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The seven grand challenges in arachnid science

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This perspective identifies the grand challenges in arachnid science: 1. Grasp the arachnid species diversity. There is a need to accelerate taxonomic research to obtain a sense of arachnid species diversity, however, at the same time, taxonomy needs to increase its quality, rigor, and repeatability. 2. Standardize arachnid systematics research. A solid phylogenetic definition and morphological diagnosis of Arachnida and its composing subgroups, usually treated at the rank of order, are needed. Studies should aim to stabilize and standardize phylogenetic efforts at all levels of hierarchy, and systematists should adopt criteria for higher level ranks in arachnid classification. 3. Interpret arachnid trait evolution through omics approaches. Among the field's grand challenges is to define the genetic diversity encoding for the diverse arachnid traits, including developmental, morphological and ecological characteristics, biomaterials such as silks, venoms, digestive fluids, or allergens and bioproducts that cause diseases. Comparative genomics, transcriptomics, and proteomics will provide the empirical basis for biotechnology to modify arachnid genomes to fit numerous applications. 4. Facilitate biotechnological applications of arachnid molecules and biomaterials. Among the grand field challenges is to define potential applications of arachnid bioproducts from therapeutics to industry. New natural and biodegradable products, e.g. from spider silks, should ease our burden on ecosystems. 5. Utilize arachnids as models in ecological and biogeographic research. Biodiversity inventory sampling and analytical techniques should be extended from spiders to other arachnid groups. Spiders and their webs could be used as environmental DNA samplers, measuring or monitoring ecosystems' overall biodiversity. Arachnids are excellent models to address biogeographical questions at the global to local scales. 6. Disentangle evolutionary drivers of arachnid diversity. Among the field grand challenges is a more precise evaluation to what extent the emergence of arachnid phenotypes is shaped by classical selection processes, and under what conditions, if any, sexual conflict needs to be invoked. 7. Define effective conservation measures for arachnids in the light of global changes. Effective conservation measures in arachnology should integrate the data from phylogenetic diversity, physiology, ecology, biogeography, and global change biology.

KEYWORDS

diversity, systematics, omics, evolutionary novelty, biomaterials, arachnid biogeography, arachnid evolution, arachnid conservation

Introduction

Arachnids are an incredibly diverse, ancient lineage of chelicerate arthropods. The phylogenetic limits of Arachnida have yet to be precisely established (Packard, 1882; Harvey, 2002; Coddington et al., 2004; Sharma et al., 2021), but Arachnida certainly contains groups of terrestrial and aquatic chelicerates including spiders (Araneae), harvestmen (Opiliones), scorpions (Scorpiones), mites (Acariformes), ticks (Parasitiformes), pseudoscorpions (Pseudoscorpiones), camel spiders (Solifugae), whip spiders (Amblypygi), vinegaroons (Thelyphonida, also Uropygi), shorttailed whipscorpions (Schizomida), microwhip scorpions (Palpigradi), and hooded tick-spiders (Ricinulei). Arachnids also include several extinct lineages of varying ranks (Wang et al., 2018), some of them marine, and may also include the marine horseshoe crabs (Xiphosura) (Ban et al., 2022). Together, arachnid lineages comprise at least hundreds of thousands, perhaps even millions of species, of which most remain undiscovered.

Arachnids contain representatives that are terrestrial and aquatic, carnivorous and herbivorous, specialized and generalist, tiny-bodied and large, sexually monomorphic and dimorphic. A selected few arachnid species are medically important, examples being venomous scorpions and spiders (Lüddecke et al., 2022), parasitic mites that transmit scrub typhus and cause pruritic dermatitis (e.g., trombiculiasis), and ticks that are vectors of debilitating, even fatal pathogens (e.g., tick-borne encephalitis virus (TBEV), *Anaplasma* spp., *Borrelia* spp., and *Babesia* spp.) (Knap et al., 2009; de la Fuente et al., 2017). Some arachnids are also considered as agricultural pests (Cornman et al., 2010; Grbić et al., 2011). Most arachnid species, of course, are neutral to humans, and constitute thousands of unique biological forms that are ecologically important within known and unknown networks. Others may hold potentially beneficial biological secrets yet to be uncovered. All of them are simply beautiful products of evolution over hundreds of millions of years.

