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REVIEW

Leveraging natural history collections to understand the impacts of global change

Parasitic flowering plant collections embody the extended specimen

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Abstract

1. The widespread digitization of natural history collections, combined with novel tools and approaches is revolutionizing biodiversity science. The 'extended specimen' concept advocates a more holistic approach in which a specimen is framed as a diverse stream of interconnected data. Herbarium specimens that by their very nature capture multispecies relationships, such as certain parasites, fungi and lichens, hold great potential to provide a broader and more integrative view of the ecology and evolution of symbiotic interactions. This particularly applies to parasite–host associations, which owing to their interconnectedness are especially vulnerable to global environmental change.
2. Here, we present an overview of how parasitic flowering plants is represented in herbarium collections. We then discuss the variety of data that can be gathered from parasitic plant specimens, and how they can be used to understand global change impacts at multiple scales. Finally, we review best practices for sampling parasitic plants in the field, and subsequently preparing and digitizing these specimens.
3. Plant parasitism has evolved 12 times within angiosperms, and similar to other plant taxa, herbarium collections represent the foundation for analysing key aspects of their ecology and evolution. Yet these collections hold far greater potential. Data and metadata obtained from parasitic plant specimens can inform analyses of co-distribution patterns, changes in eco-physiology and species plasticity spanning temporal and spatial scales, chemical ecology of tripartite interactions (e.g. host–parasite–herbivore), and molecular data critical for species conservation. Moreover, owing to the historic nature and sheer size of global herbarium collections, these data provide the spatiotemporal breadth essential for investigating organismal response to global change.
4. Parasitic plant specimens are primed to serve as ideal examples of extended specimen concept and help motivate the next generation of creative and impactful collection-based science. Continued digitization efforts and improved curatorial practices will contribute to opening these specimens to a broader audience, allowing integrative research spanning multiple domains and offering novel opportunities for education.

KEYWORDS
digitization, extended specimen, global change biology, haustorium, herbarium, natural history collections, parasitic plants, species interaction

1 | INTRODUCTION

Natural history collections underpin most biodiversity investigations, serving as crucial resources for species identification, taxonomy, biogeography and evolutionary history (Heberling et al., 2019; Meineke, Davies, et al., 2019). These collections are also critical for education and promotion of inquiry-based training and active learning (Lacey et al., 2017; Powers et al., 2014). These well-established and common applications of natural history collections have, in recent decades, been complemented by a variety of new approaches facilitated by technological advances, including next generation sequencing and isotope analysis, as well as by extensive efforts in specimen digitization and online data sharing (Hedrick et al., 2020; Hilton et al., 2021; Meineke et al., 2018; Nelson & Ellis, 2019). As a result of these developments, studies in a variety of realms such as functional ecology, ecological modelling, phenology, morphometrics and education have been greatly stimulated by the increasing availability of big data captured from specimens (Heberling, 2022; Hedrick et al., 2020; Monfils et al., 2017).

The ongoing revolution in the application of natural history collections in cutting edge and timely research is framed in the concept of the 'extended specimen'. Proposed by Webster (2017), the idea represents the totality of data types associated with a specimen, including frequently overlooked data streams, which together provide a broader view of the individual's extended phenotype. This framework is a great motivator for deeper exploration of biodiversity data via innovative preparations and analyses of natural history collections (Lendemer et al., 2020). In particular, the practice of 'holistic sampling' builds on the extended specimen by advocating for the collection and analysis of closely associated symbionts in addition to the focal species, such as parasites/hosts, that are preserved but frequently overlooked in the specimen (Schindel & Cook, 2018). In fact, natural history collections that 'extend' the main specimen by preserving and curating its collection of associated species not only optimize sampling efforts, but also have the potential to promote new interdisciplinary approaches (Thompson et al., 2021). As specimens that inherently contain multispecies relationships, such as lichens, and certain parasites and fungi, we suggest that parasitic plant species serve as key examples in the development of the extended specimen. From a parasite specimen (Figure 1a), the first extension is digitization, including the digital specimen image and its record (Lendemer et al., 2020). Secondary extensions relate to molecular, isotopic and chemical data, as well as anatomical, phenological and environmental information about the species and its symbiont(s) (Figure 1b). These data further enable tertiary extensions, stimulating research areas like biogeography, species distribution, ecological modelling and functional ecology of parasites and hosts (Figure 1c). Here, we use parasitic plant specimens as an iconic ideal representation of the Extended Specimen concept as well as an example that can be expanded to many other specimen types that capture ecological interactions.

Our focus on parasitic species as key 'specimen extensions' is warranted by the fact that parasitism is the most common form of symbiosis and feeding modality; indeed, all organisms engage in parasitic relationships at some level by being either hosts and/or parasites (Combes, 2001). These interactions are essential to biodiversity, ecosystem functioning and evolutionary processes. Specifically, parasites have repeatedly been shown to modulate intraspecific competition, community composition, species migration and local abundance of both host and non-host species thereby providing key ecosystem services (Combes, 1996; Frainer et al., 2018; Karvonen & Seehausen, 2012; Phoenix & Press, 2005). In the face of continued global change, parasitic interactions are expected to play an even greater role in ecological and evolutionary dynamics, leading to a cascade of potentially community-wide effects that may outweigh direct effects of global change upon a single species (Gilman et al., 2010). For instance, many parasites depend on intermediary hosts or mutualistic species to complete their life cycles; increased temperatures can cause ecological mismatches among species, thus aiding the accelerated evolution of parasite resistance by host populations (Mateos-Gonzalez et al., 2015) or restricting future parasite distributions (Ornelas et al., 2018). In turn, changes in parasite abundance and distribution can modify the outcome of species competition, triggering ecosystem instability (Combes, 1996). At the same time, recent research in conservation biology demonstrates that parasites face increased extinction risk and are vulnerable to both direct impacts due to climate change, and indirect impacts through coextinction with hosts (Carlson et al., 2017, 2020). Thus, parasite collections are especially important for understanding changes in complex biological systems over broad spatial and temporal scales (Brooks & Hoberg, 2007; Harmon et al., 2019).

