



Phylogenomics and genetic admixture of the invasive fireweed complex (*Senecio inaequidens*–*Senecio madagascariensis*) at a global scale

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Abstract The southern African *Senecio inaequidens*–*S. madagascariensis* complex, (‘fireweed complex’), contains several species that have established as weeds outside of their native ranges. *Senecio madagascariensis* is the most widespread, found in Mexico, South America, Japan, Australia, New Zealand, and the Hawaiian Islands. Species delimitation in the complex is controversial, and identification of specimens is difficult. Biological control researchers have worked under the assumption that

invasive populations of *S. madagascariensis* originated in the KwaZulu-Natal province of South Africa. Recently, phylogenetic analysis of target capture data from hundreds of genes found the KwaZulu-Natal specimens of *S. madagascariensis* forming a sister group to nearly all specimens of the invasive lineage of that species, raising doubt about the established provenance of the latter. Here, we vastly expanded geographic sampling of the fireweed complex. Our results confirm that Madagascan *S. madagascariensis* is distantly related to continental African and invasive populations. If the two were taxonomically separated, the name *S. ruderalis* would be available for the invasive populations. Most continental African populations formed one clade with South American and few Australian specimens. All other specimens from invaded areas formed a clade with a single specimen from Eastern Cape province, South Africa, suggesting that invasive populations outside of South America may mostly be derived from the southernmost part of the native range. Taken together with recent studies showing differences in defence chemistry and performance of a candidate biocontrol agent between KwaZulu-Natal and Australian populations, these results imply that more research is needed into the area of origin of invasive populations and their associated candidate biocontrol agents.

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Introduction

Understanding the taxonomic identity and provenance of invasive weeds is crucial for weed research and management. To be able to design biological control (biocontrol) programmes for weeds, highly specific potential control agents need to be selected for the correct species and ideally from the correctly identified area of provenance of invasive populations, because of possible infraspecific variation in the native range (Le Roux et al. 2006; McCulloch et al. 2020). Similarly, transfer of knowledge and research results across countries is based on the assumption that the relevant countries have all correctly inferred the identity of a supposedly shared weed species (Gildenhuys et al. 2015). Unfortunately, a detailed understanding of phylogenetic relationships, genetic diversity, provenance, and sometimes even basic taxonomy is lacking for many weeds, which inhibits research and management, e.g., Hoste and Verloove (2022) and Verloove et al. (2023).

The southern African *Senecio inaequidens*–*Senecio madagascariensis* species complex (Asteraceae tribe Senecioneae), subsequently ‘fireweed complex’, contains several species that have established as introduced weeds outside of its area of origin. However, the exact circumscription of the complex is unclear, and species delimitation inside the complex has been questioned (Radford et al. 2000; Lafuma et al. 2003). Species concepts and identification of individual specimens in the fireweed complex remain broadly based on a taxonomic monograph of Asteraceae that is now 48 years old and was geographically restricted to the KwaZulu-Natal province of South Africa (Hilliard 1977).

The fireweed complex comprises the following species

Senecio madagascariensis Poir. is an annual to short-lived perennial herb with lanceolate to oblanceolate leaves. It is invasive in South America, Japan, the Hawaiian Islands, and Australia (Wijayabandara et al. 2022) and has recently been documented from New Zealand (Schmidt-Lebuhn et al. 2024). *Senecio madagascariensis* is also the species that has established in Mexico, although the name *S. inaequidens* is being misapplied to records from that country, both in scientific specimen collections and on iNaturalist

(inaturalist.org, accessed 18 Sept 2025). This is because, when first reporting on the weed introduction, Rzedowski et al. (2003) adopted a broad concept and treated the entire fireweed complex as a single species, exemplifying the aforementioned disagreements about its taxonomy.

Particularly troublesome on pastures, *Senecio madagascariensis* is classified as a Weed of National Significance in Australia and has long been the subject of biocontrol research (Holtkamp and Hosking 1993; McFadyen and Sparks 1996; McFadyen and Morin 2012). *Senecio madagascariensis* is currently considered to be a single species with a native range including both Madagascar and several countries of southern continental Africa. However, in its current circumscription, the species has two taxonomic synonyms, *S. jumodanus* O.Hoffm. and *S. ruderalis* Harv. (Red List of South African Plants, <http://redlist.sanbi.org/species.php?species=3152-272>, accessed 16 June 2024). Whereas the name *S. madagascariensis* is based on a type specimen from Madagascar, the two synonyms are based on type specimens from continental Africa.

Senecio inaequidens DC. is a perennial herb with narrowly lanceolate to linear leaves. It has spread across large parts of Europe as a weed of train tracks, roadsides, and urban areas (Lachmuth et al. 2010). The species is a polyploid complex (Lafuma et al. 2003). *Senecio harveianus* MacOwan, closely related to *S. inaequidens*, differs primarily in having more and longer calycular bracts. It is not currently considered to occur outside of southern Africa, but the name has previously been applied to other invasive species of the complex (Rzedowski et al. 2003). *Senecio skirrhodon* DC. is a perennial with broadly elliptic to oblanceolate, fleshy leaves and in southern Africa is a coastal species. It has become widespread and firmly established in New Zealand (Webb 1987).

Hilliard (1977) discussed *Senecio burchelli* DC. and *S. pellucidus* DC. as species from the Cape region that were frequently confused with members of the complex. The former is a dwarf shrub well differentiated by its smaller number of involucre bracts (ca. 13 v. ca. 20 in the other species). Its name has previously been misapplied to *S. madagascariensis* in Mexico and Argentina (Rzedowski et al. 2003). The name *S. pellucidus* is not currently being used by South African taxonomists and is therefore of uncertain application (Nicola Bergh, pers. comm.).

The majority of research into the diversity of the fireweed complex has focused on *Senecio madagascariensis*, generally to inform biocontrol research. In Australia, early work resolved taxonomic confusion, as the species had originally been considered part of a species complex native to Australia (Michael 1981). Its currently assumed identity as *S. madagascariensis* was based on analysis of nuclear ribosomal Internal Transcribed Spacer (ITS1) data, and the provenance of the invasive populations narrowed down to South Africa, as opposed to Madagascar (Scott et al. 1998).

A more broadly sampled study of the fireweed complex using clustering analyses of isozyme and morphological data concluded that Australian fireweed populations were most closely related to *Senecio madagascariensis* of KwaZulu-Natal but more distantly related to Eastern and Western Cape and Madagascan populations (Radford et al. 2000). This conclusion informed the design of subsequent studies, such as one of chloroplast microsatellite haplotypes from historical herbarium records that concluded several introduction events of *S. madagascariensis* to Australia (Dormontt et al. 2014). Based on Radford et al.'s (2000) inference, Dormontt et al. (2014) sampled nearly entirely from KwaZulu-Natal except for one near-coastal population far to the south (Boesmansriviermond).

Independently, Hawaiian populations of *Senecio madagascariensis* were inferred to be derived from KwaZulu-Natal (Le Roux et al. 2006). However, that conclusion was based on phylogenies of nrITS sequences that showed large, partly zero branch-length polytomies that support the rejection of a Madagascan origin but had insufficient resolution to differentiate between areas in continental southern Africa. In addition, sampling of continental areas was at any rate restricted to KwaZulu-Natal and Eswatini, neglecting several other regions where *S. madagascariensis* is known to occur. A phylogeographic study of populations of *S. madagascariensis* in southern South America concluded two waves of invasion, one from South Africa, the other “likely from various origins” (Brem et al. 2025).