Given the enormous diversity of arachnids, their ubiquity in most ecosystems, the recent developments in biological sciences, and the biodiversity declines in the era of habitat destruction and global climate changes, I hereby identify the seven grand challenges in the field of arachnid science.

Grand challenge 1: Grasp the arachnid species diversity

The arachnid species diversity is overwhelming, with taxonomists having only discovered and described a small portion. For example, while about 50 thousand spider species are catalogued (WSC, 2022), the true spider species diversity is estimated to exceed 120 thousand (Agnarsson et al., 2013). Although arachnids also contain some species-depauperate lineages such as Uraraneida, Palpigradi, Thelyphonida, Schizomida and Ricinulei, whose species diversity will not exceed tens or hundreds, the taxonomic incompleteness noted above in spiders may be even more extreme in other arachnids. About 10 thousand species of oribatid mites are described, yet estimates of their true diversity range from 50 to 100 thousand (Schatz and Behan-Pelletier, 2008). By 2010, taxonomy had catalogued roughly 92 thousand extant arachnid species (Adis and Harvey, 2000) and today this number exceeds 110 thousand. However, if the above established measures of taxonomic completeness (42% in spiders and perhaps less than 10% in Acari) are typical of all arachnids, then, by extrapolation, the true species diversity of Arachnida must lie between 262 thousand and 1.1 million. Other approximations are even higher: estimates for species richness in Acari alone are 1 to 1.5 million (Krantz and Walter, 2009; Walter and Proctor, 2013). Arachnids are a truly mega-diverse lineage.

With only a fraction of the true arachnid diversity catalogued and considering the rate of habitat destruction worldwide, taxonomy is obviously not going to detect all species in our lifetimes. Taxonomic efforts need to be dramatically accelerated, and immediately (Agnarsson and Kuntner, 2007). Rapid species discovery now uses massive sampling and DNA barcoding (Cao et al., 2016). However, accelerating dissemination should not be achieved at the expense of taxonomy's rigor. Arachnological taxonomic practices have recently been scrutinized with some focus on spiders (Bond et al., 2021) and the results are not encouraging with much left to be desired in terms of integrating data sources, data availability, and repeatability. These authors called for higher taxonomic standards though specific recommendations: *i*) All taxonomic works should clearly state the species concept being applied; *ii*) All data should be made electronically accessible; *iii*) Descriptions of new species based on singleton specimen data that are described outside a clear context should be discouraged; and *iv*) Taxonomy should become integrative (Bond et al., 2021). These recommendations, and the general calls for the importance of taxonomy, should be adopted by the arachnological community in order to provide scientific rigor in untangling species diversity.

Grand challenge 2: Standardize arachnid systematics research

Phylogenetic progress in arachnids has shifted from predominantly morphological cladistics in the 1990s, through targeted use of a selected few genes during the first two decades of the century, towards the use of subgenomic and transcriptomic data in the past years (Agnarsson et al., 2013; Bond et al., 2014; Fernández et al., 2014; Fernández and Giribet, 2015; Starrett et al., 2017; van Dam et al., 2019). Even though arachnology has decisively ventured into the genomic era, many regions of the arachnid tree of life remain unresolved and the field still lacks a consensus on the phylogenetic definition of many higher taxa.

Take the limits of Arachnida as an example, and the results are conflicting (Sharma et al., 2021). While morphological evidence for arachnid monophyly (i.e. Arachnida traditionally excluding Xiphosura) has once been deemed solid (Shultz, 2001; Coddington et al., 2004), most molecular studies do not recover it (Ballesteros et al., 2022; Ban et al., 2022), nor do they recover some of the classical groups within Arachnida (Ballesteros et al., 2019; Ballesteros and Sharma, 2019). Monophyly and phylogenetic placement of several arachnid lineages continue to be ambiguous due to long branch attraction artifacts (Ontano et al., 2022). Additionally, a divide seems to persist between students of fossils and morphologies on the one hand and the proponents of genomics on the other, hampering a total evidence resolution of the problem.

