

# International Barcode of Life: Evolution of a global research community

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**Abstract:** The 6th International Barcode of Life Conference (Guelph, Canada, 18–21 August 2015), themed Barcodes to Biomes, showcases the latest developments in DNA barcoding research and its diverse applications. The meeting also provides a venue for a global research community to share ideas and to initiate collaborations. All plenary and contributed abstracts are being published as an open-access special issue of *Genome*. Here, I use a comparison with the 3rd Conference (Mexico City, 2009) to highlight 10 recent and emerging trends that are apparent among the contributed abstracts. One of the outstanding trends is the rising proportion of abstracts that focus upon multiple socio-economically important applications of DNA barcoding, including studies of agricultural pests, quarantine and invasive species, wildlife forensics, disease vectors, biomonitoring of ecosystem health, and marketplace surveys evaluating the authenticity of seafood products and medicinal plants. Other key movements include the use of barcoding and metabarcoding approaches for dietary analyses—and for studies of food webs spanning three or more trophic levels—as well as the spread of next-generation sequencing methods in multiple contexts. In combination with the rising taxonomic and geographic scope of many barcoding initiatives, these developments suggest that several important questions in biology are becoming tractable. “What is this specimen on an agricultural shipment?”, “Who eats whom in this whole food web?”, and even “How many species are there?” are questions that may be answered in time periods ranging from a few years to one or a few decades. The next phases of DNA barcoding may expand yet further into prediction of community shifts with climate change and improved management of biological resources.

*Key words:* DNA barcoding, conference, research trends, ecology, evolution, socio-economic applications, market substitution, next-generation sequencing, plant barcoding, ethnobotany genomics, marker selection.

**Résumé :** Le 6e congrès international « Barcode of Life » (Guelph, Canada, 18 au 21 août 2015), dont le thème est « Des codes à barres aux biomes », permet de présenter les plus récents développements en recherche sur les codes à barres de l'ADN et leurs diverses applications. Ce congrès se veut également un lieu de rencontre pour une communauté internationale de chercheurs afin d'échanger des idées et d'initier des collaborations. Tous les résumés, tant des conférences plénières que des autres contributions, sont réunis pour publication dans un numéro spécial de *Génome* à accès libre. Dans ce qui suit, l'auteure dresse une comparaison avec le troisième congrès (Mexico, 2009) pour mettre en relief 10 tendances récentes et émergentes qui ressortent parmi les résumés soumis. L'une des tendances qui ressort est la proportion croissante de résumés qui portent sur des applications ayant des retombées socioéconomiques du codage à barres de l'ADN. Cela inclut des études sur des ravageurs en agriculture, des espèces de quarantaine ou envahissantes, les causes de mortalité de la faune, des vecteurs de maladies, la biosurveillance de la santé des écosystèmes ainsi que des analyses de l'authenticité des produits de la mer ou des plantes médicinales qu'on retrouve sur le marché. D'autres tendances clés incluent l'emploi du codage à barres et du méta-codage à barres dans le cadre d'analyses nutritionnelles – dont des études de réseaux trophiques comprenant trois niveaux ou plus – ainsi que le déploiement de méthodes de séquençage de nouvelle génération dans de nombreux contextes. Conjointement à la portée taxonomique et géographique croissante des initiatives de codage à barres, ces développements suggèrent qu'on peut maintenant s'attaquer à plusieurs questions importantes en biologie. « Quel est ce spécimen de denrée agricole ? », « Qui mange qui dans ce réseau trophique ? », et même « Combien existe-il d'espèces ? » sont des questions auxquelles il devient possible de répondre sur l'horizon de quelques années à une ou plusieurs décennies. Les prochaines phases du codage à barres de l'ADN pourraient ouvrir de

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nouveaux chantiers dans la prédiction de l'évolution des communautés biologiques liée aux changements climatiques et dans la gestion des ressources biologiques. [Traduit par la Rédaction]

*Mots-clés* : codage à barres de l'ADN, congrès, tendances en recherche, écologie, évolution, applications socioéconomiques, substitution de produits, séquençage de nouvelle génération, codage à barres chez les plantes, ethnobotanique, génomique, sélection de marqueurs.

## Introduction

The 6th International Barcode of Life Conference, held 18–21 August 2015 in Guelph, Ontario, Canada—themed Barcodes to Biomes—highlights key recent expansions to the DNA barcoding research program, including large-scale investigations of entire assemblages of species. The sum of the abstracts reveals that substantial work remains to be done to understand the full extent of species diversity and to build DNA barcode reference libraries to enable specimen identifications to the species level. Nevertheless, for focal ecosystems and taxonomic groups, DNA barcode libraries are mature enough to move beyond library building, towards questions about trophic interactions and the structure of food webs. Moreover, key socio-economically important applications of DNA barcoding are galloping forward, such as wildlife forensics investigations and marketplace surveys of seafoods and medicinal plants.

In this introductory article, I present a brief introduction to the history of DNA barcoding and comment upon its international spread. I also review the most intriguing trends that I have observed during the review of contributed abstracts. Being the largest of this biennial conference series to date, the 6th Conference received 500 oral and poster presentations by presenting authors representing 56 nations. The special open-access volume of conference abstracts to follow showcases a truly international research movement reflective of the diverse individual and national interests of the participants.

### DNA sequences as barcodes: the origin of an idea

The ability to organize and recognize biological entities is essential for basic biological research and for diverse socio-economic applications in which humanity and biodiversity intersect. The need to identify species is perhaps particularly strong in the fields of systematics, conservation, invasion biology, ecology, and evolutionary biology as well as for applications such as the forensics of food, pest, and medicinal species. While estimates of total global species diversity vary greatly (e.g., see Mora et al. 2011 for a summary), there is a growing community consensus that the number is sufficiently vast—and contemporary extinction risk alarmingly high—such that the incorporation of digital methods is required to speed up the process of species discovery as well as to store and retrieve information about species collected at any life stage (e.g., Tautz et al. 2003; Janzen et al. 2005; Packer et al. 2009; Padial et al. 2010).

One key form of digital information about biodiversity is DNA itself, which stores vast biological information as

an information string consisting of four characters (A, C, G, T). Genetic information in various forms has been used for at least half a century for systematics research. Early contributions in the 1970s and into the 1980s included investigations of gross similarity and differences in entire genomes through DNA–DNA hybridization experiments, leading, for example, to an influential proposal regarding the higher-level systematics of birds (Sibley and Ahlquist 1990). Protein data, such as revealed through allozyme analysis, also featured prominently in earlier genetic studies. The invention of Sanger sequencing (Sanger et al. 1977) marked a critical point in the use of genetic data for systematics, providing direct rather than indirect evidence of the underlying DNA sequence information.