Recently, we conducted a broadly sampled phylogenetic study based on the traditionally used high-copy markers nrITS, nrETS, and chloroplast *psbA-trnH* and *trnL* to clarify the relatedness of Australian native species of *Senecio* to *S. madagascariensis* (Schmidt-Lebuhn et al. 2020). However,

as in previous work discussed above, these traditional molecular markers were insufficient to resolve relationships within the fireweed complex with confidence.

We therefore explored target capture data from hundreds of low-copy nuclear genes (Johnson et al. 2019) and were able to use this approach to confirm the contested presence of *Senecio madagascariensis* in New Zealand (Schmidt-Lebuhn et al. 2024). Although focused on *S. madagascariensis* and *S. skirrhodon* from New Zealand and Australia, the dataset also included specimens from the South African province of KwaZulu-Natal and *S. inaequidens* from Europe. In the fireweed complex, the target capture data were able to resolve with high confidence three major clades representing *S. inaequidens* from Europe, *S. skirrhodon* from South Africa and New Zealand, and *S. madagascariensis*. All samples of *S. madagascariensis* were divided into two sister clades, one predominantly from KwaZulu-Natal but with two Australian samples, the other entirely of Australian and New Zealand samples. This result cast doubt on the established view of the provenance of invasive populations of *S. madagascariensis*. We also noted that European populations of *S. inaequidens* aligned morphologically with Hilliard's (1977) description of *S. harveianus* but were unable to draw firm conclusions, because we had sampled only a single specimen of that species and no southern African material of *S. inaequidens*.

In the present study, we expanded our dataset to the global scale to resolve uncertainties around the phylogenetic associations and likely invasion pathways of the fireweed complex, by including samples obtained from South America, Japan, the Hawaiian Islands, Madagascar, and a broader range of areas in continental southern Africa. The aims of our study are to (1) resolve genetic lineages in the fireweed complex, (2) clarify their taxonomy, and (3) infer the likely area of origin of invasive populations. These aims ultimately serve to inform biocontrol research. Accurate understanding of taxonomy—which entity in southern Africa has been introduced where?—underlies all communication and research, and an accurate understanding of weed provenances is critical for the exploration of candidate biocontrol agents.

Materials and methods

Sampling

We re-used sequence data from our previous study focused on New Zealand (Schmidt-Lebuhn et al. 2024), which included data published by the Plant And Fungal Tree Of Life consortium (PAFTOL) and the Genomics for Australian Plants consortium (GAP). Most newly added specimens were destructive samples of herbarium sheets kindly provided by the following collections: Bishop Museum, Honolulu, USA (BISH; herbarium acronyms according to Index Herbariorum, <https://sweetgum.nybg.org/science/ih/>), for the Hawaiian Islands; Queensland Herbarium, Australia (BRI), to expand sampling in the north of Queensland, Australia; Bews Herbarium of the University of KwaZulu-Natal, South Africa (NU), to expand geographic coverage of South Africa and Argentina; Royal Botanic Gardens & Domain Trust, Australia (NSW), for samples collected for biocontrol research in the 1990s in southern Africa, especially Madagascar; and National Museum of Nature and Science, Tsukuba (TNS), for Japan. Newly collected samples were obtained during field work in South Africa by co-author Daniella Egli, and Uruguayan specimens were kindly provided by Mauricio Bonifazino, Universidad de la República, Uruguay. Voucher information and Sequence Read Archive accession numbers for data newly generated for this study are available as Supplementary Data S1.

Three South African herbarium specimens were re-examined morphologically after being placed in unexpected positions in preliminary phylogenetic analyses and found to be *Senecio skirrhodon* that had been misidentified as *S. madagascariensis*. On updated identifications and following Hilliard's (1977) species concepts, our dataset included four specimens of *Senecio harveianus*, 19 of *S. inaequidens* (but see discussion below for their morphological variation), 83 of *S. madagascariensis*, and 15 of *S. skirrhodon*. In addition, the dataset included available data for other species of Asteraceae tribe Senecioneae to provide a phylogenetic context for the fireweed complex. We used four samples of three species of *Abrotanella* Cass. as outgroup for both orthology inference and phylogenetic analysis.

Lab procedures and bioinformatics

Part of the samples were processed by the Australian Genome Research Facility (AGRF, Melbourne). Genomic DNA was extracted using the NucleoSpin Plant II Kit (Macherey–Nagel, Düren, Germany) following the manufacturer's instructions and using Lysis Buffer PL2. Libraries were prepared using the NEBNext Ultra II FS Library Prep Kit (New England Biolabs, Ipswich, MA, USA), following the manufacturer's instructions and targeting a fragment size of up to 350 bp in the enzymatic fragmentation step. Libraries were enriched in pools of 12–16 using the Angiosperms353 MyBaits probe kit (Johnson et al. 2019) (Daicel Arbor Biosciences, Ann Arbor, MI, USA) with 65 °C hybridisation temperature, following the manufacturer's instructions.

For samples processed at CSIRO Black Mountain Laboratories, genomic DNA was extracted from 5–15 mg silica dried leaf tissue or herbarium material using Invisorb Spin Plant Mini Kit (Stratec, Berlin, Germany) or DNeasy Plant Mini Kit (Qiagen, Clayton, Australia) following the manufacturer's instructions. Some libraries were built from <1–5 ng of DNA using the QIAseq FX DNA Library UDI-A Kit 96 (Qiagen, Clayton, Australia) that included a DNA digestion step to a fragment size of approximately 200 base pairs. The remainder of DNA samples were sonicated to approximately 250 bp using the Covaris LL220 ultrasonicator with the following conditions: 55 µL DNA extract in 8 microTUBE-50 AFA Fiber Strip V2 tubes, PIP 450, DF 15%, CPB 1000, TT 120, 0.5 mm X-dither + 0.5 mm Y-dither at 10 mm/sec. Libraries were built from <1–5 ng of sonicated DNA using the QIAseq Ultralow Input Library Preparation kit (Qiagen, Clayton, Australia). All libraries were prepared in miniaturised format on the Echo 525 Acoustic Liquid Handler following the kit manufacturer's instructions with minor modifications to allow for automated high-throughput processing. Sequence capture was conducted on pools of sixteen libraries using the Angiosperms 353 MYbaits kit, following the manufacturer's "Standard-Plant" protocol (v5). Enriched libraries were sequenced on Illumina NovaSeq 6000 SP with v1.5 paired-end 2×150 cycle chemistry.

Raw sequence reads were quality filtered and paired with TRIMMOMATIC ver. 0.39 (Bolger et al. 2014) with illuminaclip: adapters, fa: 4: 20:10,

minimum length of 30, and average quality of 25, and then further filtered with bbduk ver. 38.90 (<https://github.com/BioInfoTools/BBMap/blob/master/sh/bbduk.sh>) with entropy of 0.8, entropy window of 20, and entropy mask t.

Phylogenetic analysis

Paired reads were assembled using hybpiper-nf (Jackson et al. 2023), a Nextflow pipeline adapted from HybPiper ver. 1 (Johnson et al. 2016) against a target file designed for broad representation of Asteraceae by mining transcriptome data for angiosperms 353 targets (McLay et al. 2021).