Intermediate level phylogenies at, say, family and genus levels, have likewise failed to stabilize despite considerable phylogenetic efforts in capturing more and more taxa and data (Hormiga and Griswold, 2014). Clearly, better datasets are paramount, but what should one emphasize given the limited data generation and computational capability? Genome scale phylogenetic analyses are possible and could be the systematists' ultimate goal, but may not yet be feasible in multidiverse non-model lineages such as arachnids due to taxon sampling constraints. Thus, immediate phylogenetic efforts should focus on reduced representation sequencing, e.g. anchored hybrid enrichment (Lemmon et al., 2012) or the ultraconserved elements (Faircloth et al., 2012). An increasing number of studies on arachnids are demonstrating that these techniques are able to resolve both deep and shallow divergencies (Hamilton et al., 2016; Maddison et al., 2017; Starrett et al., 2017; Kuntner et al., 2019; Kulkarni et al., 2020; Xu et al., 2021; Chamberland et al., 2022; Li et al., 2022). These data should continue to be accumulated with the ultimate goal of openness and compatibility of datasets.

Phylogenetic instability aside, there is also a need for consensual classifications that would provide nomenclatural stability. Because the International Code of Zoological Nomenclature does not mandate the ranks above the genus level, systematic practice should adopt clear classification criteria, examples being monophyly, information content, diagnosability, stability, and lineage age (Kuntner et al., 2019). Arachnids are an old phylogenetic entity with numerous clades of widely varying ages and compositions, but this fact should not preclude systematists from creating order from chaos.

Grand challenge 3: Interpret arachnid trait evolution through omics approaches

Since 2010, when the first arachnid genome was published, 34 additional genomes have been sequenced and assembled (Table 1; Google Scholar search on 17 October 2022), and this pace is accelerating exponentially (Figure 1). Recent analyses demonstrate the power of large-scale comparative genomics in uncovering the links between the genotype and phenotype in arthropods (Thomas et al., 2020).

Comparative arachnid genomics is just taking flight given the diversity of arachnid karyotypes (Král et al., 2019) and genome sizes [Table 1; see also (Cerca et al., 2021)]: these range from the smallest known arthropod genome at 90 megabases (Mbp) in the mite *Tetranychus urticae* (Grbić et al., 2011) to a sizeable 4.29 gigabases (Gb) in the velvet spider *Stegodyphus dumicola* (Liu et al., 2019). The currently limited number of arachnid genomes reveal high rates of methylation in spiders and scorpions, perhaps suggesting epigenetic control of large portions of arachnid genes (Thomas et al., 2020). Current evidence furthermore points towards rampant gene duplication and loss in arachnids, with at least one whole genome duplication event at the branch subtending Arachnopulmonata, a clade that unites spiders and amblypygids (Schwager et al., 2017; Harper et al., 2021) as well as additional whole genome duplications in horseshoe crabs (Shingate et al., 2020; Nong et al., 2021). Nuclear genome sequencing in ticks has revealed expansions of gene families associated with vector-host interactions (Gulia-Nuss et al., 2016). Evidence has been found for ancient lateral gene transfer events to arachnids from bacteria or fungi (Dong et al., 2018). Genomic and transcriptomic studies have so far focused on annotating gene families that encode for morphological development (Hoy et al., 2016; Zhang et al., 2019; Harper et al., 2021), for venom neurotoxins (Cao et al., 2013; Yu et al., 2019), for silks (Babb et al., 2017; Garb et al., 2019; Kono

TABLE 1 Current tally of arachnid genomes with their assembled or estimated sizes.