Interestingly, the idea that DNA sequences can be used as unique “barcodes” for identifying biological groups has appeared at least three times independently in the literature, i.e., without cross-citation. To my knowledge, the first appearance of the term barcode—as used referring to genetic information rather than a commercial product code—was by Arnot et al. (1993). They proposed using hypervariable tandemly repeated sequences as barcodes for identifying strains of the parasite *Plasmodium*. Second, Floyd et al. (2002) used the term barcodes in their study proposing the use of nuclear small subunit ribosomal DNA (18S) sequences for defining Molecular Operational Taxonomic Units for a taxonomically difficult group of animals, the nematodes. Third, the most recent and most general independent introduction of the concept was presented in two papers published by Hebert and colleagues (Hebert et al. 2003a, 2003b). These multiple origins of the concept of codifying biological forms through DNA, and the use of the barcode analogy, attest to the utility inherent in the digital signal of DNA.

### DNA barcoding: the spread of an idea (2003–2015)

The contributions by Hebert et al. (2003a, 2003b) are considered the most influential and are commonly cited as representing the origin of the DNA barcoding approach and movement. What distinguished these contributions from earlier treatments of DNA data as codes in other systematics contexts (whether or not the term barcodes was employed) was in providing a bold and general proposal: that standardized DNA regions could be used for identification of specimens to the species level across all (or at least the vast majority) of animals. Prior treatments tended to be more specific in their taxonomic scope. The more general proposal involved standardization of genetic regions to be sequenced, meaning

that, in principle, any specimen of any life stage representing any taxon collected anywhere in the world could be identified. Such a system would open new avenues for research and for the detection of species at critical places by non-taxonomic experts, such as at agricultural quarantine and international customs stations.

In their abstract entitled “Diffusing barcoding: the global spread of a good idea”, Bubela et al. formally analyze publication patterns in the barcoding literature, including all papers that cited four key papers. Bubela et al. conclude “Barcoding is an exemplar of the rapid and global spread of an innovation in the absence of formal proprietization. Its diffusion is not only in volume but in scope of applications. Institutional structures and opinion leaders have been key drivers. Further diffusion is likely with regulatory acceptance of the technology.” (Unless otherwise indicated, all citations in this article are to abstracts being published in this special volume.)

In this article, I delve into the contributed conference abstracts in more detail to highlight emerging trends, some of which are not yet apparent in the published literature. The global spread of the idea of DNA barcoding is clear, as evidenced by the diversity of nations represented among the authors and the varied study sites, taxa, and research questions included in this conference volume.

#### International Barcode of Life Conference series

A global research community was founded shortly after the publication of the first formal works proposing DNA barcoding as a global, standardized initiative (Hebert et al. 2003a, 2003b). Beginning in 2005, the International Barcode of Life Conference has been held every other year. Prior meetings have been hosted by cities spanning four continents: London, UK, in 2005; Taipei, Taiwan, in 2007; Mexico City, Mexico, in 2009; Adelaide, Australia, in 2011; and Kunming, China, in 2013.

As the 6th Conference will be hosted in Guelph, Canada, the upcoming meeting represents a symbolic homecoming for the DNA barcoding community. The Biodiversity Institute of Ontario (BIO), University of Guelph, is the home institution of Paul Hebert and colleagues. BIO is also home to the Secretariat of the International Barcode of Life (iBOL) project ([www.ibol.org](http://www.ibol.org)) as well as iBOL's largest sequencing facility.

The International Barcode of Life Conferences have grown in both participation and scientific scope over time. For example, there were 215 attendees of the 1st Conference in London, while there were ~340 participants at both the 2nd and 3rd Conferences. By the 4th Conference, in Adelaide, the number of conference delegates totaled 463, with 375 scientific presentations delivered. As of 22 July 2015, there are >500 registered participants for the 6th Conference as well as 500 accepted abstracts.

#### Research trends: Mexico City (2009) versus Guelph (2015)

As Guest Editor of this special volume, it was my privilege to review the contributed abstracts for publication. During this process, I noticed several intriguing trends to share with the broader community. I have elected to partially quantify these emerging trends by comparing the 6th Conference with the 3rd Conference. I selected the Mexican conference for comparison because DNA barcoding as a large-scale, standardized approach was first proposed in 2003. Therefore, 2009 represents the half-way point between 2003 and the present day, 2015. Moreover, as both conferences were held in North America, inter-continental travel costs would be more similar for these two conferences than for the other conferences. I am assuming here that this would increase the consistency of the pool of conference delegates at the continental level, improving comparisons of conference delegate composition across years. Nevertheless, I would still expect that travel costs remain an important factor influencing the representation of ongoing research within these conference proceedings.

For each contributed, accepted abstract (both oral and poster) for both conferences, I recorded key information and “scored” the abstracts on several scales. First, I recorded the country of the presenting author. Second, I assigned each abstract a score in terms of its taxonomic scope: (1) 1–9 species, (2) 10–99 species, (3) 100–999 species, (4) 1000–4999 species, and (5) 5000+ species. Third, I scored each abstract with regards to its geographic/political scope: (1) local, (2) regional, (3) national, (4) continental, and (5) global. Fourth, I categorized all abstracts in terms of their dominant theme: (1) barcode reference library building, systematics, and (or) marker selection/testing; (2) ecology (includes dietary analysis and community assembly); (3) evolutionary biology (includes molecular evolution and phylogeography); (4) socio-economic applications of DNA barcoding (e.g., agricultural pests, disease vectors, medicinal species, wildlife forensics, quarantine applications, invasive species detection; this category included library building when the socio-economic applications were stressed in the abstract); and (5) methods development. Fifth, and lastly, I recorded whether or not each abstract used next-generation sequencing (NGS) methods.