The results of HybPiper's paralog finder were analysed with the Monophyletic Outgroups (MO) algorithm as implemented in paragone-nf (Jackson et al. 2023), a Nextflow pipeline for the four gene-tree based paralogy resolution algorithms collated by Yang and Smith (2014). Custom-written Python scripts (<https://github.com/csiro/nrca-bioinformatics-and-phylogenetics>) were used to ensure that gene alignments were in frame and to concatenate them into a supermatrix.

A phylogeny of the concatenated supermatrix was inferred with IQTREE 2.2.0.5 (Minh et al. 2020), partitioning the alignment by codon positions and under automatic partition and model testing (Lanfear et al. 2017). Testing resulted in the three codon position partitions being maintained, with all three under the GTR+I+G4 model. One thousand UltraFast Bootstrap (UFB) replicates were used to estimate branch support (Minh et al. 2013).

As we observed that some specimens had an unstable phylogenetic position across preliminary analyses, we first conducted phylogenetic inference on all specimens originally intended for inclusion and examined the resulting UFB tree samples with RogueNaRok 1.0 (Aberer et al. 2013). We removed from the concatenated data matrix any terminals flagged as 'rogues' and repeated the phylogenetic inference, with identical partitioning and substitution model.

Genetic admixture

To examine the possibility of genetic admixture between lineages or specimens, we extracted Single Nucleotide Polymorphism (SNP) data of only the specimens of the fireweed complex for 324 of

the genes enriched using target capture and analysed population structure. Reference sequences for variant calling were created as consensus sequences across all sequences of a gene from *Senecio madagascariensis* using the gap_consensus function of BioPython. Align.AlignInfo. Variants were called following the same approach as Chen et al. (2025) using freebayes 1.3.7 (Garrison and Marth 2012).

Variants were filtered using VCFtools 0.1.16 (Danecek et al. 2011) and vcflib 1.0.1 (Garrison et al. 2022). Low-quality sites were removed (QUAL/DP>0.25 and -minQ 20-min-meanDP 4-max-meanDP 40-max 2-max-missing-count 55-remove-indels). Filtering was also performed for allelic balance (AB>0.25 and AB<0.75 | AB<0.01) and discrepancy in mapping quality between reference and alternative alleles (MQM/MQMR<2 and MQMR/MQM<2).

The resulting variant file was converted to geno format using a custom-written script (available at <https://github.com/csiro/nrca-bioinformatics-and-phylogenetics>). Population structure was analysed using sparse Non-Negative Matrix Factorization (sNMF) with the function snmf from the R library LEA v.3.18.0 (Frichot and François 2015) for values of K from 1 to 10 under default settings.

Cypselas morphology

Because we found the Madagascan and non-Madagascan specimens of *Senecio madagascariensis* to be placed in distant clades within the fireweed complex (see below), we explored if the two groups could be distinguished morphologically. Leaf division is highly variable in both clades, and we did not perceive any consistent difference in phyllary and calyculus traits. Because hairiness of the cypselas (fruits) and length and width of the hairs had previously been suggested as a potentially useful differentiating character (Radford et al. 2000; Le Roux et al. 2006), we focused our efforts on these. Preliminary examination of cypselas of Madagascan and Australian specimens available to us suggested that the former have more prominent ridges and grooves, thicker hairs, and lighter colouration than the latter.

Photos of 14 cypselas from five Madagascan and 28 cypselas from twelve Australian herbarium specimens (1–6 cypselas per specimen) were taken with a Galaxy A15 smartphone mounted with a

200×microscope lens (Apexel, Hong Kong). To maintain consistent conditions, all images were taken at an optical zoom level of 3.9x, with ring light activated, and on white herbarium sheets as a background.

For each cypsel, the width in pixels of five representative hairs was measured using ImageJ 1.52r (imagej.nih.gov/ij), and the mean calculated. This value was then converted into μm by calculating its ratio to the mean of five ImageJ measurements of a 1 mm scale photographed under the same conditions. To reduce surface colouration to a single gradient of lightness, all cypsel images were converted to greyscale using GIMP 2.10.18 (gimp.org). For each cypsel, the greyscale colour value of 0–255 of a representative part of the surface between hairs was measured with GIMP's Color Picker tool set to a radius of 20 pixels and the sample average setting. We conducted *t*-tests of hair width and surface colour in Madagascan *versus* Australian specimens and created box plots in R 4.2.1 (r-project.org).

Results

For the 111 new samples, we sequenced a total of ca. 648,000,000 reads, with on average 6,161,436 reads per sample (5, 500, 00–6, 820, 000 95% CI). The average percentage of on-target reads recovered was 57.87% (53.81%–61.93% 95% CI, median 64.41%, minimum 1.10%, maximum 87.31%). Only seven samples had fewer than 10% on-target reads recovered: *Abrotanella forsteroides* (Hook.f.) Benth. (CBG 9012273), *Senecio condylus* I.Thomps. (CANB 389276), *S. crassiflorus* (Poir.) DC. (CANB 521284), *S. hamersleyensis* (CBG 8503829), *S. macroglossus* DC. (CANB 546253), *S. madagascariensis* (NSW1005735, NSW1005751). In the case of NSW1005735, this resulted in the assembly of so few loci that it was excluded from analysis, but the other low-recovery samples were represented with 35–64 loci.

Phylogenetics

The concatenated target capture dataset comprised 210 terminals and 173,343 characters, of which 48,752 were parsimony informative, 35,849 variable but uninformative, and 88,742 constant. Missing or

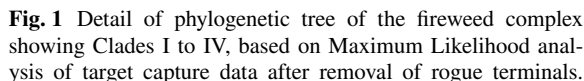
ambiguous nucleotide data comprised 29.54% of the concatenated data matrix. Terminals had data for 35–327 loci (median 296), and loci had data for 20–208 terminals (median 194). The Maximum Likelihood phylogeny of the concatenated data (Figs. 1, 2; Supplementary Figs. 1, 2) showed the fireweed complex as monophyletic with maximum support (UFB 100). A single sample from Western Cape Province originally doubtfully identified as *S. inaequidens* and labelled “perhaps more like *S. Burchellii*?” was sister to the remainder of the complex. Re-examination of the specimen confirmed that it is likely *S. burchellii*. Most other samples of the complex formed six major clades arranged along a grade, with some specimens placed in isolated positions with poor branch support.

In our first analysis (Supplementary Fig. 1), RogueNaRok flagged eight specimens as rogue terminals, i.e., as having an unstable phylogenetic position: a specimen identified as *Senecio leptophyllus* DC. based on absence of ray florets, a *S. skirrhodon* from New Zealand, two of *S. madagascariensis* from southern Africa and one from Australia, one of uncertain identity from southern Africa, and two specimens not belonging to the fireweed complex. Removal of rogue terminals slightly decreased the UFB support of some of the clades but increased it strongly from 69 to 100 for one clade and also strongly increased support for the backbone of the phylogeny (Supplementary Fig. 2). We therefore in the following present the phylogeny re-inferred after removal of rogue terminals.

Maximally supported Clade I included all samples of *Senecio madagascariensis* from Madagascar. Sister to it was a sample of *S. madagascariensis* from KwaZulu-Natal, albeit with poor support (UFB 60; Fig. 1).