Sort	Year	Lineage	Species	Genome size (Gb)	Reference
1	2010	Mesostigmata	*Varroa destructor*	0.57	(Cornman et al., 2010)
2	2011	Trombidiformes	*Tetranychus urticae*	0.09	(Grbić et al., 2011)
3	2013	Scorpiones	*Mesobuthus martensii*	1.13	(Cao et al., 2013)
4	2014	Araneae	*Stegodyphus mimosarum*	2.74	(Sanggaard et al., 2014)
5	2016	Mesostigmata	*Metaseiulus occidentalis*	0.15	(Hoy et al., 2016)
6	2017	Araneae	*Trichonephila clavipes*	2.44	(Babb et al., 2017)
7	2017	Araneae	*Parasteatoda tepidariorum*	1.45	(Schwager et al., 2017)
8	2017	Scorpiones	*Centruroides sculpturatus*	0.93	(Schwager et al., 2017)
9	2018	Trombidiformes	*Leptotrombidium deliense*	0.12	(Dong et al., 2018)
10	2018	Trombidiformes	*Dinothrombium tinctorium*	0.18	(Dong et al., 2018)
11	2019	Araneae	*Araneus ventricosus*	3.66	(Kono et al., 2019)
12	2019	Araneae	*Stegodyphus dumicola*	4.29	(Liu et al., 2019)
13	2019	Araneae	*Anelosimus studiosus*	2.22	(Purcell and Pruitt, 2019)
14	2019	Araneae	*Dysdera silvatica*	1.7	(Sánchez-Herrero et al., 2019)
15	2019	Araneae	*Pardosa pseudoannulata*	4.26	(Yu et al., 2019)
16	2019	Parasitiformes	*Neoseiulus cucumeris*	0.17	(Zhang et al., 2019)
17	2020	Parasitiformes	*Ixodes persulcatus*	2.04	(Jia et al., 2020)
18	2020	Parasitiformes	*Haemaphysalis longicornis*	2.59	(Jia et al., 2020)
19	2020	Parasitiformes	*Dermacentor silvarum*	2.76	(Jia et al., 2020)
20	2020	Parasitiformes	*Hyalomma asiaticum*	1.78	(Jia et al., 2020)
21	2020	Parasitiformes	*Rhipicephalus sanguineus*	2.12	(Jia et al., 2020)
22	2020	Parasitiformes	*Rhipicephalus microplus*	2.56	(Jia et al., 2020)
23	2020	Parasitiformes	*Ixodes scapularis*	1.77	(Jia et al., 2020)
24	2020	Xiphosura	*Carcinoscorpius rotundicauda*	1.67	(Shingate et al., 2020)
25	2020	Araneae	*Loxosceles reclusa*	3.26	(Thomas et al., 2020)
26	2020	Araneae	*Latrodectus hesperus*	1.14	(Thomas et al., 2020)
27	2021	Araneae	*Tetragnatha kauaiensis*	1.08	(Cerca et al., 2021)
28	2021	Araneae	*Trichonephila antipodiana*	2.29	(Fan et al., 2021)
29	2021	Araneae	*Caerostris darwini*	1.58	(Kono et al., 2021)
30	2021	Araneae	*Caerostris extrusa*	1.42	(Kono et al., 2021)
31	2021	Xiphosura	*Carcinoscorpius rotundicauda*	1.7	(Nong et al., 2021)
32	2021	Xiphosura	*Tachypleus tridentatus*	1.7	(Nong et al., 2021)
33	2021	Araneae	*Argiope bruennichi*	1.67	(Sheffer et al., 2021)
34	2022	Araneae	*Caerostris darwini*	1.81	(Babb et al., 2022)
35	2022	Araneae	*Uloborus diversus*	1.98	(Miller et al., 2022)

et al., 2021; Babb et al., 2022), for dietary characteristics (Grbić et al., 2011; Hoy et al., 2016; Fan et al., 2021), for enzymes that cause allergies in vertebrates (Dong et al., 2018), for candidate genes for sex determination (Hoy et al., 2016; Miller et al., 2022), and for genes important for the innate immune system (Shingate et al., 2020). Large scale comparative genomics has also started to understand the genetic basis for tick-borne diseases (Jia et al., 2020).

Rapid genomic progress in the recent years as depicted in Figure 1 predicts hundreds and thousands of newly sequenced arachnid genomes in the coming years and decades, respectively. The new genomic data will facilitate more accurate interpretations of genetic architectures of arachnid traits and augment our understanding of the genetics of extreme arachnid diversity, ecological specialization, parasitism, disease transmission, metabolism, and biomaterials (Garb et al., 2018). Comparative genomics in itself, however, will not suffice to understand trait evolution. For this, a systems biology approach combining genomics, transcriptomics, and proteomics is best (Wilson and Daly, 2018; Mans, 2020). Such omics insights, combined with species interactions and ecology, will pave the way to discover novel biotechnological, biomedical, and pest control applications of arachnid bioproducts, such as venoms, silks, and allergy causing biomolecules.