Some abstracts did not receive a score in all categories. When the above information was not explicitly provided, yet there was some reasonable indication of taxonomic or geographic scope in the prose, I performed some educated guessing. Therefore, the specific abstract “scores” were somewhat subjective. Nevertheless, as I conducted all of the scoring, the below comparison of the 3rd and 6th Conferences will be at the least internally consistent and revealing of general trends. Further details regarding the abstract scoring can be found in the

Supplementary data<sup>1</sup>. The 2015 numbers included here represent all accepted abstracts as of 22 July 2015; due to unforeseen circumstances, some of these abstracts may not be presented at the 6th Conference. As well, I omitted plenary abstracts, as those abstracts reflect in large part the strategic vision for the conference that is crafted by the individual organizing committees. By contrast, contributed abstracts may be more comparable across the conferences and more reflective of global research activities in progress. Moreover, research by the plenary speakers will be highlighted in a separate special issue of full articles. While the Mexico City meeting featured 229 contributed presentations, the Guelph conference is more than twice as large, with 470 contributed abstracts (including both poster and oral presentations for both meetings). Therefore, comparison in composition between the meetings is made in percentages.

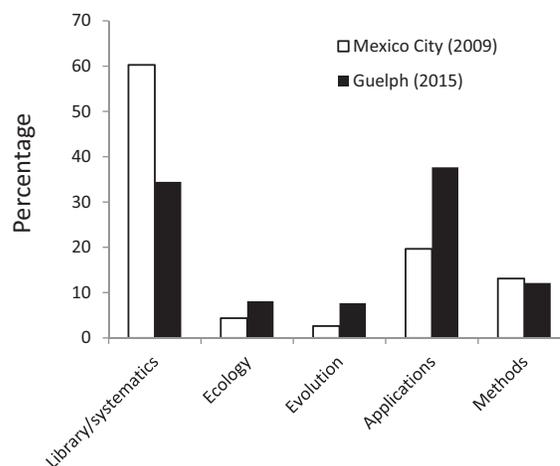
Below, I highlight 10 of the most salient observations and trends that I noted in the evolution of the International Barcode of Life community. For space considerations, I emphasize trends apparent since the 2009 conference, acknowledging that many excellent abstracts are not highlighted or cited below. I present these observations as a commentary in the hope of promoting reflection, discussion, collaboration, and research planning.

### 1. Rise in socio-economic applications of DNA barcoding

The increased focus upon the socio-economic applications of DNA barcoding was one of the dominant trends noted in the 2009 versus 2015 comparison. Contributed abstracts for the 3rd Conference heavily featured library building, genetic marker evaluation and comparisons, and methods development, including primer design and informatics tools for species-level identification. By contrast, in the 6th Conference, there is a distinct rise in the number of abstracts that emphasize the socio-economic applications of DNA barcoding (Fig. 1). For example, there is a marked increase in both the number and diversity of marketplace surveys, with a particular emphasis upon herbal medicinal plants (Dhivya et al.; Ghorbani et al.; Kumar et al.; Lekganyane et al.; Melo Palhares et al.; Osathanunkul et al.; Ratsoma et al.; Schori et al.; Shiba et al.) and fish products (Cawthorn et al.; Santos et al.; Sarmiento Camacho and Valdéz-Moreno) but also including spices (Saravanan et al.) and wild edible mushrooms (Xu et al.). In 2015, the total quantity of studies on medicinal plants—including reference library building, marker testing, methods development for mixed-species products, and marketplace studies—was striking.

The Fish Barcode of Life (FishBOL) initiative played a prominent role in both conferences. While both conferences include important studies that are building DNA

Fig. 1. Distribution of contributed presentations among research themes in Mexico City (2009) versus Guelph (2015). The number of abstracts in every category is higher in Guelph, with a total of 470 contributed abstracts, in comparison with Mexico, having a total of 229. The results are therefore shown by percentage here to highlight trends. Mexico more prominently featured DNA barcode reference library building and systematics works, while in Guelph there is a higher focus upon socio-economically important applications of DNA barcoding as well as the usage of barcoding for ecological and evolutionary research.



barcode reference libraries for fish from various geographic regions, some shifts in research focus relating to fish and other commercially important aquatic taxa are apparent. In particular, varied applications of DNA barcoding are apparent in 2015. These include developing protocols for the barcoding of fish eggs and larvae (Naaum et al.), using barcoding to investigate the larval distributions of fish species (Bourque and Hanner; Cota-Valentin et al.; Malca et al.; Steinke et al.) and also lobsters (Vasquez-Yeomans et al.), and unraveling trophic interactions through dietary analysis in fish (Bartley et al.; H. Liu et al.; Shortridge and Miner; Thielman et al.). As well, several marketplace surveys are detailed in the 2015 conference proceedings (Cawthorn et al.; Santos et al.; Sarmiento Camacho and Valdéz-Moreno), and the contribution that barcoding can make to understanding medicinal uses of fish is also highlighted under the term ethnoichthyogenomics (Ravitchandirane and Thangaraj).

Studies on vectors of human and veterinary diseases; agricultural pests, pathogens, and parasitoids (agricultural biological control agents); and agricultural soil microbiota featured in both conferences, with an overall increase towards the present in the frequency of studies directed towards such socio-economically important groups of organisms. As well, in 2009, there was a tendency for abstracts to focus primarily on methodological

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/gen-2015-0094>.

development and library building for these taxonomic groups. In comparison, 2015 features more abstracts reporting studies conducted in real agricultural settings, including cultivated fields (e.g., Bennur et al.; Gutiérrez Gutiérrez et al.; Jindal et al.; Kamenova et al.; Shinde and Khedkar; Wang et al.), greenhouses (Lenin et al.), fruit tree orchards (Aslam et al.), and vineyards (Gutiérrez Gutiérrez et al.). Such studies are uncovering new information about species-level diversity and the specificity of biological associations within agricultural systems. Possibly, in future conferences we may see yet a further shift—going beyond elucidating the diversity inhabiting agricultural systems towards directly applying barcoding for agricultural management and for making pest mitigation decisions.

Numerous studies also specifically highlight barcoding progress, methods development, analysis of policy, and (or) training programs relating to the detection or understanding of quarantine and invasive species (Bezeng et al.; Chain et al.; Deiner et al.; Frewin et al.; Furlan et al.; Glover et al.; Gutiérrez Gutiérrez et al.; Hodgetts et al.; Jalali and Venkatesan; Kumar and Smrithy; Layton et al.; Marinich et al.; Masson et al.; Park et al.; M. Roy et al.; Salisbury et al.; Sambandan et al.; R. Santos et al.; M.D. Santos et al.; Shimura and Duthie; Sutou and Ito; Thomas et al.). Interest in the topic of invasive and quarantine species spans many countries, focal taxa, and molecular approaches (DNA barcoding, metabarcoding of mixed-species assemblages, and eDNA detection using both qPCR and NGS methods).