Clade II included *Senecio harveianus* and most specimens of *S. inaequidens* both of South Africa and Europe; it received strong support (UFB 97), but within the clade, the two species were not reciprocally monophyletic (Fig. 1). Conversely, three other specimens morphologically matching *S. inaequidens* and collected in the South African province of Mpumalanga were placed outside of Clade II, sister to Clades II–VI.

Clade III comprised several samples collected for this study near Makhanda, Eastern Cape, that are characterised by leaves linear or divided into 4–6 narrow lobes and as such suggestive of *Senecio*

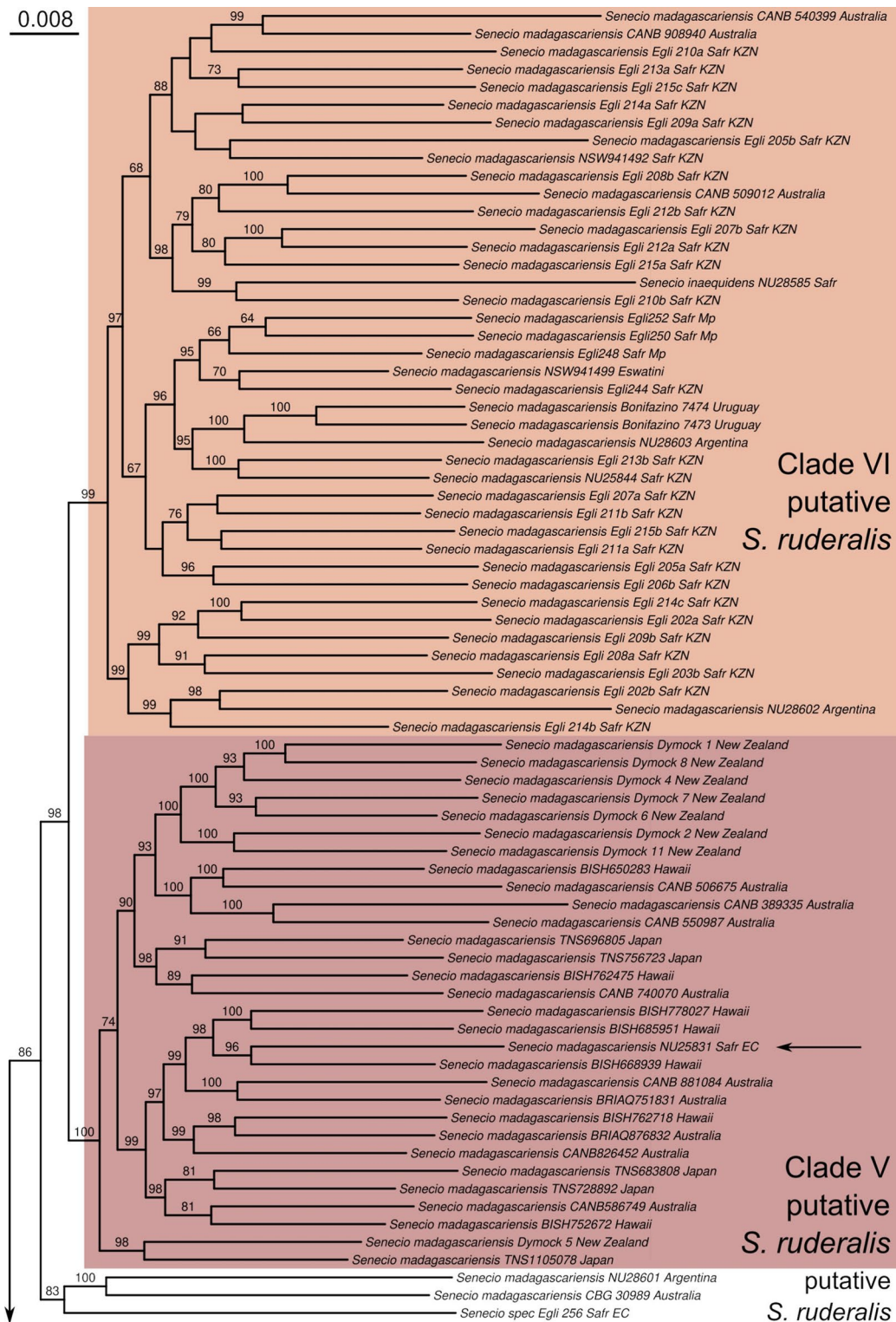


Numbers above branches indicate UltraFast Bootstrap values.
Abbreviations: EC=Eastern Cape, KZN=KwaZulu-Natal,
Mp=Mpumalanga, Safr=South Africa

Clade IV included all samples of *Senecio skirrhodon* both of South Africa and New Zealand but received only weak support (UFB 72; Fig. 1). A South African specimen in this clade, NSW 941930, had been misidentified as *S. madagascariensis*, but closer examination of its morphology in the light of its placement in the phylogeny revealed the characteristic habitat (beach dunes) and perennial habit of *S. skirrhodon*. Another specimen from Eastern Cape Province previously identified as *S. madagascariensis*, NU 25811, was similarly revealed to be *S.*

Clade V included a single sample of *Senecio madagascariensis* from Eastern Cape Province (close to the border of KwaZulu-Natal), NU 26831, all samples of *S. madagascariensis* from the Hawaiian Islands, Japan, and New Zealand, and nearly all samples from Australia (Fig. 2). Clade V received maximum support.

Sister to Clade V with high support (UFB 98), Clade VI included *Senecio madagascariensis* from South America, three Australian samples, and all continental southern African *S. madagascariensis*



◀**Fig. 2** Detail of phylogenetic tree of the fireweed complex showing Clades V and VI, based on Maximum Likelihood analysis of target capture data after removal of rogue terminals. Numbers above branches indicate UltraFast Bootstrap values. The arrow indicates the only sample in Clade V from the native range of the complex, Eastern Cape province of South Africa. All specimens in this figure except NU28585 are *Senecio madagascariensis* under current taxonomy but would become *S. ruderalis* if the two lineages are taxonomically recognised as separate species. Specimen NU28585 matches *S. inaequidens* morphologically but is strongly genetically admixed by Clade V, suggesting introgression. Abbreviations: EC=Eastern Cape, KZN=KwaZulu-Natal, Mp=Mpumalanga, Safr=South Africa

except the two aforementioned samples respectively placed in Clade V and sister to Clade I (Fig. 2). It also contained a single specimen of *S. inaequidens*, NU28585. Clade VI received high support (UFB 99).

Genetic admixture

Variant calling retrieved 35,705 SNPs at mean depth of coverage for each site of 49.12, of which 2,643 remained after quality filtering. Cross-entropy of sNMF results was lowest for $K=5$. The five ancestry clusters were roughly equivalent to (1) Clade I (Madagascan *Senecio madagascariensis*), (2) *S. inaequidens* and *S. harveianus* (Clade II and three specimens of *S. inaequidens* placed outside of Clade II in the phylogeny), (3) *S. skirrhodon* and Clade III, (4) Clade V (mostly continental African *S. madagascariensis*), and (5) Clade VI (mostly invasive *S. madagascariensis*) (Fig. 3; Supplementary Figure S3).