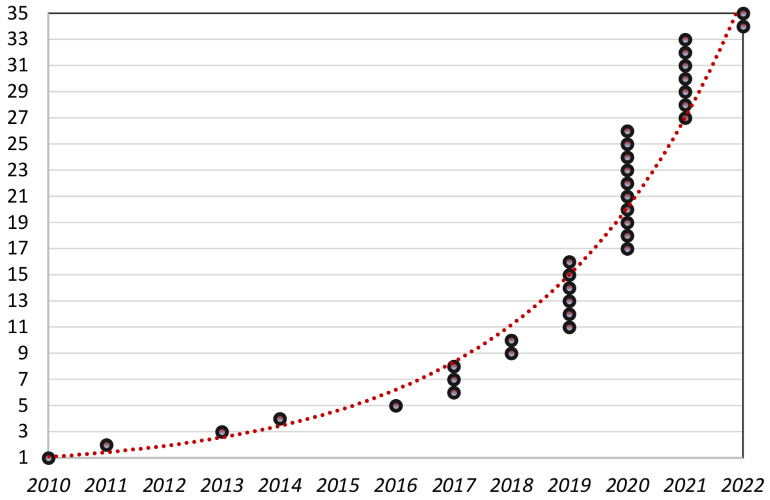

FIGURE 1
Cumulative numbers of arachnid genomes per year of publication (Table 1).

Grand challenge 4: Facilitate biotechnological applications of arachnid molecules and biomaterials

Arachnids produce biomolecules and biomaterials that show applied potential in industry and biomedicine. Tick saliva, for example, contains proteins, peptides, lipid derivatives, and non-coding RNAs, that combined act to inhibit vertebrate immune reactions (Chmelař et al., 2019; Aounallah et al., 2020). These bioproducts could be genetically modified to fit numerous therapeutic requirements, perhaps as drugs for human immune diseases. Other arachnid biomolecules show antimicrobial potential (Leannec-Rialland et al., 2021).

Silks are natural materials that have independently evolved multiple times in arthropods (Craig, 1997). Most research has focused on understanding and exploiting spider silks. All spiders have abdominal silk glands (up to seven types in a single species) that produce silks for different uses (Sethy and Ahi, 2022). The glands connect with the spinnerets where a biologically unique spinning process solidifies the silken gland products (Vollrath and Knight, 2001). Dragline silk is used by all spiders—even those that do not spin prey-capture webs—, as a safety line. Spun out of the major ampullate glands (Ayoub et al., 2007), it is the toughest silk type known (Agnarsson et al., 2010; Blackledge et al., 2011) and therefore forms those architectural elements of orb webs that absorb the kinetic energy of impacting prey. Orbweaving spiders have also evolved glands specific for other silks (Vollrath and Knight, 2001; Lewis, 2006) such as minor ampullate glands that produce auxiliary spirals, flagelliform silk glands that produce extremely stretchy capture spirals, piriform silk glands that produce cement silk, aciniform silk glands that produce attack wrapping and eggsac insulation silk, tubuliform and cylindrical silk glands that produce silks for eggsac coating, and finally, aggregate silk glands that produce viscous glue (Sethy and Ahi, 2022).

Classical knowledge suggested a one-to-one correspondence between the seven silk glands in spiders and the different genes that encode spider silk proteins (spidroins). Genomic studies have already refuted this simplistic presumption. Babb et al. (2017) annotated 28 spidroin genes in *Trichonephila clavipes* and found their expression in several silk glands to be complex, as well as sex-specific (Correa-Garhwal et al., 2021). The genomes and transcriptomes of bark spiders (genus *Caerostris*) reveal a repertoire of no fewer than 31 spidroins (Garb et al., 2019; Kono et al., 2021; Babb et al., 2022). In comparison, studies of the genomes of other spiders have annotated fewer spidroins: 11 in *Araneus ventricosus* (Kono et al., 2019), 10 in *Uloborus diversus* (Miller et al., 2022), 16 in a non-web-building wolf spider (Yu et al., 2019).

Beyond spiders, other arachnids can produce silks. The silk fibers of the spider mite *Tetranychus urticae*, for example, have diameters on the nanometer scale, representing the thinnest natural silk fiber produced by arthropods (Lozano-Pérez et al., 2020). Combined with a Young's modulus almost double that of spider *Trichonephila clavipes* silk, the spider mite silks show great potential in pharmacological and biomedical application (Lozano-Pérez et al., 2020).

