crucial for understanding how organisms acquire and utilize resources throughout their lifetime, and why they form species with narrow niches over longer timescales (Futuyma & Moreno, 1988; Agrawal *et al.*, 2010). Field transplants of ecotypes of *S. lautus* have shown developmental mismatches with the environment that result in mortality during seedling establishment. Such mortality reflects fitness trade-offs between contrasting environments and life stages, suggesting specialization for environment-specific resource allocation strategies (Walter *et al.*, 2018b). How variation in resource allocation across environments is mediated by biotic challenges (e.g. immunity or resistance to fungi) remains a key issue in understanding ecological range margins.

4. Genetic constraints to adaptation

Trait correlations bias the distribution of genetic variation towards certain multivariate phenotypes, at the expense of other phenotypes. If genetic variance is orientated away from the direction of natural selection, there will be little genetic variance for fitness, and the rate of adaptation will be slowed (Lande, 1979; Walsh & Blows, 2009). For much of the 20th century, genetic correlations were thought to be stable, making it difficult to see how rapid evolution in novel directions could occur (Arnold *et al.*, 2008). However, recent comparative evidence has shown that genetic correlations can evolve rapidly (Doroszuk *et al.*, 2008; Eroukhmanoff & Svensson, 2011), and experiments with *Senecio* suggest that changes in genetic correlations could overcome constraints to adaptation, allowing rapid ecological diversification (Walter *et al.*, 2018a). By integrating the approaches outlined earlier, experiments can capitalize on the tractability of *Senecio* to identify how the environment affects genetic variation in traits and fitness, identify the conditions that alter genetic correlations, and assess how and when the evolution of trait correlations lead to rapid evolutionary responses to novel environments.

VIII. Conspectus

Senecio is a powerful but as yet underutilized model system that has a unique potential to answer many fundamental questions in ecology and evolutionary biology. Most recently, four studies using Australian species of *Senecio* in field and glasshouse experiments combined artificial hybridization with molecular and quantitative genetics to identify mechanisms underlying adaptive divergence leading to speciation (Roda *et al.*, 2017; Melo *et al.*, 2019; Walter *et al.*, 2019; Wilkinson *et al.*, 2019). In Europe, the development of genetic and genomic resources for *S. squalidus* and its close relatives has facilitated comparative genomics of species adapted to contrasting environments, and the identification of candidate genes underlying adaptation (Hegarty *et al.*, 2008; Chapman *et al.*, 2013; B. Nevado *et al.*, unpublished). Meanwhile, detailed genomic and ecological analyses of closely related but ecologically divergent species in Sicily have revealed how selection acts across different genomic and ecological backgrounds (Brennan *et al.*, 2009), the role of gene flow and geological processes in promoting adaptive divergence (Chapman *et al.*, 2013; Osborne *et al.*, 2016), and the way that gene expression variation may be involved in these processes. Alongside these studies, focused ecological analyses can use *Senecio* to better understand the biotic and abiotic factors that limit species distributions across taxa and biogeography, and ongoing next-generation sequencing can further develop *Senecio* as a system for studying genome evolution within a phylogenetic context. Quantitative genetic research can develop *Senecio* by taking clones of individuals from breeding designs and transplanting them across environments to identify genetic variation that can promote adaptive evolutionary responses to environmental change. Combining transcriptomic analyses with such experiments can then identify the genetic basis of plasticity. Such experiments using the *Senecio* model will ultimately yield an integrative 'triangle' linking genotype, phenotype, and fitness.

IX. Acknowledgements

We would like to thank Lynda Delph, Jeannine Cavender-Bares, and three anonymous reviewers for valuable comments on earlier versions of this paper. We apologize that we cannot name all contributors, but we are especially thankful to those scientists who have contributed to advancing *Senecio* as a system for research: L. Ambrose, B. Britain, D. Bernal, M. James, H. Liu, M. Melo, H. North, P. Pelser, P. Prentis, T. Richards, F. Roda, and M. Wilkinson in Australasia; and P. Ashton, M. Coleman, H-P. Comes, S. Cozzolino, P. Crisp, A. Cristaudo, D. Forbes, P. Gibbs, A. Gillies, S. Harris, M. Hegarty, R. Ingram, J. Irwin, J. James, J. Kadereit, M. Kim, G. Liu, A. Lowe, D. Tabah, S. McInnis, O. Osborne, G. Barker, A. Allen and D. Marshall in Europe. We also acknowledge the national funding bodies that have supported this work, including NERC, The Genetics Society, BBSRC, and the Leverhulme Trust in the UK, NSF in the USA, and ARC in Australia.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Photo credits for Figs 1 & 4.

Notes S2 Details of the methods to produce Fig. 2.

Notes S3 References cited in Table 1.