Although the majority of all studies from both meetings were contributed by university-based researchers, 2015 witnesses an increase in the number of abstracts that were either written or coauthored by researchers working within governmental agencies or other institutions concerned with the regulation of biological materials, protection of biological resources, and protection of environmental health. Using Canada as an example, multiple contributions by Canadian teams highlight barcode-related research within federal and provincial governmental agencies, including both government-led projects and strong academic-governmental collaborations. These projects are diverse, including: library building and species delineation in aquatic (Castelin et al.; Young et al.) and terrestrial (Barrio et al.; Fernandez-Triana et al.; Landry et al.; Solecki et al.) taxa, the trophic ecology of fishes (Bartley et al.), the detection of threatened (Boothroyd et al.; Currier et al.; Serrao et al.) and invasive (Marinich et al.; Masson et al.; M. Roy et al.) species, and a study revealing the composition of mixed-species assemblages being used in freshwater ecotoxicological assays (Capretta et al.).

Finally, there is a strong trend in using DNA barcoding for wildlife forensics. Schindel and Trizna outline a dedicated six-country initiative to barcode endangered species, particularly those regulated under the Convention

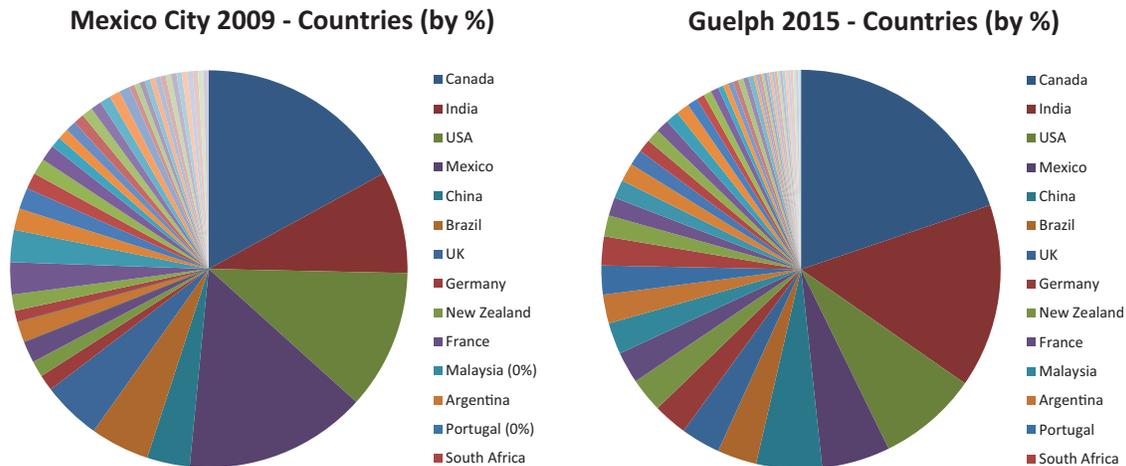
on International Trade in Endangered Species of Wild Fauna and Flora (CITES), as well as related and “look-alike” species. The strong data standards for this project (Trizna and Schindel) are designed to enable barcodes to be used in the prosecution of wildlife crimes to reduce the trade of endangered species. As a participant in this initiative, Mwale et al. report that all CITES-listed mammal, bird, and reptile species of South Africa have been barcoded. Shiba et al. expose the illegal presence of CITES-listed species within a medicinal plant market in South Africa. Other works relating to wildlife forensics include the barcoding of captive animals at a zoo in India (Kumar et al.) and the usage of barcodes to identify claw samples originating from large cats in India (Hange and Khedkar). Mendoza et al. focus upon increasing barcode coverage for CITES-listed species within Colombia, with particular emphasis upon a highly traded animal group, the birds. Also, within India, Kalyankar et al. outline investigations relating to the ornamental fish trade. Beyond its conservation importance, wildlife forensics also encompasses human safety-related investigations, including understanding the identities of birds involved in air strikes (Beentjes et al.). Arulandhu et al. outline a strategy for identifying seized forensics samples, while Topan provides an overview of the rising demand for forensics-related services at the Biodiversity Institute of Ontario.

## 2. International participation enhanced in 2015

The number of nations represented among presenting authors of contributed presentations grew by 22% between Mexico City (44) and Guelph (54). These results confirm that the Barcode of Life is indeed a highly international research discipline. Moreover, the distribution of presentations among countries reflects broad participation among many nations, while several countries emerge as being highly involved in DNA barcoding (Fig. 2). Nations that are well represented (>2% of all contributed abstracts) in both 2009 and 2015 are Canada, India, the United States, Mexico, China, Brazil, the United Kingdom, Germany, and New Zealand. As hosts of the 2009 meeting, Mexico was prominently represented at the 3rd Conference.

Several nations have become more heavily involved in the 2015 conference. In particular, the rise in participation by India is striking; this increase in barcoding activities may be linked to the recent establishment of a dedicated barcoding institute (see trend No. 4 below). Interestingly, neither Malaysia nor Portugal are recorded having any contributed abstracts in 2009, while both reach >2% representation in 2015. An examination of co-authorship patterns suggests that the rise of Malaysia as a strongly represented nation is to a large degree due to the establishment of a barcoding-intensive research program at the University of Malaya. This group of researchers is investigating the biodiversity of Southeast Asia, including novel studies of wildlife harboured within

**Fig. 2.** Distribution of countries that are represented by the presenting authors of contributed abstracts in Mexico City (2009) versus Guelph (2015). The legend to the right of each pie chart can be associated with the figure by reading the legend from top to bottom and comparing with the pie slices in a clockwise fashion, starting at the top. The 14 most represented countries from 2015 (>2% of contributed abstracts) are shown in both charts, with the countries placed in the same order to facilitate comparison.



large urban centres (Brandon-Mong et al.; Jising-See et al.; Lee et al.; Lim and Wilson; Ng et al.; Sing et al.; Wilson et al.). With multiple institutions involved from from mainland Portugal and the Azores, Portugal exhibits particular strength in using DNA barcoding to explore the diversity and evolution of marine life (Antunes et al.; Costa et al.; Lobo et al.; Moura et al.; Oliveira et al.; Paupério et al.; R. Santos et al.; Vieira et al.).