Understanding the genetic basis for arachnid silk material properties over a larger taxonomic breath is essential for genetic modification and biotechnological use of silks. In fact, this grand challenge has already begun in a study that sequenced over a thousand spider species over their phylogenetic breath in order to map their spidroins and link their genetics with silk properties

(Arakawa et al., 2022). This study launched the Spider Silkome Database (https://spider-silkome.org/), a new, vast resource that could help to identify applications for silks of a particular species, gland, and sex. The field is moving towards the possibility of genetic modification of silks of desired properties.

Applicative potentials of genetically modified arachnid silks are numerous. Being biodegradable and purportedly neutral to the human immune system, silks could encapsulate drugs and deliver them to targeted tissues (Leal-Egaña and Scheibel, 2010; Omenetto and Kaplan, 2010). Further potential medical applications are self-absorbing wound stitches (Omenetto and Kaplan, 2010), scaffolding for tissue engineering, and artificial nerve construction (Schacht and Scheibel, 2014). Electric conductivity, antibiotic, and insecticidal properties are among the least understood silk properties with great potential (Marques et al., 2004; Salles et al., 2006; Ortega-Jimenez and Dudley, 2013). Finally, being tough yet light, synthetic silks could replace nylon and rubber materials in the industries, and perhaps replace most plastic products thereby lowering humanity's burden on ecosystems.

Grand challenge 5: Utilize arachnids as models in ecological and biogeographic research

Biodiversity inventories routinely sample arachnids. Works focusing on spider communities in tropical and temperate ecosystems have fine-tuned the sampling and the analytical protocols (Coddington et al., 1996; Scharff et al., 2003; Cardoso, 2009; Cardoso et al., 2009; Malumbres-Olarte et al., 2016), and explained that rare species in tropical inventories are artefacts of undersampling (Coddington et al., 2009). These techniques should be extended to other arachnid groups such as mites, ticks, scorpions, and harvestmen for a bigger picture of arachnid alpha and beta diversity.

The ease of sequencing has brought forth protocols to define food webs from predator gut contents, and arachnids are excellent model predators for such ecological application (Krehenwinkel et al., 2017). Less invasive sampling techniques are also being developed, one example being spider webs that can potentially monitor overall biotic diversity in ecosystems. Functioning as an extended phenotype targeting specific or nonspecific prey (Blackledge et al., 2011; Blamires et al., 2018), and being suspended in air or on substrates (Eberhard, 2020), spider webs passively filter organisms other than the spider host and its prey. Gregorič et al. (2022) demonstrated that spider webs harbor environmental DNA (eDNA) of hundreds or thousands of animals, fungi, bacteria, and most likely, viruses. Given the web architecture diversity, and the durability of silks, future studies should design ecological experiments where spider webs serve as non-invasive samplers of the total eDNA in ecosystems. Alternatively, spider webs could be used for more targeted monitoring of environmentally or medically important species of pests, parasites or pathogens.

Given the immense diversity of arachnid forms, ecologies, life histories, and evolutionary imprints, arachnology has had little trouble selecting suitable model species or clades to address some of the fundamental biogeographic questions relating to dispersal, vicariance, and extinction. As examples, biogeographic patterns in hooded tick-spiders (Ricinulei), the harvestmen lineage Cyphophthalmi, as well as in certain ground-burrowing lineages of spiders (Mesothelae and Mygalomorphae) seem to be heavily imprinted by vicariant events (Boyer et al., 2007; Opatova et al., 2013; Fernández and Giribet, 2015; Xu et al., 2015). The biogeographic patterns in these lineages are often interpreted as direct consequences of historic tectonic events, or events such as mountain uplifts, sea level fluctuations or river formation (Xu et al., 2016; Xu et al., 2018). In contrast, numerous groups of spiders that regularly disperse aerially and thus more easily maintain gene flow over bodies of land or water have been more informative about speciation on oceanic islands (Gillespie, 2002; Hormiga et al., 2003; Kuntner and Agnarsson, 2011; Casquet et al., 2015). Arachnids also play prominently in subterranean biology research (Arnedo et al., 2007; Harms et al., 2018; Mammola et al., 2020).