Specimens of *Senecio harveianus* and some European specimens of *S. inaequidens* showed higher levels of admixture from other clusters than African specimens of *S. inaequidens*. Several Australian specimens of *S. madagascariensis* and NU 26831 from Eastern Cape Province appeared admixed between the two continental African and invasive clusters of *S. madagascariensis*. The specimen morphologically matching *S. inaequidens* but placed in Clade VI in the phylogeny, NU28585, was admixed to approximately equal degree between *S. inaequidens* and Clade VI. Several specimens morphologically matching *S. madagascariensis* but placed outside of Clades I, V, and VI in our phylogenetic analyses showed strong admixture from various clusters.

Cypselas morphology

Madagascan (Clade I) and Australian (Clades V and VI) specimens of *Senecio madagascariensis* had hairs of significantly different and non-overlapping thickness, at $17.34 \pm 1.64 \mu\text{m}$ versus $12.46 \pm 1.46 \mu\text{m}$, $p = 1.76 \times 10^{-9}$ (Fig. 4a; Table 1). Although Madagascan specimens had on average lighter cypselas surfaces, the difference was not significant, and there was a large amount of overlap, at greyscale colour values of 84.43 ± 22.44 versus 70.68 ± 21.41 , $p = 0.07$ (Fig. 4b; Table 1).

Discussion

Non-monophyly of *Senecio madagascariensis*

All Madagascan samples of *Senecio madagascariensis* formed a distinctive Clade I separated from Clades V and VI comprising the continental southern African and invasive populations of *S. madagascariensis*, and after removal of rogue terminals, this divergence was maximally supported (UFB 100 for grouping of Clades II–IV to the exclusion of Madagascan Clade I). The Madagascan specimens also formed a separate ancestry cluster in sNMF, albeit with high degrees of admixture in three of the seven specimens. This confirmed previous studies indicating that Madagascar is not the area of origin of the invasive populations (Scott et al. 1998; Le Roux et al. 2006). More than that, however, it confirmed with greater confidence previous suggestions (Scott et al. 1998; Radford et al. 2000) that these continental and invasive populations of *S. madagascariensis* are more closely related to *S. skirrhodon*, and perhaps also to *S. harveianus* and *S. inaequidens*, than they are to Madagascan *S. madagascariensis*.

The taxonomic implication is that the Madagascan and non-Madagascan populations currently treated under that name may not constitute a single species. An alternative interpretation is that the entire fireweed complex is a polymorphic species (Lafuma et al. 2003). However, we consider this unlikely in light of the strong ecological divergence between species as currently accepted (Red List of South African Plants, <http://redlist.sanbi.org/genus.php?genus=3152>, accessed 18 March 2025), ranging from fleshy-leaved coastal dune plants in *Senecio skirrhodon* to narrow-leaved highland

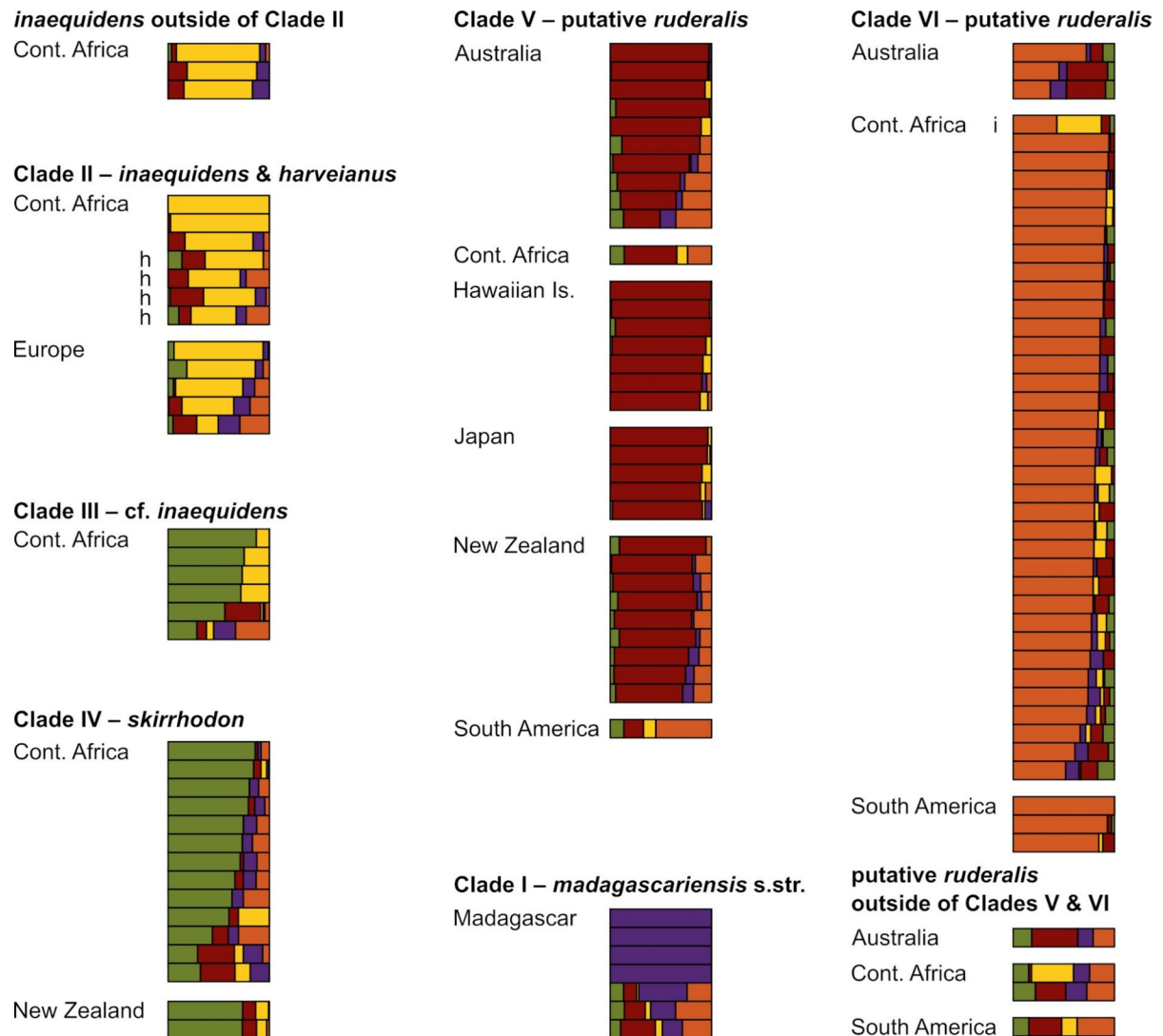


Fig. 3 Bar plot showing genetic admixture of samples of the *Senecio inaequidens*–*S. madagascariensis* complex at $K=5$ as inferred by sNMF analysis of 2,643 SNPs using the R library LEA. Cont.=continental. Specimens marked with h indicate

S. harveianus. The specimen marked with i morphologically matches *S. inaequidens* but was placed in Clade VI of *S. madagascariensis* (*S. ruderalis*) in phylogenetic analysis of target capture data

plants in *S. harveianus* and from annuals in *S. madagascariensis* to perennials in *S. harveianus*, *S. inaequidens*, and *S. skirrhodon*.