A comparison of 2009 versus 2015 also reveals an increase in the number (but not the proportion) of continental- and global-scale projects (Fig. 3). Several authors specifically stress the importance of international collaboration. For example, Lavinia et al. highlight the role of international collaboration (among Argentina, Bolivia, Brazil, and Mexico) in achieving a novel study of evolutionary diversification in their abstract entitled “From a local barcoding initiative to a continental-scale, multi-institutional assessment of avian diversification in the Neotropics”. Perez et al. describe a global-scale study to elucidate terrestrial arthropod diversity, Schindel and Trizna describe a six-country initiative to protect endangered species, and Park et al. and Frewin et al. describe continental or global efforts to generate species lists and barcode libraries for pest and quarantine species. Such initiatives are important for understanding and protecting biodiversity, especially in the face of increasing global trade and associated invasion risk (Shimura and Duthie).

Interestingly, in 2015, there is an increasing proportion of abstracts of narrow taxonomic focus (1–9 species) and geographic scope (local or regional scale) (Fig. 3). This may be reflective of the growing interest in DNA barcoding; new researchers, institutions, and countries are joining the 6th International Barcode of Life Conference. As well, a variety of the applied studies are highly targeted; for example, several contributions relate to select taxonomic groups of agricultural pests collected

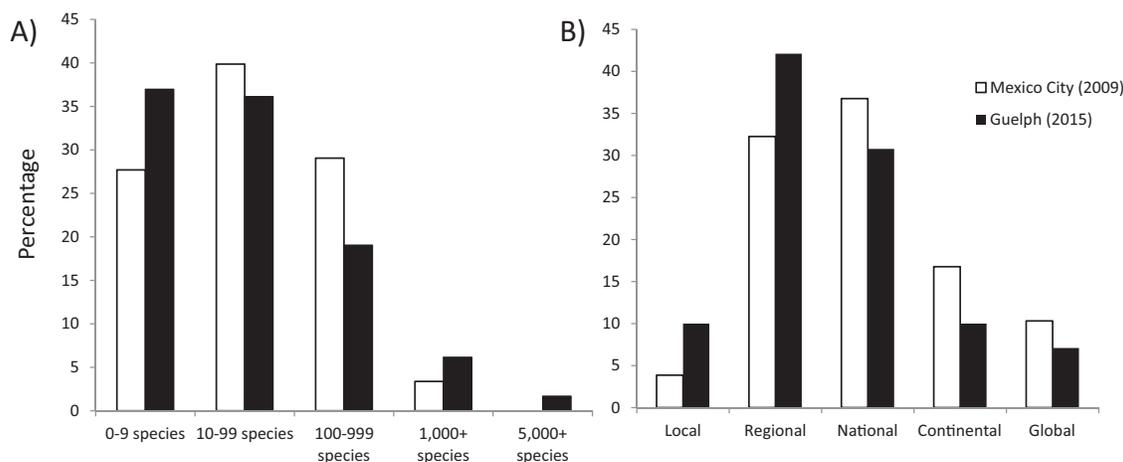
from fields in specific geographic regions. By contrast, researchers from several “established” barcoding nations are presenting very large-scale projects, representing a decade of barcoding-related research as well as collaborations spanning multiple research teams.

### 3. Different countries/continents lead in specific disciplines

While DNA barcoding as a whole is a highly international endeavour, it is clear that institutional and national research priorities can vary. For example, India, China, and South Africa have all emerged as leaders in plant barcoding, and this includes the barcoding and analysis of medicinal plant products. This result may partially reflect institutional and (or) personal research priorities; however, this finding also underscores international variability in the strength of association between human communities and biodiversity. Particularly in rural communities in developing regions of the world, plant-derived treatments are more common than synthetic or industrially produced medicines, and this trend is likely mirrored in research resources being directed towards medicinal plants. Davies et al. present a study entitled “Human population density in Africa correlates with the evolutionary history of its flora”, again highlighting the close association between humans and biodiversity.

As another example of regional leadership, South and Central American researchers are global leaders in the DNA barcoding of birds. Based upon patterns in abstract coauthorships, this effort is to a large degree catalyzed by Argentina, specifically the team at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, but this effort has now expanded far beyond Argentina’s borders and involves multiple institutions and research teams. The building of more complete barcode reference libraries enables not only wildlife forensics applications

**Fig. 3.** A comparison of the scope of contributed abstracts in Mexico City (2009) versus Guelph (2015) using two metrics: (A) taxonomic scope, and (B) geographic/political scope. For both metrics, the absolute number of abstracts was higher in every bin in Guelph than in Mexico. The results are shown in percentages to demonstrate trends in the composition of abstracts.



but also excellence in fundamental scientific research. This conference volume reports novel insights into the systematics, phylogeography, species ages, diversification patterns, molecular evolution, and barcodes of endangered species within birds from the Neotropics, including contributions from across South and Central America (e.g., Barreira et al.; Bukowski et al.; Lavinia et al.; Mendoza et al.; Salinas et al.).

#### 4. New DNA barcoding centres rise to prominence

The 2015 abstracts volume also reveals emerging new centres of DNA barcoding. I highlight here the research scope and contributions of two key dedicated barcoding centres, whose strongly prominent role in the conference proceedings has arisen since 2009.

The Paul Hebert Centre for DNA Barcoding and Biodiversity Studies (at the Dr. Babasaheb Ambedkar Marathwada University in Aurangabad, India) has emerged as a major contributor to the 2015 conference proceedings, which is especially noteworthy as its grand opening was held only recently, in 2011. As authors from this institution submitted ~20 abstracts to the conference, this represents institutional participation second only to that of the conference hosts, the University of Guelph. Moreover, a wide-ranging and diversified research program on DNA barcoding and its socio-economic applications is apparent, with conference contributions encompassing the following: barcoding of mosquito disease vectors (Ahirrao et al.); barcoding of both pest species (Shinde and Khedkar) and parasitoids (Devi et al.) in agricultural settings; reference library building, phylogenetic/systematics works, and (or) barcoding methods development for diverse taxa including aquatic plants (Kadam et al.), freshwater and marine fishes (Khedkar; Mohekar et al.; Rathod et al.), freshwater zooplankton (Khobragade et al.), and corpse flies relevant for forensics investigations (Zambare and Khedkar); conservation applications including a wildlife forensics investigation involv-

ing large cat species (Hange and Khedkar) and studies on the trade of ornamental fishes (Kalyankar et al.); and a marketplace survey of meats to evaluate law enforcement (Naikwade et al.).