Considering how different biological traits affect the evolutionary imprints of organisms, the most powerful approaches to biogeography would overlay as many different lineages as possible over the same geographic area, and seek for congruence over conflicts amongst datasets. One such massive sampling in the Caribbean archipelago (http://www.islandbiogeography.org/) offered reconstructed biogeographic histories of numerous arachnid clades of varying dispersal propensities (Dziki et al., 2015; Agnarsson et al., 2016; Čandek et al., 2019; Tong et al., 2019; Čandek et al., 2020a; Chamberland et al., 2020; Crews and Esposito, 2020; Čandek et al., 2021; Shapiro et al., 2022). Such multi-clade studies can powerfully test the ultimate biogeographic hypotheses specific to a particular archipelago. Among the grand field challenges, therefore, is to perform similar massive field samplings along other major global biogeographic hotspots to address fundamental biogeographical questions.

At the same time, next-generation biogeography should improve on the accuracy of analytical tools. Kuntner and Turk (2022) argue that among the elements needed for historical biogeographic inference, the estimations of organismal dispersal probabilities are particularly vague, representing the bottle neck in historical biogeography. Their appeal for dispersal probability estimations that are better informed and biologically meaningful has so far only been tested on spiders (Turk et al., 2020; Turk et al., 2021; Magalhaes and Ramirez (2022)). If the better devised estimations of dispersal probability are accepted by this community, then perhaps arachnids will be established as the model lineage of choice for applications of the next-generation biogeography (Kuntner and Turk, 2022).

Grand challenge 6: Disentangle evolutionary drivers of arachnid diversity

What arachnid traits, or what extrinsic factors may predict, or even drive, the extreme diversity of certain lineages? In spiders, comparative research points towards a correlative link between small male body size and extreme species diversity: Čandek et al. (2020b) tested the predictive power of 22 variables deriving from morphological, genetic, geographic, ecological, and behavioral landscapes on species richness of 45 spider genera. Within their sample, no variable that described spider-specific biologies predicted species richness, but one biologically universal trait—small male body size—did. Comparative research on other arachnid groups should test whether this finding is generally valid for arachnids, or even broader, for arthropods.

Research shows that body size of an average spider female is 6.9 mm and of a male is 5.6 mm (Kuntner and Coddington, 2020). This overall modest sexual size dimorphism has repeatedly evolved to extremes in orb-weaving spiders, with females in some species overgrowing males 10 or even 14-fold. If size differences are measured in mass, they are even more dramatic: while attached on the host, 'gluttonous' female ixodid ticks increase their mass 100 times of the original size, while the males remain comparatively tiny (Sojka et al., 2013). In spiders, *Nephila* females on average outweigh their male partners 125 times (Kuntner et al., 2012b). This female biased, extreme sexual size dimorphism (eSSD) in arachnids is the greatest among all terrestrial life.

The evolution of eSSD in spiders is explained through the differential equilibrium model, whereby sex-specific selection pressures, relating to the processes of both natural and sexual selection, act additively or antagonistically to sum up the overall selection (Kuntner and Coddington, 2020). Once the genetic correlation between the sexes is broken, eSSD emerges through runaway selection. Whether this or similar evolutionary models can be more broadly generalized to apply to body sizes in arachnids is among the field's grand challenges. But it is possible that, rather than a driver of diversity, extreme phenotypes such as eSSD may in fact be evolutionary dead ends, driving lineages towards extinction (Kuntner and Coddington, 2020). A similar phenomenon has been detected in the evolution of sociality in otherwise solitary and cannibalistic spiders (Agnarsson et al., 2006).

Much remains to be learnt from variation in body size among arachnids, particularly how it is inherited and how plastic versus canalized body sizes are and in what context (Walzer and Schausberger, 2014; Turk et al., 2018; Quiñones-Lebrón et al., 2021). Body sizes affect other phenotypic traits, notably behaviors. eSSD, for example, may be linked to the levels of sexual conflict that arises when male and female interests in the mating context diverge (Parker, 1979; Chapman et al., 2003; Tregenza et al., 2006). At least in arachnids, this field is somewhat controversial as it explains behavioral and evolutionary patterns though intersexual arms race (Kuntner et al., 2009a) rather than cryptic female choice (Eberhard, 2004; Peretti and Aisenberg, 2015).