The type specimen of *Senecio madagascariensis* is from Madagascar, so that unless the name were to be protected as referring to the invasive entity here resolved as Clades V and VI, the continental African and invasive entity would require a different name. Of the two available taxonomic synonyms applying to continental African populations, *S. junodianus* and

S. ruderalis, *S. ruderalis* is the older name and would consequently have priority.

The name *Senecio ruderalis* is based on material from Durban, South Africa (W.T.Gerrard 324 & M.J.Mckenzie, [NH0011054-0](#), image seen; [TCD0001096](#) page 1, image seen), “Natal”, South Africa (*J.Sanderson* 326, [TCD0001096](#) page 2, image seen), and “near Delagoa Bay”, Mozambique (*W.B.Grant s.n.*, D, not seen). The three herbarium sheets of which images were available to us match the

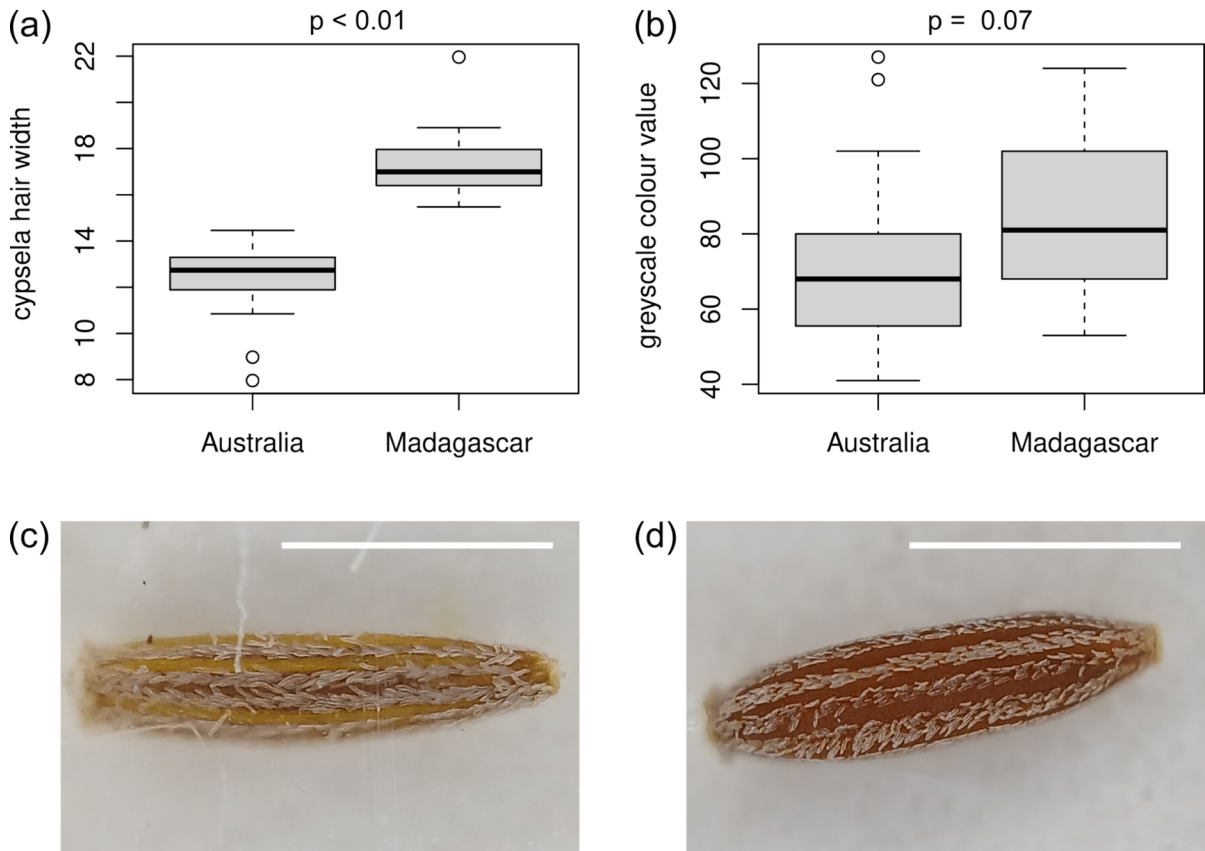


Fig. 4 Box plots of (A) mean hair thickness in μm and (B) cypselar surface colouration converted to greyscale colour values of *Senecio madagascariensis* as currently circumscribed for 14 cypselas from five specimens collected in Madagascar

and 28 cypselas from twelve specimens collected in Australia. Cypselas of selected (C) Madagascan (NSW 1005746) and (D) Australian (CBG 8323) specimens. Scale bars indicate 1 mm

morphology of Clades V and VI, sharing their leaf shape, number of involucre bracts and ray florets, and overall annual, top-branching growth habit. This suggests that the name *S. ruderalis* would apply to them if the taxonomic concept of *S. madagascariensis* were narrowed to only Clade I.

There are two caveats to this conclusion. First, our sampling from Madagascar was limited to specimens from only three locations, Toliara and the vicinity of Taolagnaro (“Fort Dauphin” and “Mandana Forest”). Wider geographic sampling could reveal several species to occur on the island. Second, we found it difficult to morphologically separate Clade I, *S. madagascariensis* s. str., from Clades V and VI, putative *S. ruderalis*, which may make it difficult to diagnose these lineages as different species or to produce a reliable identification key. Both lineages are annual and share narrowly

elliptic to oblanceolate or lanceolate leaves with serrate margins, involucre of ca. 20 bracts, and relatively few, short, lanceolate calycular bracts with a narrow scarious margin. Radford et al. (2000) were unable to morphologically differentiate Madagascan and continental populations of the species in their study. Following Le Roux et al. (2006) and Radford et al. (2000), we examined cypselar morphology and found that the thickness of the cypselar hairs may be a promising character to explore further on specimens of Clades V and VI from areas other than Australia (Fig. 4c, d).

Origins of invasive populations of “*Senecio madagascariensis*”

One of the aims of our study was to resolve the area(s) of origin of invasive populations of *Senecio*

madagascariensis (or putative *S. ruderalis*, i.e., Clades V and VI). Unfortunately, despite expanding our sampling in southern Africa, we resolved an invasive Clade V that included only a single sample from the native range of the species, from Eastern Cape province. The vast majority of samples from the native range, and all from KwaZulu-Natal and Mpumalanga provinces, were instead placed in Clade VI. Our data suggest the following conclusions:

The invasive populations currently called *Senecio madagascariensis* in the Hawaiian Islands, Japan, and New Zealand represent the same lineage, Clade V (Fig. 5). The populations introduced to South America constitute a second, separate lineage, Clade VI

(Fig. 5). Australian samples are found in both Clades V and VI, and in some cases placed in a small clade that is sister to Clades V and VI. It is possible that Australian populations are the result of repeated introductions, as has been suggested previously (Dormontt et al. 2014). As indicated by the results of the analysis of admixture, the isolated placement of some Australian specimens in the phylogeny is likely due to gene flow between Clades V and VI after introduction.