Another important continental centre is the African Centre for DNA Barcoding (University of Johannesburg, South Africa). With eight presented or coauthored abstracts in 2015, compared to two from 2009, the University of Johannesburg team and collaborators are well represented in the conference proceedings. Contributed abstracts that include one or more coauthors from the African Centre for DNA Barcoding are far-reaching and build upon a solid foundation enabled by dedicated DNA barcode library building. Specifically, this research group and their collaborators have emerged as global leaders in creating regional species-level plant phylogenies and using these to investigate the evolutionary history and ecological mechanisms that underlie community assembly (Bello et al.; Davies et al.; Maurin et al.; Yessoufou and van der Bank) as well as species invasion success (Bezeng et al.). Members of this research group have also investigated plant species identification success and product authenticity from a traditional medicinal market (Lekganyane et al.; Ratsoma et al.; Shiba et al.), revealing some trade in species with declining populations as well as the illegal sale of CITES-listed species.

The University of Waikato (New Zealand), with 10 contributed abstracts, also features prominently among the institutions participating in the 6th Conference, with research focused upon the biodiversity of New Zealand (Beet et al.; Doyle and Hogg; Doyle et al.; Mc Cormack et al.; Podmore et al.; Riding et al.; West et al.; Woods et al.) and Antarctica (Beet et al.; Collins and Hogg; Collins et al.). Due to variability in the way institutions were entered by authors into the abstract submission form, the assessment in this section should be consid-

ered a qualitative rather than a comprehensive assessment of institutional involvement. Nevertheless, the trends reported here showcase several highly active research programs and institutions.

### 5. Increase in the number of large projects

Both the number and proportion of taxonomically broad projects, those including 1000+ species or even 5000+ species, has increased markedly between 2009 and 2015 (Fig. 3). This rise is not explained by an increase in adoption of next-generation sequencing (NGS) methods. Many studies that feature NGS were not included in the “taxonomic scope” analysis, as the numbers of species or MOTUs detected were not reported. Moreover, among the nine contributed abstracts reporting work involving 5000+ species or Molecular Operational Taxonomic Units (MOTUs) or 20 000+ specimens, all but one (Deiner and Altermatt, a contribution on river biomonitoring) used Sanger sequencing.

Among the contributed abstracts from 2015, these large-scale projects include an overview of the Mexican Barcode of Life (MexBOL) initiative (Eliás-Gutiérrez and León-Règagnon; Martínez-Arce and Eliás-Gutiérrez), a large and active national network that includes regional barcoding facilities. The progress of another large national network, the Norwegian Barcode of Life (NorBOL), which is tasked with advancing knowledge of Norwegian and polar biodiversity, is also highlighted in a dedicated presentation (Ekrem et al.). Although the Netherlands were not represented among the presenting authors of contributed abstracts in 2009, in 2015 a summary is provided regarding the substantial barcoding program at the Naturalis Biodiversity Center, which is focused upon the flora and fauna of the Netherlands (Beentjes et al.).

Interestingly, beyond these overviews of large institutional programs and national networks, there are also cases of specific research projects that are extensive in their taxonomic scope. For example, Fernandez-Triana et al. present a large study (10 000+ specimens) investigating cryptic diversity and Holarctic distribution patterns in a group of parasitoid wasps. Bukowski et al. report progress in studying the diversity of terrestrial arthropods as part of the Global Malaise Trap Program, with a finding of >5000 MOTUs to date at a site in the Atlantic Forest biome of Argentina. Perez et al. provide an overview of the Global Malaise Trap Program, which includes collaborators from 30 countries and which has documented >65 000 MOTUs to date. Given these large programs, the oft-posed but elusive question of “how many species are there?” (e.g., Mora et al. 2011) may be within reach within the coming few years, at least for select taxonomic groups amenable to collection via standardized methods.

### 6. Continued “hub” role for University of Guelph, Canada

About 18% (~84 of 470) of the contributed presentations include one or more coauthors from the University

of Guelph, particularly with representation from the Biodiversity Institute of Ontario (BIO), which span all five of the research subject categories described above. This predominance in the scientific program in part reflects the geographic reality that the host institution is expected to contribute proportionally more abstracts due to lower travel costs (Fig. 2). However, this also reflects the continued role of BIO as a hub for both research and for high-throughput sequencing for the global barcoding community. The Biodiversity Institute of Ontario (or Canadian Centre for DNA Barcoding, housed within) is acknowledged for providing sequencing support within approximately 25% of all publications relating to DNA barcoding (Dirk Steinke, pers. comm., 17 July 2015).

BIO’s role as a high-throughput DNA barcoding centre is enabling new, large-scale research projects that have been developed since 2009. One such project being highlighted at this conference is the Global Malaise Trap Program for elucidating terrestrial arthropod diversity, which is featured in several abstracts led by researchers from BIO (D’Souza; Perez et al.), Argentina (Bukowski et al.), Bangladesh (Bhuiya and Mazumdar; Mazumdar et al.), and the United States (Zlotnick et al.). The capacity of BIO as biological repository—with a digitized, highly barcoded specimen collection and an active loan program—is also presented (Telfer et al.). BIO-based researchers are also sharing new methodological developments, including new NGS-based protocols for barcoding type specimens (Prosser et al.), revealing the composition of herbal medicines (Ivanova et al.), and non-destructively sequencing DNA from bulk environmental samples (Shokralla et al.).

University of Guelph researchers are also strongly involved in building extensive plant (e.g., Kuzmina et al.; Warne et al.) and animal (e.g., Blagoev et al.; Fernandez-Triana et al.) barcode reference libraries; assessing the uses and authenticity of medicinal plant species (e.g., Dhivya et al.; Sambandan et al.; Tahir et al.); studying patterns of molecular evolution (e.g., Loeza-Quintana and Adamowicz; Mitterboeck et al.; Young et al.) and community assembly (e.g., Bringloe et al.; Martin et al.; Pare and Smith; Smith et al.); developing approaches for the biomonitoring of ecosystem health (e.g., Fahner et al.; Gibson et al.); establishing methodological approaches (e.g., Naaum et al.), species checklists (Frewin et al.), and best practices (Naaum et al.) relating to quarantine applications, product validation, and marketplace surveys; and using DNA barcoding to enhance scientific education (Berzitis et al.).