In the case of many zoonotic parasites, collections are hindered by poor representation relative to other taxa, lack of vouchered specimens and other curatorial difficulties (Bell et al., 2018; Thompson et al., 2021). On the other hand, a wealth of parasite specimens in other collections is already available but is seldom explored in the context of global change biology (Andrew et al., 2019). This is the case of parasitic angiosperm specimens in herbaria, which despite attracting research in the areas of plant taxonomy, phylogenetics and biogeography, remain frequently ignored in general discussions about parasitism and overlooked in their potential for integrative research. With the development of the extended specimen concept and increasing interest in novel applications of natural history

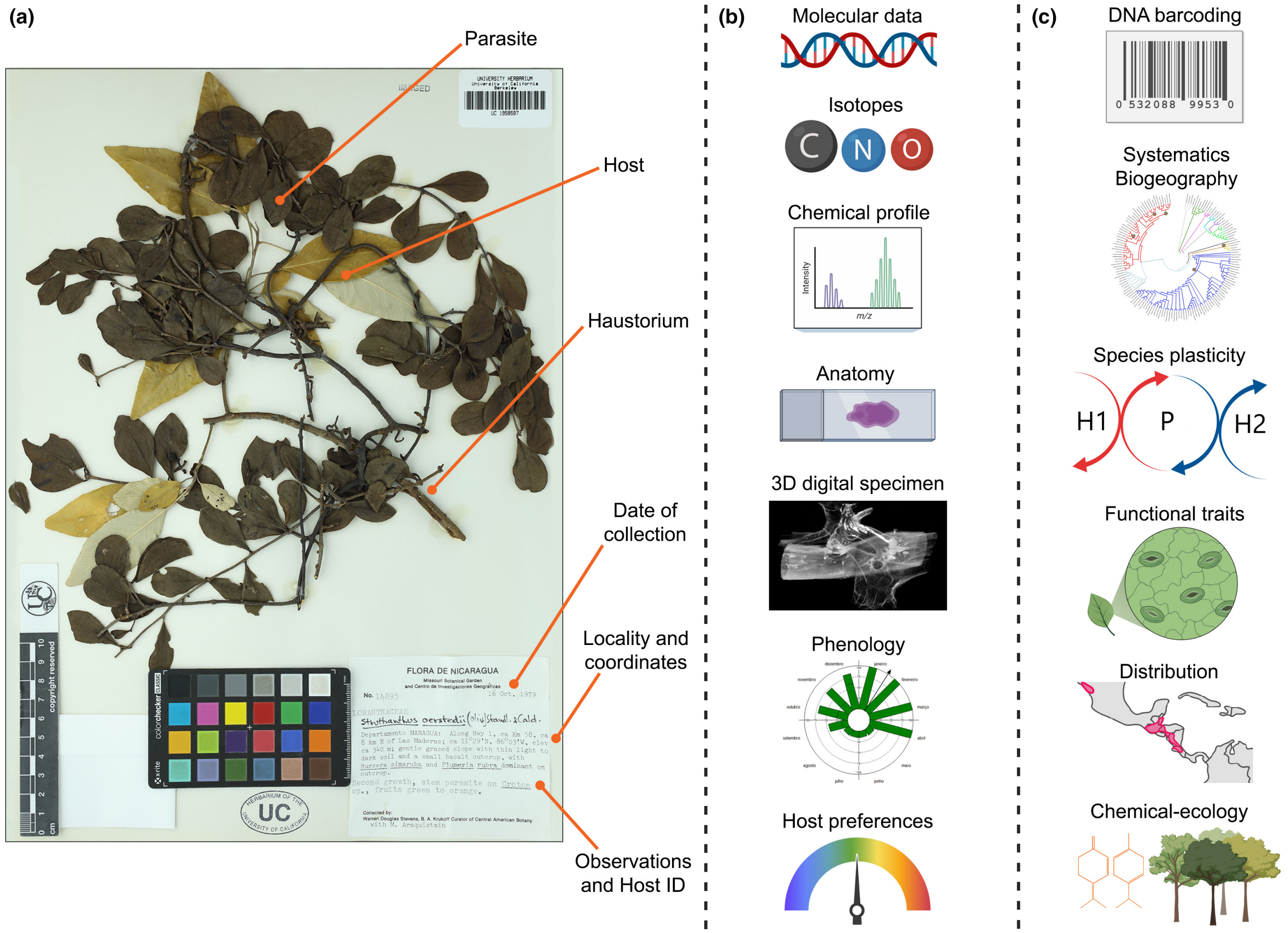

FIGURE 1 Parasitic plant specimen (a) including parasite and host material, as well as the haustorium connection between the two plants. From these, secondary extensions (b) in the form of molecular, isotopic, chemical, anatomical, phenological and environmental data can be generated. Tertiary extensions (c) emerge from the combination of these data, stimulating broader research in ecology and evolution

collections, now is the time to view parasitic plant specimens in a new light.