The provenance of the South American populations (Clade VI) can be narrowed down to the area of Eswatini and the South African provinces of KwaZulu-Natal and Mpumalanga. The provenance of the other invasive populations, however, cannot be

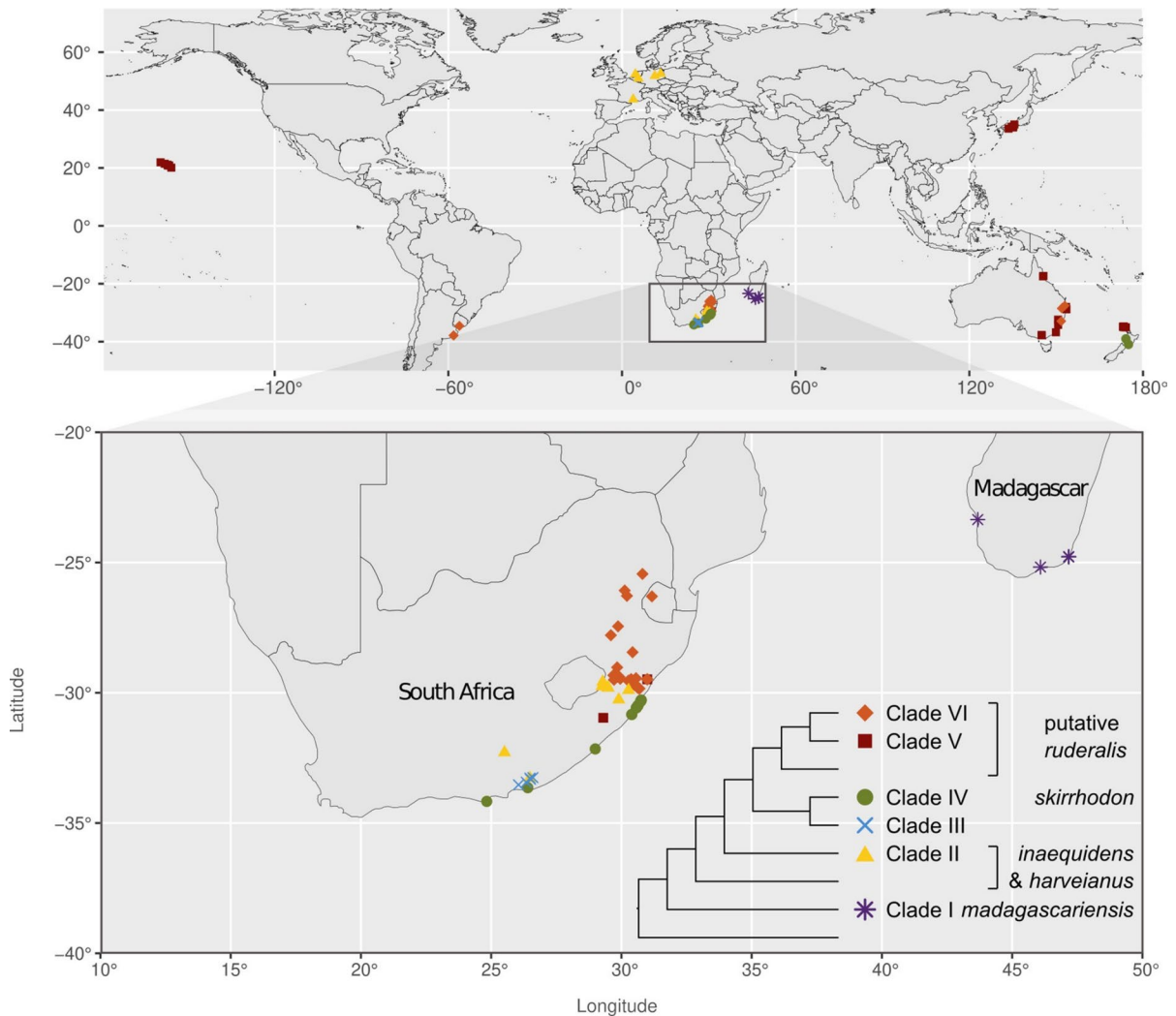


Fig. 5 Map showing global distribution of the specimens comprising the six clades resolved in the fireweed complex

deduced with certainty. There are two possible interpretations of the difficulty of inferring the provenance of Clade V. First, our sampling in southern Africa may remain insufficient. The single South African sample placed in Clade V is the southernmost sample of *S. madagascariensis* in our dataset, the only from Eastern Cape province (Fig. 5). It is possible that if additional specimens from the same area were sequenced, they would also be placed in Clade V, confirming this province as the area of origin.

Second, it is possible that the entire Clade V is of hybrid origin. An allopolyploid origin has been observed in other invasive taxa (Ainouche et al. 2009; Welles and Ellstrand 2016) and has been suggested for related *Senecio inaequidens* (Lafuma et al. 2003), as discussed below. A similar origin of Clade V would explain the difficulty of placing it in the phylogeny relative to samples from the area of origin. However, we currently have no firm evidence supporting this interpretation. Although all South African populations of *Senecio madagascariensis* examined by Lafuma et al. (2003) were diploid, and the species has been reported to be both diploid and tetraploid in Argentina (López et al. 2008), four counts of Australian specimens were diploid (Radford et al. 1995). It is possible that all of the Australian specimens counted by Radford et al. would have been placed in Clade VI if included in our study, but this appears improbable given the predominance of Clade V among Australian samples. sNMF did not reveal a higher degree of admixture in Clade V than in other clades or species and therefore did not support a hybrid origin of Clade V. It therefore seems more likely on current evidence that the problem remains insufficient sampling from Eastern Cape province, where Clade V may have originated.

Summary of taxonomic implications

Our study began with the specimens of Madagascan Clade I and continental African and invasive Clades V and IV identified and labelled as *Senecio madagascariensis*, reflecting the current taxonomy that treats all of these populations as a single species under that name. Our phylogenomic and admixture analyses subsequently revealed that these populations form two deeply divergent clades, indicating they should be recognised as distinct species. Applying taxonomic principles, we confirmed that the name

Senecio madagascariensis Poir. is typified by Madagascan material, meaning that the Madagascan lineage retains that name after taxonomic segregation. *Senecio ruderalis* Harv. is, to our knowledge, the oldest taxonomic synonym based on continental African specimens, which after taxonomic segregation makes it the name that has priority for the continental and invasive populations currently treated as *S. madagascariensis*. However, we refrain from making a formal taxonomic change until southern African plant taxonomists can be consulted on the matter and therefore refer to these populations as “putative *S. ruderalis*” in this study.

Senecio harveianus and *senecio inaequidens*

In a previous publication, we observed that the invasive European populations currently named *Senecio inaequidens* would key out to *S. harveianus* due to their several rows of long calycular bracts, the main morphological difference between the two species (Schmidt-Lebuhn et al. 2024). We added specimens of both species to the present dataset to test if South African specimens of both species could be differentiated genetically and which of them would group with the European material.

In our phylogeny, specimens of *Senecio harveianus* were nested inside those of *S. inaequidens*, and three samples of *S. inaequidens* were placed sister to Clades II–VI. This indicates that target capture data may not be sufficient to differentiate the two species, either because species are too recently diverged to have progressed lineage sorting to a sufficient degree or because of reticulate evolution. Similarly, sNMF did not separate *S. harveianus* and *S. inaequidens*, although it is possible that this is partly due to the small number of specimens of *S. harveianus* included in the analysis.