### 7. Animal and fungal barcode markers: broad consensus

In the six years between 2003 (Hebert et al 2003a, 2003b) and 2009 (3rd Conference), the animal research community widely adopted the standardized animal barcode marker, the 5’ region of cytochrome c oxidase subunit I (COI). This was despite the trend that earlier barcoding-style works on species-level identification

systems for animals (Bartlett and Davidson 1992; Parson et al. 2000; Branicki et al. 2003), as well as phylogeography studies of vertebrates, generally used a different mitochondrial gene, cytochrome b. This subsequent adoption of COI for a broad DNA barcoding program in animals may have been facilitated by the relatively similar pattern of molecular evolution between the two mitochondrial protein-coding genes (e.g., see Lavinia et al.). The greater conservatism of COI amino acid sequences may assist with higher taxonomic placements (Hebert et al. 2003a). Phylogenetic signal of COI has previously been explored in the literature (e.g., Wilson et al. 2011 and other works), and the possibility of identifying specimens to the family level based upon their DNA barcodes is further developed at this conference (Kekkonen).

The barcoding community in general adopted the notion of standardization as being important for creating globally relevant DNA barcode reference libraries. In both 2009 and 2015, most animal-focused contributions used COI, either solely or in combination with other markers. While a small number of contributions in 2009 solely explored “alternative” animal barcode markers, the vast majority of animal contributions from 2015 use COI. Some authors included the study of additional genomic regions, often nuclear, to further their specific study goals, such as using nuclear DNA sequences to detect hybridization (e.g., Aguilar-Velasco et al.). Terms such as complementary rather than alternative, when referring to markers other than COI, are more commonly employed in 2015 compared to 2009 among animal-related abstracts.

While COI is broadly used as the barcode region for most animal phyla, consideration of barcode markers is apparently ongoing for nematodes. The nuclear small subunit rRNA gene (18S) is typically used, sometimes in combination with other markers, for studying free-living nematodes in marine settings (Zhou et al.) as well as in agricultural soils (Gutiérrez Gutiérrez et al.). Zhou et al. contrast 18S and COI for marine nematodes and highlight the trade-offs that may occur; they found lower sequence variation (discrimination signal) in 18S but a higher rate of sequence recovery compared to COI. Marker evaluation is also ongoing in parasitic nematodes. COI, ITS-1, and ITS-2 are used in a study of parasitic nematodes infecting pelicans (Valles Vega et al.), while Velarde-Aguilar and León-Règagnon evaluate the effectiveness of the barcode region of COI for discriminating nematode parasites of frogs.

Similar to the case in animals, there is broad consistency in marker usage for fungi. Whether using Sanger sequencing or NGS methods, most authors use one or more ITS regions for fungi (Aslam et al.; Ivanova et al.; Korpelainen and Pietiläinen; Mark et al.; Meyer et al.; Porter et al.; S. Roy et al.; Xu et al.; Yu et al.), sometimes in combination with other markers, especially nuclear rRNA gene sequences. In light of the widespread usage of

ITS2 for fungal and plant barcoding, Ankenbrand et al. present an extended informatics workbench for ITS2 sequences. However, Irinyi et al. report insufficient species-level resolution of ITS within pathogenic fungi and explore alternative markers. Although alternative or complementary marker exploration is ongoing, ITS is apparently now firmly established as the “core” marker in use by the fungal barcoding community.

#### 8. Plant barcode markers: community consensus remains elusive

In contrast to the situation in animals, a consensus regarding marker choice has not emerged in plants. In 2009, the CBOL Plant Working group published a dedicated contribution in which they compared and tested the merits of multiple candidate genetic regions. They recommended that two chloroplast gene regions serve as the “core” DNA markers for plant barcoding: *rbcl* and *matK*. Given their study was published in 2009, it is not surprising that at the 2009 conference, plant marker choices were diffuse among studies. It is somewhat more surprising that, six years later, this remains the case. Many plant-related contributions in the present volume employ or test a variety of different markers. Some studies do not even include the core markers as candidates. Without marker standardization, it is difficult to achieve a reference library that would enable identification anywhere in the world, such as at international customs check-points.

Standardization also enables large-scale research into entire biomes. In their contribution on the applications of DNA barcoding for ecology, Yessoufou and van der Bank point out: “Since the pair *rbcl* and *matK* has been accepted as the core DNA barcode for terrestrial plants, many studies, perhaps surprisingly, continue to test the discriminatory power of these markers in many lineages. In Africa, and specifically in South Africa, we have moved on with the application of the core barcode in phylogenetic ecological studies.” As highlighted above in the section on the African Centre for DNA Barcoding, the approach of this research group in using consistent markers has yielded multiple intriguing findings. They have used phylogenies to reveal mechanisms underlying community assembly and to provide new knowledge in invasion biology. As well, consistent marker usage enables comprehensive regional libraries to be built, facilitating marketplace surveys of medicinal plants and other biological products.

There are several potential reasons for the lack of consensus. The primary reason may be that even when using the recommended two-marker “core” plant barcode, species discrimination rates for plants tend to be lower than for animals. The [CBOL Plant Working Group \(2009\)](#) indicated a species discrimination rate of 72% for the recommended two-marker barcode among their test species, with 100% success for genus-level assignments. [Fazekas et al. \(2009\)](#) also reported species discrimination rates of

~70% in plants, while species-level discrimination rates for animal species in their review were much higher, 90%–98%. While lower rates of molecular evolution may contribute, they attributed this difference primarily to differences in hybridization rates between plants and animals. Unfortunately, [Fazekas et al. \(2009\)](#) indicate this issue cannot be readily addressed through adding a small number of additional loci.

These typical plant “success” rates may not be high enough for many purposes, such as distinguishing closely related species that may have different medicinal properties and in cases where geographic information about the source location is not available (e.g., biological forensics). The majority of plant authors either explicitly evaluate and compare markers or comment upon the species discrimination success rate. Upon seeking higher resolution, some authors may forego global concerns over marker standardization in favour of markers that serve as taxon-specific “local optima” for species discrimination. While many contributions in this conference volume use *rbcl*, *matK*, or both, and demonstrate the significant discriminatory signal in these markers, some plant contributions did not employ either one of the core barcode regions for plants.