The parasitic lifestyle has evolved multiple times within land plants, involving at least two different modes of resource acquisition (Heide-Jørgensen, 2013). A first mode includes mycoheterotrophic plants, which have adopted an indirect procurement of nutrients via mycorrhizal fungal intermediaries (Merckx et al., 2009). In contrast, the more specialized of these parasitic nutritional modes depends on development of the haustorium, a hybrid root–shoot organ that acts as a living bridge, connecting parasite and host plants (Teixeira-Costa, 2021). These haustorial parasitic plants, which are the focus of this review, penetrate and remain physically attached to their hosts via the haustorium from initial stages of parasitism onwards. Shortly after penetration, a vascular connection is established between the two plants, thus allowing water and resource uptake by the parasite, as well as the bilateral exchange of hormones, proteins and genetic material (Yoshida et al., 2016). This highly specialized organ, and the parasitic lifestyle coupled with it, is associated with a wide variety of life histories, host specificities, morphological traits and eco-physiological attributes (Teixeira-Costa & Davis, 2021). These peculiar characteristics have long captured the attention of naturalists and plant collectors. Perhaps not surprisingly, parasitic plant species are among the first known herbarium collections in modern history (Stefanaki et al., 2018).

The morphological and functional diversity of these parasites is further mirrored by the wide network of interdependencies they form, which goes far beyond host relationships to include pollinators, seed dispersers, herbivores and pathogens (Watson & Herring, 2012). Field studies have also demonstrated that parasitic plants might extend their impact to other plant, animal and fungal species with which they are indirectly associated (Cullings et al., 2005; Hartley et al., 2015; Spasojevic & Suding, 2011). It is noteworthy that while most plants are ecologically interconnected to other species, such as pollinators and seed dispersers, parasitic plants can also have an impact on multiple trophic levels including species with which they are only indirectly associated, such as invertebrate and microbes. For this reason, as well as for their disproportionally large effect in modulating community structure and ecosystem function, both in natural and urban areas, parasitic plants are often considered keystone species (Phoenix & Press, 2005). In this context, parasitic plant specimens represent ‘information hubs’ from which a broad swath of secondary and tertiary extensions (Figure 1, sensu Lendemer et al., 2020) can be gathered and applied to studies ranging from co-evolutionary dynamics to macro-ecology and plasticity of both directly and indirectly associated species (Figure 2).

Global change research can benefit from well-curated parasitic plant collections and the richness of data they preserve. Here, we review how parasitic plant diversity is represented in natural history collections, especially herbarium records. We then discuss the various ways these collections can be applied to understand global change impacts at multiple scales. Finally, we comment on best practices for sampling parasitic plants in the field, and subsequently preparing and digitizing specimens.

2 | PARASITIC PLANTS IN HERBARIA: A GLOBAL ASSESSMENT USING GLOBAL BIODIVERSITY INFORMATION FACILITY

The most recent account of parasitic plant taxonomic diversity recognizes nearly 5,000 species, classified in 12 distinct clades and constituting *c.* 1.6% of all extant angiosperm species (Nickrent, 2020; Teixeira-Costa & Davis, 2021). This large number of species is distributed across all continents (except Antarctica) and several remote islands, spanning all terrestrial biomes, from large deserts to the high arctic (Heide-Jørgensen, 2013; Teixeira-Costa & Davis, 2021). Owing to their broad distribution, parasitic plants are well represented in most major herbarium collections. Although the vast majority of the 396+ million specimens spanning more than 3,000 herbaria globally (Thiers, 2021) have yet to be digitized and mobilized online, a significant number of records are already available in biodiversity aggregators enabling large, synthetic analysis addressing basic questions and novel ideas (Heberling & Isaac, 2017; Hedrick et al., 2020; Soltis, 2017). To stimulate novel research using parasitic plant herbarium specimens, we present an overview of how these plants are represented in digitized collections around the globe and discuss biases in their representation to guide future priorities for collection and digitization efforts.

To accomplish our goal, preserved specimen records for all 12 parasitic plant clades were obtained from the Global Biodiversity Information Facility (GBIF.org, 2021: https://doi.org/10.15468/dl.dpsg3s). The dataset was initially filtered to exclude records without species identity below family (e.g. genus and species), and