Behavioral literature on spiders has ample examples of the imprints of sexual conflict. For example, sexual conflict is the best explanation for the occurrence of sexual cannibalism (Elgar, 1991; Elgar and Schneider, 2004; Kralj-Fišer et al., 2012; Kralj-Fišer et al., 2013; Schneider, 2014; Kralj-Fišer et al., 2016), and for evolution of opportunistic mating (Uhl et al., 2015; Sentenská et al., 2021). Further adaptations that could be interpreted as sexually conflicted are male self-sacrifice and male spontaneous death (Andrade, 1996; Welke and Schneider, 2010; Schwartz et al., 2013; Schwartz et al., 2014; Neumann and Schneider, 2020), genital mutilation and plugging (Uhl et al., 2007; Kuntner et al., 2009b; Uhl et al., 2010; Kuntner et al., 2012a), emasculation (Lee et al., 2012; Kuntner et al., 2015b; Kuntner et al., 2015a), remote copulation (Li et al., 2012), mate guarding, binding, or biting and other coercive acts (Zhang et al., 2011; Sentenská et al., 2020), male strategic allocation of sperm depending on levels of perceived cannibalism (Zhang et al., 2022b), and finally, males catapulting to safety to avoid being cannibalized (Zhang et al., 2022a). Whether or not these adaptations are merely spider specific or indicative of broader evolutionary patterns in arachnids is yet to be established.

Among the field grand challenges, thus, is a more precise evaluation to what extent the emergence of arachnid phenotypes is shaped by classical selection processes, and under what conditions, if any, sexual conflict needs to be invoked.

Grand challenge 7: Define effective conservation measures for arachnids in the light of global changes

Impediments to arachnid conservation mirror those for most invertebrates, and so do the proposed solutions (Cardoso et al., 2011). Arachnid science should attempt to redefine the role of arachnids in biological conservation given their genetic and functional diversity, as well as their known and unknown roles in ecological webs. The conservation measures should be assessed repeatedly in the light of global changes. Namely, research on arachnids and insects reveals that changes in temperature affect all behavioral interactions in a mating context (Leith et al., 2021). As a result of urbanization, anthropogenic noise also impacts negatively the functioning of arthropod communication by altering their soundscape (Classen-Rodríguez et al., 2021), and, likely, their vibroscape (e.g. Šturm et al., 2021). The effects of human degradation of the planet are thus directly manifested in the communities of arachnids, which are known to employ complex multimodal communication (Hebets et al., 2006). Finally, arachnid species are predicted to either go locally extinct or shift their ecological and geographical optima in response to global changes (Gobbi et al., 2006; Kuntner et al., 2014; Krehenwinkel et al., 2015; Mammola et al., 2019). These shifts will create new species communities with unknown consequences.

Among the field's challenges is to define appropriate and effective conservation measures for arachnids by integrating data from (phylogenetic) diversity, physiology, ecology, biogeography, and global change biology.

Conclusions

This perspective identifies the seven grand challenges in arachnid science: 1. Grasp the arachnid species diversity; 2. Standardize arachnid systematics research; 3. Interpret arachnid trait evolution through omics approaches; 4. Facilitate biotechnological applications of arachnid molecules and biomaterials; 5. Utilize arachnids as models in ecological and biogeographic research; 6. Disentangle evolutionary drivers of arachnid diversity; 7. Define effective conservation measures for arachnids in the light of global changes. Additional grand challenges in arachnid science will be defined, more specific to arachnid diversity and conservation, to arachnid morphology and systematics to arachnid micriobiota and vector-borne diseases, and to arachnid ecology and behavior. *Frontiers in Arachnid Science* is a new, open access venue to unite for the first time the scientific advances in all of arachnid science. It aims to become the main scientific forum for publishing high quality research bearing on arachnids and their chelicerate cousins. It will advance the basic knowledge on arachnid biology and their roles in ecosystems, strive to better understand and preserve their genetic, phenotypic, ecological, and functional diversity, and move towards applications of arachnid evolutionary novelties.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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