In a study of genome sizes, *Senecio inaequidens* was found to be diploid and tetraploid in its home range but only tetraploid in Europe (Lafuma et al. 2003). Based on the existence of diploid genotypes with slightly different genome sizes and the additive genome size of European plants, the authors hypothesised that invasive tetraploids are derived from a cross between two diploid genotypes overlapping near Lesotho. A subsequent study of the invasion history of *S. inaequidens* using AFLP and microsatellite data

concluded that it was characterised by multiple introductions and high gene flow (Lachmuth et al. 2010).

The failure of *Senecio inaequidens* and *S. harveianus* to form distinct clades and clusters may therefore be due to frequent gene flow between its two constituent species. Too much uncertainty remains to suggest a new identification for the European populations of *Senecio inaequidens* despite their calyculus morphology matching Hilliard's (1977) concept of *S. harveianus*.

In sNMF, the isolated specimen of *Senecio inaequidens* placed in Clade VI of the phylogeny (NU 28585) was strongly and approximately evenly admixed between the clusters dominated by *S. inaequidens* and by Clade VI. This suggests that it may be a hybrid between the two lineages that favors *S. inaequidens* morphologically.

Clade III consists mostly of specimens collected near Makhanda, Eastern Cape, that have an annual habit but sometimes branch strongly from the base and have narrowly linear to narrowly lobed leaves that are reminiscent of perennial *Senecio inaequidens* and *S. harveianus*. In sNMF, they were shown as admixed between *S. skirrhodon* and the cluster dominated by *S. inaequidens*. These specimens may constitute a distinct species or the result of hybridization. A dedicated study of more comprehensively sampled South African material would be required to confirm the taxonomic identity of this lineage and resolve the delimitation of *S. inaequidens*.

Implications for biocontrol research

Biocontrol has been investigated as a potential management tool for fireweed since the early 1990s (Sheppard et al. 2011). Clarity around the taxonomy of the fireweed complex and the provenance of invasive populations is still needed to advance research into the establishment of biocontrol agents and weed management more broadly, for example by pinpointing where native range exploratory surveys of candidate biocontrol agents should be undertaken, (e.g., Schmidt-Lebuhn et al. 2024).

Based on previous studies using isozyme and Sanger sequence data with limited geographic sampling, biocontrol researchers had in recent decades assumed that invasive populations of *Senecio madagascariensis* originate from the South African

province of KwaZulu-Natal (Radford et al. 2000; Le Roux et al. 2006; Dormontt et al. 2014). However, the different performance of the priority candidate biocontrol agent (a stem-boring weevil, *Gasteroclisus tricostalis*) on Australian and KwaZulu-Natal populations (Singh et al. 2024) and a recent study demonstrating differences in chemical defences between the Australian and KwaZulu-Natal populations (Egli et al. 2022) suggested that weevils sourced from KwaZulu-Natal were not genotypically matched to the invasive Australian populations of *S. madagascariensis*.

The placement of *S. madagascariensis* specimens from KwaZulu-Natal in Clade VI of our phylogeny and of most of the Australian specimens in Clade V adds support to the hypothesis that previous surveys of invasive populations for candidate biocontrol agents with a highly restricted host range may not have sampled broadly enough throughout southern Africa and/or used molecular markers with insufficient resolution to pinpoint optimal source location(s). Indeed, in a study of field host-plant affinities of stem-boring weevils and moths associated with *S. madagascariensis* in KwaZulu-Natal, Singh et al. (2022) found that there was a high degree of genotypic variability (based on maximum likelihood COI phylogeny) in populations of the candidate biocontrol agent *Gasteroclisus tricostalis* both within and between different host plant taxa. Such genotypic variability was sympatric, occurring within the same plant populations. This implies that *G. tricostalis* is a diverse species complex, likely with a high degree of spatial variation across the native range of *S. madagascariensis* in southern Africa.

We recommend, therefore, that any future research on *G. tricostalis* or other candidate biocontrol agents should be expanded geographically across southern Africa, focused on areas with *S. madagascariensis* (=putative *S. ruderalis*) populations most closely related to those in Australia, New Zealand, and elsewhere. Further research is also required to characterise the variation in population-level associations between the weevil *G. tricostalis* and *S. madagascariensis* populations across South Africa, given the high degree of genotypic variation in both the weevil and host plant (Singh et al. 2023). Addressing such uncertainties would help pinpoint locations and genotypes for future candidate biocontrol agent exploratory surveys (Table 1).

Table 1 Voucher information, mean cypselar hair width (n = 5) and cypselar surface greyscale colour values for Madagascan and Australian specimens of *Senecio madagascariensis* as currently circumscribed

Geography	Specimen	Image	Cypselar hair width [μm]	Cypselar surface
Australia	CANB 474501	20241015_172921	11.3	102
	CANB 474501	20241015_172944	11.7	121
	CANB 474501	20241015_172958	8.0	89
	CANB 474501	20241015_173026	9.0	127
	CANB 474501	20241015_173046	12.6	93
	CANB 506675	20241015_175154	11.0	72
	CANB 540399	20241015_174327	12.8	77
	CANB 550987	20241015_174125	14.0	69
	CANB 550987	20241015_174137	12.3	83
	CANB 550987	20241015_174149	12.6	69
	CANB 710131	20241015_172506	14.3	88
	CANB 710131	20241015_172650	13.7	74
	CANB 810447	20241015_174842	12.1	48
	CANB 866598	20241015_173548	13.1	57
	CANB 866598	20241015_173633	12.7	62
	CBG 30989	20241015_174544	13.4	74
	CBG 30989	20241015_174555	13.2	60
	CBG 46160	20241016_144454	14.5	54
	CBG 46160	20241016_144502	14.0	47
	CBG 8323	20241016_144828	12.9	52
	CBG 8323	20241016_144835	12.8	65
	CBG 8323	20241016_144851	12.7	75
	CBG 9403116	20241016_144018	13.4	48
	CBG 9403116	20241016_144028	13.0	57
	CBG 9403116	20241016_144045	11.7	49
	CBG 9403116	20241016_144112	12.7	41
	CBG 9407224	20241016_144224	12.8	67
	CBG 9407224	20241016_144305	10.9	59
Madagascar	NSW 1005734	20241015_155950	22.0	80
	NSW 1005734	20241015_160101	16.7	68
	NSW 1005734	20241015_160140	15.5	124
	NSW 1005734	20241015_160225	16.1	82
	NSW 1005737	20241016_140002	15.9	69
	NSW 1005737	20241016_140017	17.2	102
	NSW 1005746	20241015_154810	17.2	116
	NSW 1005746	20241015_154831	16.4	117
	NSW 1005751	20241016_140837	18.9	85
	NSW 1005751	20241016_140853	18.4	89
	NSW 941500	20241016_140256	16.8	64
	NSW 941500	20241016_140312	16.4	53
	NSW 941500	20241016_140347	18.0	64
	NSW 941500	20241016_140400	17.3	69

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Author's contribution A.N.S.L. and B.G. designed the study. D.E. collected plant material. A.G. conducted lab work. A.N.S.L. conducted analyses. All authors contributed to writing and approved the final version of the manuscript.

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Data availability Raw sequence read data generated newly for this study are available at the Sequence Read Archive under accession numbers SRR31282202 to SRR31282312. Detailed voucher information is provided as Supplementary Data S1. Phylogenetic trees, sequence data alignments, and cypselas are available on the CSIRO Data Access Portal at <https://doi.org/10.25919/pzpk-tg88>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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