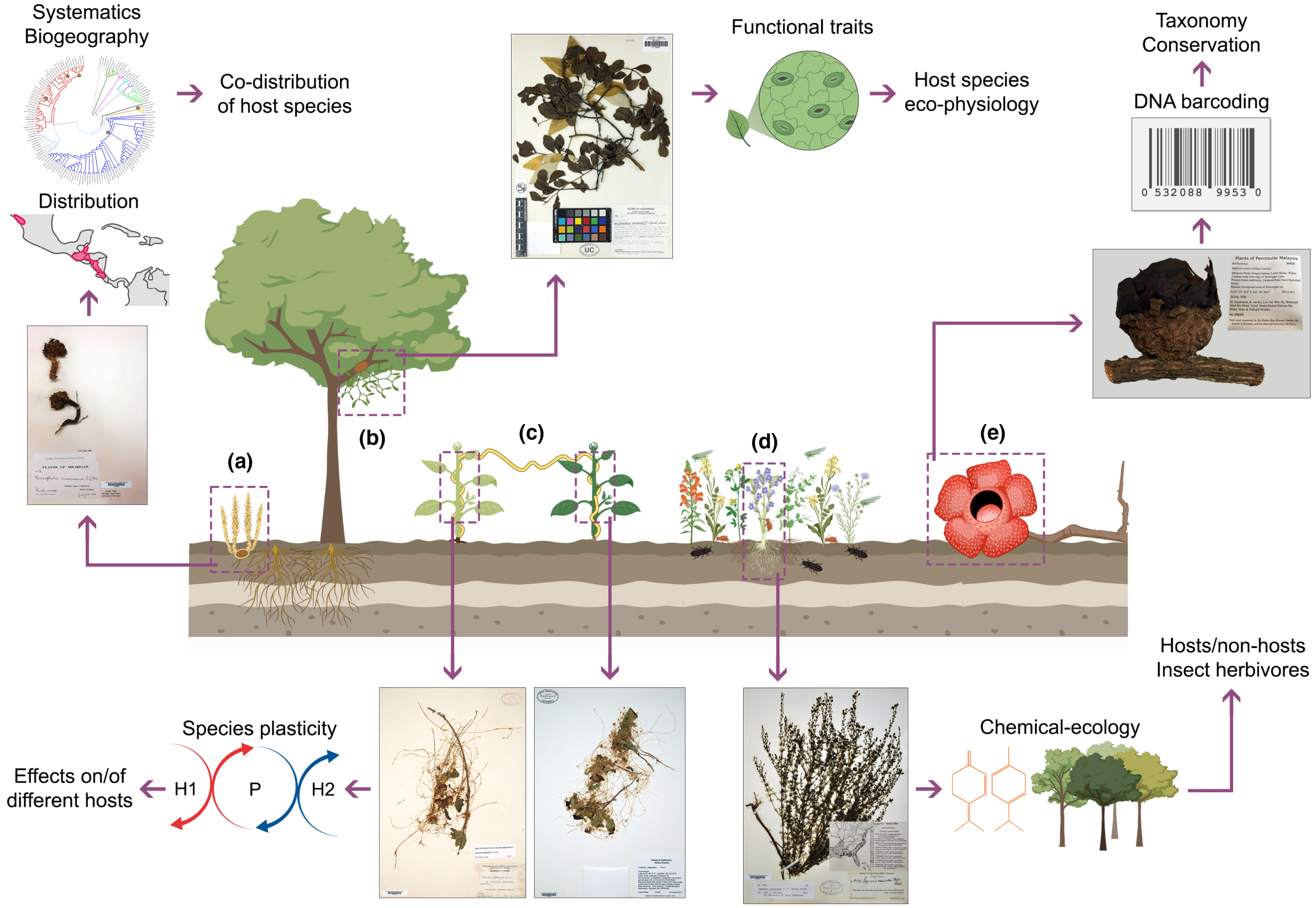

FIGURE 2 Secondary and tertiary extensions of parasitic plant specimens can be applied to a range of studies focusing on parasite–host co-distribution patterns (a); host eco-physiology (b); plant phenotypic plasticity (c); chemical ecology of tripartite relationships (d); host taxonomy; and species conservation (e)

records with no information on the institutional provenance of the specimen. In cases when the field 'institution code' was empty, an attempt was made to obtain this information by analysing other fields, namely 'collection code', 'catalogue number', 'record number' and 'rights holder'. Collections belonging to the same institution were grouped under a single institutional code (e.g. A, AMES, ECON, FH, GH and NEBC collections were classified as 'HUH'—Harvard University Herbaria). A total of 1,017,028 records were included in our final analysis (Table 1).

Considering the total number of currently recognized species of parasitic flowering plants (Nickrent, 2020; Teixeira-Costa & Davis, 2021), the overall representation of digitized herbarium specimens of parasites in GBIF results in an average of 206 specimens/species. This ratio vastly surpasses the number of digitized specimens representing other symbiotic associations, indicating that parasitic plants are a well collected and mobilized functional category of plants. Parasitic animals and protozoans, for instance, are estimated to include a massive 3.5 million species (Dobson et al., 2008; Mora et al., 2011) but are represented by only ~2.8 million specimen lots on GBIF (Bell et al., 2018). Nevertheless, we observe that collections of parasitic plants are not uniformly distributed: 11.6% of these species are absent from GBIF (Table 1). This lack of records might be partially explained by unresolved issues in taxonomically complex genera, especially within the Orobanchaceae (Robart et al., 2015; Tank & Olmstead, 2009; Yu et al., 2018). Differences in digitization efforts and priorities among institutions are also likely to play a role in the absence or under-representation of species in the analysed data. As more specimens become digitized world-wide and available online, we will have a better understanding of what strengths, biases, and gaps exist in parasitic plant collections (Nelson & Ellis, 2019).

Most of the analysed records belong to Orobanchaceae (53.7%; Table 1), a large family with a cosmopolitan distribution and the only parasitic plant clade to occur in high latitude areas, including the coast of Greenland (Heide-Jørgensen, 2013, 2014). The Santalales, despite being the largest and most functionally diverse parasitic plant clade (Teixeira-Costa & Davis, 2021), is represented by 32% less records when compared to the Orobanchaceae (Table 1). This difference could be explained by the fact that, within GBIF, Orobanchaceae is present in 98 more institutions than Santalales (Table 1). Differences in digitization efforts among institutions (due to insufficient funding or staffing, etc.) could also account for these differences. Furthermore, because all Orobanchaceae species are annual or perennial herbs, sampling efforts are comparatively easier than what is required to collect samples from large trees and aerial parasitic shrubs (i.e. mistletoes) which comprise the bulk of Santalales. The pronounced tropical (Santalales) versus temperate (Orobanchaceae) distributions in the abundance of species between these groups may further help to explain these differences.

Another interesting comparison can be made among clades composed exclusively of endoparasites (i.e. Apodanthaceae, Cytinaceae, Mitrastemonaceae and Rafflesiaceae). Species in these four families have independently evolved a strategy similar to that of many biotrophic fungi, that is, growing incognito within their host plants and only becoming visible to the human eye during short reproductive phases (Thorogood et al., 2021). These four clades have similarly restricted distributions and many of their species are considered rare (Burgoyne, 2006; Hidayati et al., 2000; Mir et al., 2016). Nevertheless, Rafflesiaceae, which includes as many species as the other three endoparasite groups combined (Table 1), is one of the least represented parasitic plant lineages in GBIF. Considering that Rafflesiaceae species are famous for developing the world's largest flowers (Nikolov & Davis, 2017), a lack of publicly available records may also be related to difficulties in creating and digitizing adequate

TABLE 1 Species diversity in each parasitic plant lineage and their representation in herbarium collections available on the GBIF database

Parasitic plant lineage	Total number of species[a]	Species represented	Collections[b]	Records[b]	% of total records
Apodanthaceae	10	10	144	2,124	0.21
Cassytha	20	19	259	17,873	1.76
Cuscuta	215	187	530	61,132	6.01
Cynomoriaceae	1	1	61	515	0.05
Cytinaceae	12	12	106	2,282	0.22
Hydnoraceae	12	12	47	421	0.04
Krameriaceae	23	16	251	14,266	1.40
Lennoaceae	4	4	82	1,020	0.10
Mitrastemonaceae	2	2	29	148	0.01
Orobanchaceae	2,183	1,880	721	545,908	53.68
Rafflesiaceae	36	22	41	252	0.02
Santalales	2,428	2,189	623	371,087	36.49
Totals	4,926	4,354	950 unique collections	1,017,028	100

[a] Based on Nickrent (2020).

[b] A total of 245,918 records were excluded from the analysis due to missing data (collection identity and/or genus identification not provided).

vouchers for large and cumbersome specimens (some of which are often preserved in spirit).

Within each parasitic plant clade, we also analysed which species are most abundant in the dataset and which institutions house the most specimens. In most cases, species with wider geographic ranges were not surprisingly the most well represented in each clade. Hydnoraceae and Krameriaceae were notable exceptions; here, the most widespread species were not the best represented in GBIF. For example, *Hydnora johannis* Becc. (Hydnoraceae), distributed across most of central and northeast Africa (Musselman & Visser, 1989), and *Krameria tomentosa* A. St.-Hil. (Krameriaceae), distributed across most of Brazil and parts of Bolivia (Simpson, 1989), represented only *c*. 3% and 13% of the records in each of their respective families (Table 1). These instances are likely to reflect collection biases, as in both cases the best represented species for these two families (*H. africana* Thunb., Hydnoraceae and *K. erecta* Willd., Krameriaceae) are distributed in areas close to larger research institutions and herbaria, which represents a well-known collecting bias (Daru et al., 2018; Musselman & Visser, 1989; Simpson, 1989).

It is also unsurprising that most records per institution were derived from the Muséum National d'Histoire Naturelle (France), the New York Botanical Garden (USA), the Missouri Botanical Garden (USA), the Smithsonian Institution (USA), and Naturalis (Netherlands), which are among the largest herbaria in the world and the earliest adopters of industrial-scale digitization (Thiers, 2021). Digitized records from these collections alone represent over 250,000 records, constituting *c*. 25% of the analysed specimen data we analysed. Nevertheless, an interesting trend was observed for five parasitic plant families, whose species collectively have restricted geographic distributions. In the case of Apodanthaceae, Hydnoraceae, Krameriaceae, Lennoaceae and Mitrastemonaceae, most records available in GBIF are held by medium-sized herbaria, each of which house less than 2 million specimens in their collections (Table 2). On the other hand, larger institutions, those with more than 5 million specimens, house greater species diversity for each of these families (Table 2). It is noteworthy that data available in GBIF does not allow us to analyse how comprehensive the digitization of these families is for each herbarium, nor how each institution has chosen to prioritize which specimens to digitize. Nevertheless, our observations suggest that, while large collections provide crucial material for phylogenetic and taxonomic investigation, medium-sized herbaria contribute valuable specimens for analyses of how morphological and functional attributes of parasitic plant species vary according to their distribution. Furthermore, small herbaria with less than one hundred thousand specimens may also contribute unique information on plant distribution and changes overtime, especially when regional holdings are strong (Marsico et al., 2020). Many collections, both large and especially small, are not yet digitized and online, or only partly so, and yet likely hold many parasitic plant specimens. Although light boxes with digital single lens reflex cameras or flatbed scanners designed for rapid imaging of herbarium specimens are standard in most large herbaria, methods using LED light banks, camera stands and mirrorless interchangeable-lens cameras offer lower cost solutions for smaller institutions (Davis et al., 2021; Takano et al., 2019). On the other hand, long-term storage of high-resolution images contributes substantially to the cost of digitizing and archiving collections calling for more infrastructural support at global and local scales to enable a truly global network of collections.

Finally, we additionally quantified records associated with images and georeferenced specimens. For most clades, less than 40%

TABLE 2 Institutions holding the largest and the most diverse collections of five parasitic plant lineages with limited distribution according to the GBIF database

Parasitic plant lineage	Geographic distribution	Institution with most records on GBIF	Institution with highest species' diversity on GBIF
Apodanthaceae (Bellot & Renner, 2014)	Southwest USA to Argentina, Arabian Peninsula, East Africa, Southwest Australia	Texas Tech University (190 records, 6 species)	Muséum National d'Histoire Naturelle (151 records, 8 species)
Hydnoraceae (Machado & Queiroz, 2012; Musselman & Visser, 1989)	Costa Rica, South America, Arabian Peninsula, Africa, and Madagascar	South African National Biodiversity Institute (76 records, 3 species)	Missouri Botanical Garden (49 records, 10 species)
Krameriaceae (Simpson, 1989)	Southwest USA to Chile and the West Indies	University of Texas (1,418 records, 10 species)	New York Botanical Garden (952 records, 14 species)
Lennoaceae (Yatskievych & Mason Jr., 1986)	Southwest USA to Mexico	California Botanical Garden (122 records, 2 species)[a]	Smithsonian Institution (79 records, 4 species)[a]
Mitrastemonaceae (Meijer & Veldkamp, 1993)	Japan, India, Southeast Asia, North and Central America	Taiwan Forestry Research Institute (42 records, 1 species)	Missouri Botanical Garden (19 records, 2 species)

[a] The California Botanical Garden holds only five records for one of the two of the species in Lennoaceae; the records from the Smithsonian Institute are more evenly distributed.

of the records on GBIF include images (Table 3). Cynomoriaceae was the clade with the largest proportion of imaged records (50.3%; Table 3). This may be partially explained by the fact that this family is represented by only 515 records, 29% of which are held by the Muséum National d'Histoire Naturelle (France) and Naturalis (Netherlands), which have digitized their entire herbaria. On the other hand, Cynomoriaceae, as well as *Cuscuta*, showed the least proportion of georeferenced records (*c*. 25% each; Table 3). Apart from these two widely distributed groups, more than 40% of the records analysed include geographical coordinates (Table 3). This percentage is in line with what has been reported for herbarium networks (Barkworth & Murrell, 2012), and is well above the general proportion reported for animal parasite collections (Bell et al., 2018; Carlson et al., 2017).

3 | EXTENDED SPECIMENS TO UNDERSTAND BASIC BIOLOGY AND GLOBAL CHANGE RESPONSE

Species delineation, classification and biogeography are among the most frequently conducted specimen extensions using herbarium collections (Figure 1; Heberling et al., 2019). Along these lines, novel distribution patterns and parasite–host co-evolution have been reported from these data (e.g. Bellot & Renner, 2014). Previously published data on the systematics and distribution of host clades have served as key baseline data for interpreting events in the evolution of their parasites. Nevertheless, the investigation of parasite specimens further offers a unique window into the ecology and evolution of their associated hosts but have been relatively less utilized (Figure 2a). Recently, Bellis et al. (2020) compiled data from digitized herbarium specimens of the parasite *Striga hermonthica* (Delile) Benth. (Orobanchaceae), noting its associated host species. Because few parasitic plant specimens included host material, the identity of the infested species was obtained from information on the specimen label (E. Bellis, pers. comm.). These data were then applied to the simultaneous creation of parasite and host species distribution models, which were combined with genome-wide association investigations, revealing long-term maintenance of diverse host resistance genes across smallholder agroecosystems compared to industrial-scale agricultural settings (Bellis et al., 2020). These findings hold important implications for preserving crucial genetic information across human-modified landscapes and are essential in the context of global change investigations. This is especially relevant considering that *S. hermonthica* causes devastating effects to food crops (Spallek et al., 2013) and that the adaptability and independency of smallholder farming systems to future climate scenarios is uncertain (Cohn et al., 2017).

Parasitic plant specimens containing information and material of the associated host species can also provide valuable information regarding functional aspects of parasite–host relationships. Although not generally collected for this purpose, herbarium specimens are becoming increasingly recognized as big data sources for functional traits (Heberling, 2022), and increasingly specimens are being used to investigate symbioses (Meineke et al., 2018; Meineke, Davies, et al., 2019). Despite the growing importance of functional trait research in ecology, functional traits of parasitic plants are scarcely measured and poorly understood relative to other plants. Given their unique strategies of resource capture (i.e. carbon, nutrients, water), it is likely that parasitic plants exhibit specialized traits and trait combinations dissimilar to their non-parasitic counterparts. Haynes (2022) recently applied a global trait database to compare trait values between parasitic and non-parasitic plant species, asking whether the former followed the same global pattern of coordinated

TABLE 3 Number of records with geographical references or images, and their percentage from the total of records obtained from the GBIF database

Parasitic plant lineage	Records with images	% with images[a]	Georeferenced records	% georeferenced[a]
Apodanthaceae	553	26.0	1,038	48.9
Cassytha	4,266	23.9	12,443	69.6
Cuscuta	28,093	46.0	15,698	25.7
Cynomoriaceae	259	50.3	130	25.2
Cytinaceae	750	32.9	930	40.8
Hydnoraceae	103	24.5	193	45.8
Krameriaceae	4,850	34.0	7,545	52.9
Lennoaceae	356	34.9	511	50.1
Mitrastemonaceae	21	14.2	62	41.9
Orobanchaceae	241,029	44.2	243,748	44.7
Rafflesiaceae	94	37.3	82	32.5
Santalales	146,872	39.6	194,498	52.4
Totals	427,246	42.0	476,878	46.9

[a] The same total of 245,918 records noted in Table 1 were excluded from the analysis due to missing data.

trait variation observed in other seed plants (i.e. the leaf economics spectrum; Wright et al., 2004). Interestingly, the study did not find evidence that parasitic plants deviate fundamentally from the general trends found across free living plants. However, parasitic trait data accounted for less than 1% of all observations, rendering their conclusions preliminary. Although studies focus on the physiology, function and evolution of the parasitic plant haustorium, relatively few studies exist on other traits, or in the context of plant functional strategy.

Herbarium specimens have long been suggested as an important resource to investigate variations in functional traits across time (Woodward, 1987). The use of these specimens for the analysis of functional traits has expanded and is now becoming increasingly widespread, as these collections are now regarded as big data repositories (Heberling, 2022). Here, we propose that parasitic plant collections may serve as especially valuable data sources for analyses of functional traits and trait variation across phylogeny, time and space of not only the parasites but also their host species (Figure 2b). Mistletoes, for instance, are particularly sensitive to prolonged drought, and the study of their eco-physiology can provide valuable insights about the consequences of global change (Fontúrbel, 2020). Considering that nitrogen and carbon metabolism are positively correlated between mistletoes and their hosts (Scalon & Wright, 2015), the analysis of functional traits of one plant can serve as a proxy for inferences about the other. Thus, incomplete parasitic plant specimens (i.e. without host material) can also be used as valuable sources of information about host eco-physiology. On the other hand, if host material is also present in the parasite collection, host functional traits can be analysed more directly and compared to data gathered from other specimens of the same host species collected in a similar area. Results from such investigations can bridge key knowledge gaps about the direct effects of plant parasitism on host eco-physiology and vice-versa.

Parasitic plants that use a wide range of host species are especially interesting in this context, because analysing the outcomes of different parasite–host combinations can reveal interesting questions about species' phenotypic plasticity (Figure 2c). One question that has attracted renewed interest in the context of global change biology is related to the phenology of symbiotic associations (Rafferty et al., 2015). The utilization of herbarium specimens to investigate plant phenology has emerged as a leading research area in recent decades (Davis et al., 2015). Because herbarium labels contain collection dates and specimens capture key phenological events (e.g. flowering, fruiting, leaf-out) they represent an underutilized, yet powerful record of phenology across time, space and phylogeny. Connecting specimen-derived phenological data to historical climate data provides insight into how associated species, such as herbivores, pollinators and dispersers respond to global change. The same is true for herbarium specimens of parasites. Indeed, due to their role as keystone species, changes in flowering/fruiting patterns of the parasite may affect a broader network of species, not only their hosts (Fontúrbel, 2020). In fact, host-associated changes in the phenology and reward production of sympatric parasite populations can influence interactions with mutualistic vectors (Yule & Bronstein, 2018). Data from herbarium specimens also support the hypothesis that different parasite species co-occurring in an urban area show a complementary phenological pattern that extends the period of flower/fruit availability for mutualistic animals (Teixeira-Costa et al., 2017). Moreover, because the cross-talk of mobile genetic elements and hormones between parasite and host may regulate the timing of phenological events (Shen et al., 2020), changes in host species can amplify the role of parasite phenology in plant and animal communities.

The range of hosts used by a parasite also influences the interactions between these plants and antagonist organisms, such as insect herbivores. Experiments designed to help elucidate the chemical ecology of such tripartite interactions have demonstrated that differences in host terpenoid production can impact the performance of insect herbivores feeding on parasitic plants (Marvier, 1996, 1998). Global change drivers, such as increased concentration of carbon dioxide, ozone and nitrogen oxides, can alter the biosynthesis, composition and levels of plant metabolites, which in turn affect plant–herbivore interactions (Jamieson et al., 2017). Herbarium specimens are thus well suited to reveal patterns and changes in insect herbivores at broad spatial and temporal scales (Meineke, Classen, et al., 2019). As technical difficulties related to the analysis of small and volatile metabolites are overcome, herbarium species are also becoming increasingly important for the investigation of plant chemical ecology (Foutami et al., 2018). In the specific case of the specimens discussed here, quantifying insect herbivory and terpenoid profiles on the parasitic plant itself, for instance, can reveal important aspects of local community ecology (Figure 2d).

Herbarium specimens also represent a crucial genetic resource and are increasingly being utilized in this context for a variety of purposes including large-scale systematic investigations (Muñoz-Rodríguez et al., 2019) and species assessments in biodiversity hotspots (Lahaye et al., 2008). Herbariomic approaches, however, have been underutilized for exploring parasite–host dynamics despite the obvious utility of these collections for untangling the cryptic biology of these plants. We anticipate that DNA barcoding methods applied to parasitic plant specimens, can greatly facilitate the identification of their associated hosts with a high degree of confidence (Figure 2e). This is likely to be especially useful for revealing cryptic host specific diversity in cases where host identity is unknown or uncertain due to either insufficient features being collected to facilitate standard host identification or complicated taxonomy of host lineages (Pelser et al., 2016). Results from such investigations can help elucidate dynamic host shifts within species, especially among those with wide geographic distributions (Schneider et al., 2016). Moreover, eDNA monitoring can be applied to determine the existence of parasitic plants of conservation concern within a given area, particularly when parasites are hidden within the body of their hosts (Osathanunkul, 2019). Similar monitoring approaches can be applied to herbarium specimens of host plants to identify novel parasite genotypes and reveal emerging conservation concerns (Barkman et al., 2017).

4 | BEST PRACTICES FOR COLLECTING, PREPARING AND CURATING PARASITIC PLANT SPECIMENS

The 'extensions' discussed in the previous section involve data gathered from parasitic plant specimens, regardless of the presence or identification of its associated hosts and other mutualist or antagonistic species. In fact, it is noteworthy that parasite specimens seldom include host material, although some level of host identification (species, genus or family) is provided in 50%–70% of the specimens (Bellis et al., 2020; Downey, 1998; Norton & de Lange, 1999). Nevertheless, as discussed for collections of metazoan parasites and other symbiotic associations (Andrew et al., 2019; Obermayer, 2002; Thompson et al., 2021), the absence of host material and/or identification of parasite vouchers can hamper innovative and integrative collections-based research. To remedy that, future collections are strongly encouraged to deposit parasite specimens with their associated host material and locality in data collections (Bell et al., 2018).

Unlike the specific practices often adopted for different animal groups in natural history collections, parasitic plants require the same overall recommendations followed for any herbarium specimen. The key differences are the sampling and identification of the associated hosts, and the collection of haustorium material. In parasitic plants with multiple haustoria, often more than one host plant is parasitized simultaneously. While it would be most informative to include all hosts, sampling conditions may not allow the identification or collection of all host plants. In these cases, the inclusion of at least one host plant will add to the knowledge of parasite–host interactions and facilitate many of the potential studies elaborated here. Parasitic plants themselves also frequently serve as hosts to other parasites, the latter of which are then broadly known as hyperparasitic plants (Krasylenko et al., 2021). If present, these plants should also be collected along with both their parasitic and non-parasitic hosts.

Haustoria should also be included with any parasite voucher because this organ represents 'the very essence of plant parasitism' (Kuijt, 1969). In the case of parasites with a solitary attachment, the entire haustorium should be collected, which might not be feasible depending on the conservation status for certain species and populations. When collection is possible, haustorium samples should include the basal-most portion of the parasitic plant, as well as a portion of the parasitized host stem/root that extends basipetally and acropetally from the haustorium. Considering the complex three-dimensional structure of the parasite–host interface, haustorium collections can be digitized in a manner similar to that of zoological collections, using technologies such as photogrammetry and computed tomography (Hedrick et al., 2020). This should be especially valuable in promoting studies aimed at understanding haustorium structure and development across different spatial and temporal scales. Preserved haustoria in herbarium or xylarium collections can also yield tissue samples for the analysis of primary and secondary metabolites, especially considering that the chemical profile of this organ can be remarkably different from that of isolated parasite and host tissues (Furlan et al., 2019). Furthermore, as DNA barcode techniques advance to include more reference libraries for wood discrimination (Jiao et al., 2018), we envisage that dried haustorium samples can potentially become a source for reasonable quality DNA in the future.

Upon sampling, and following curatorial best practices for plant material preservation, parasite specimens and their hosts can be mounted together on a single sheet, or separately on two sheets. Depending on its volume and overall size, haustoria can either be mounted onto the specimen sheet directly or incorporated into separate collections. Woody haustoria can be air- dried and placed in archival boxes, while small and succulent haustorium material can undergo tissue fixation and be preserved in spirit collections. For endoparasites and root parasites with bulky, succulent haustoria, preservation in spirits is also important. Due to the large volume of these specimens, however, subsamples consisting of small tissue fragments should also be prepared to ensure good fixation. Regardless of the collection type, both the parasite and the host plant should receive unique labels and identifiers (and be cross-referenced in collections accordingly). This practice can facilitate many of the applications discussed here for parasitic plant specimens by allowing easy identification of parasite–host pairs. If hyperparasites are present, they also require separate labels and barcodes, probably necessitating a separate sheet for the primary host. To avoid confusion, labels must include information connecting the various types of parasite/host/hyperparasite specimens and additional material in dry or wet collections.

Vouchers should then be imaged, with images and associated data digitized and mobilized online. At this point, the question of how to best annotate the associated host species becomes especially important. Our analysis of parasitic plant records in GBIF revealed that host identification appears under five different fields: 'associated taxa', 'occurrence remarks', 'habitat', 'field notes' and 'event remarks'. Each of these fields is defined in Darwin Core, a standard intended to facilitate the sharing of information about biological diversity (Darwin Core Maintenance Group, 2021). According to their definitions, 'associated taxa' or 'ResourceRelationship' would be the most appropriate fields to list host identity in a digital specimen record. We prefer the 'ResourceRelationship' field but agree with Downey (1998) that a field for 'host plant' in databases and specimen labels would eliminate confusion with species that are only associated. An extension to the Darwin Core controlled vocabulary framework for parasitic plants with standardized terms for these important interrelationships would provide a more information-rich description of their ecologies and greater accuracy for web-based applications and data analysis protocols (Myltsev & Mozzherin, 2016; Pearson, 2018) that extract taxon information from digitized records. It is crucial, however, that both the original voucher label and the digitized specimen host taxa are annotated similarly, as to avoid confusion. This is particularly important for multispecies parasitism where there are hyperparasitic taxa as well as parasites and hosts are present.

5 | CONCLUSIONS AND FUTURE PERSPECTIVES

Parasite specimens in natural history collections represent a valuable, albeit overlooked resource for integrative research in ecology and evolution (Bell et al., 2018). These specimens have the peculiarity of capturing symbiotic associations in a single collection event, thus providing data that can be explored to address multiple questions about the biology, ecology and evolution of both parasite and host species. Here, we have focused on parasitic flowering plants due to their taxonomic, morphological and functional diversity, as well as their fundamental ecological role as keystone species (Press & Phoenix, 2005). We proposed that specimens of these plants can be used to analyse patterns of species co-distribution to eco-physiology and phenotypic plasticity. Furthermore, because the network of interactions established by parasitic plants include several other mutualistic and antagonistic species beyond those directly associated with the parasites themselves, data gathered from specimens can also inform studies in a wide range of topics, from tripartite chemical ecology to species conservation.

To increase the value of these collections and help realize the integrative potential of these specimens, continued digitization efforts, and improved curatorial practices are crucial. Next generation technologies, such as computed tomography, already an important component of the digitization of zoological collections, can also be applied to parasitic plants (Hedrick et al., 2020). Sample preparation protocols focusing on the structural and physiological complexity of the haustorium (Teixeira-Costa, 2022) can be incorporated into digitization pipelines to generate three-dimensional digital derivatives. Additionally, explicit annotation of host species during sampling and digitization of can be improved by the inclusion of digital images of both parasite and host species to the specimen metadata as a way to provide verification of associated taxa (Heberling & Isaac, 2018). These practices can contribute to new 'extensions' of parasitic plant specimens and motivate the next generation of collection-based science. In summary, parasitic plant specimens nicely exemplify the extended specimen concept, providing an ideal framework for further development and implementation across a wide variety of taxa and symbioses across the tree of life.

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CONFLICT OF INTEREST

The authors have no conflict of interests to disclose.

AUTHORS' CONTRIBUTIONS

L.T.-C. and J.M.H. conceived the central idea of parasitic plants as a manifestation of the extended specimen concept; L.T.-C. led the writing of the manuscript and prepared the figures; J.M.H., C.A.W. and C.C.D. contributed to the development of the manuscript and helped write particular sections. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

All data used in this manuscript are available at the Global Biodiversity Information Facility (GBIF.org, 2021; https://doi.org/10.15468/dl.dpsg3s).

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