A large number of plant contributions in this volume have used a hybrid approach between standardization and discrimination. These studies use the two “core” plant barcode markers across the species in their study, but also evaluated or added additional markers to increase species-level discrimination in difficult groups (e.g., [Awad et al.](#); [Gao et al.](#); [Gawhari et al.](#); [Kadam et al.](#); [Kress et al.](#); [Kuzmina et al.](#); [Malik and Babbar](#); [Martínez de la Vega et al.](#); [Mitchell and Alemseged](#); [Şahin et al.](#); [Schori et al.](#); [Shaw et al.](#); [Sheth and Thaker](#); [Sheth et al.](#); [Shiba et al.](#); [Silvis et al.](#); [Vinitha et al.](#); [Warne et al.](#); [Zhou](#)). [Fahner et al.](#) also highlight the value of including multiple markers in environmental assessments of below-ground plant communities using NGS. These studies could possibly serve as a model for future trends in plant DNA barcoding, in which the core markers are always included even when the specific study aims dictate addition of markers. One can hope that funding towards plant barcoding projects can reflect the need for global standardization of markers—for both scientific gain and for enabling socio-economically important applications of DNA barcoding—as well as the need for researchers to achieve better species discrimination rates for plants for their individual studies and specific applications.

### 9. Next-generation sequencing methods are becoming widespread

In 2009, next-generation sequencing (NGS) methods were used in just five presentations (2% of the 229 contributed abstracts). During the intervening years, research that featured NGS methods were typically included within dedicated oral presentation sessions. By contrast, in 2015, NGS usage is widespread, being used in

19% (88 of 470) of all contributed abstracts by presenting authors from 24 countries. Moreover, NGS methods are widely distributed across various research themes. Topics in which NGS usage is particularly prevalent include dietary analysis of mammals, fish, and terrestrial arthropods (see trend No. 10 below); simultaneous detection of animal and microbe DNA in support of food authenticity and safety analysis ([Kaepfel et al.](#)); restoration ecology ([Eaton et al.](#); [McGee et al.](#)); biodiversity assessment and biomonitoring of entire communities for ecosystem health (e.g., [Bowser et al.](#); [Gibson et al.](#); [Ledger et al.](#); [Lobo et al.](#); [Pawlowski et al.](#); [Rougerie et al.](#); [Wright et al.](#)); and environmental DNA (eDNA) analysis, in which DNA is sampled directly from the environment, such as from sediments or water, rather than from specimens (e.g., [Alsos et al.](#); [Bista et al.](#); [Deiner and Altermatt](#); [Deiner et al.](#); [Fahner et al.](#); [King et al.](#); [Morey and Hanner](#); [Pansu et al.](#)).

An interesting research avenue emerging at the 2015 conference is that several contributions use DNA for historical reconstructions. [Pansu et al.](#) use sediments to reconstruct vegetation community shifts and to detect changes in mammal species presence over 10 000 years, with shifts detected that are corroborated with the known history of human activities in the area. Similarly, [Alsos et al.](#) demonstrate that eDNA in sediments can be used to detect changes in vegetation communities, such as planting of forests, over the past two centuries. Using NGS barcoding of pollen from historical bee collections, [Gous et al.](#) investigate shifts in plant usage by bees over a 93-year period. Finally, historic usage of different fish species by humans is investigated through sequencing mini-barcode regions from ancient fish remains from archaeological sites ([Puncher et al.](#); [Royle et al.](#)).

Several promising new technologies are also highlighted in 2015. [Ramgren et al.](#) and [Boutain and Boutain](#) showcase diverse uses of the Oxford Nanopore Technologies’ MinION device, which is a sequencing instrument “about the size of a smartphone” ([Ramgren et al.](#)). [Sirrianni and Wangh](#) also present an intriguing technology in which species may be discriminated in a single closed-tube reaction. Based upon such developments, the hoped-for “hand-held field-friendly barcoder” ([Janzen et al. 2005](#)) may be within reach, which would open remarkable opportunities for both research and applications of barcoding by diverse user groups.

### 10. Species interactions are being studied across multiple trophic levels

In Mexico, only one or possibly a small number of studies investigated diet. Searches for the word “diet” and for the phrase “gut content” in the titles/abstracts spreadsheets yielded only a single match (barring a case that mentioned that specific tissues were sampled for earthworm barcoding to avoid amplifying gut contents). The sole 2009 abstract on this topic presented a published study on dietary analysis for eight sympatric

species of bats (Clare et al. 2009). By contrast, in 2015, there are enough dietary analyses among the contributed abstracts for a dedicated parallel presentation session (plus there are posters and presentations in other sessions) on the trophic interactions of mammals (Arrizabalaga-Escudero et al.; Bennett et al.; Jung; Kartzinel and Pringle; Magalhaes de Oliveira et al.; Mallott et al.; Mata et al.; Mitchell and Alemseged; Salinas-Ramos et al.). Moreover, there are at least four abstracts reporting fish dietary analysis as well (cited above).

The 2015 conference also witnesses the expansion of dietary analysis beyond vertebrates, including dietary analysis within marine copepods (Zhang et al.), squids (Braid and Bolstad), and terrestrial arthropods. Kamenova et al. use diet analysis to characterize the ecosystem services (pest regulation) provided by carabid beetles in managed wheat and oilseed rape fields, and Wang et al. investigate the diet of generalist predators (spiders) in rice paddies. Other studies investigate dietary breadth in herbivorous terrestrial arthropods collected in wild ecosystems (Burgess et al.; Garcia-Robledo et al.; Kishimoto-Yamada and Ito; McClenaghan et al.), yielding novel insights. For example, in their study investigating the diets of chrysomelid beetles in Costa Rica, Garcia-Robledo et al. found that barcoding “revealed several cryptic insect herbivore species with narrow diets and elevational distributions”. By contrast, Kishimoto-Yamada and Ito emphasize the broad diets of several species of chrysomelid beetles in a rainforest in Borneo (e.g., “four species fed on several families of gymnosperms and (or) ferns together with multiple angiosperm families”). While more research is needed to understand broader patterns of specialization/generalization in insect herbivores across taxonomic groups and sites, it is clear that DNA barcoding and metabarcoding can play a prominent role in uncovering feeding associations.

Species interaction studies have also expanded beyond the (primarily) two trophic levels that are considered during dietary analyses. For example, Roslin and Wirta outline how they first constructed a comprehensive barcode library of terrestrial animals and vascular plants in a focal High Arctic region of Greenland. They went on to use this library to document predator–prey relationships in animals, finding that the “the structure of the food web proved extremely complex, showing dense linking and no compartmentalization”. Beyond illuminating new information about this Arctic food web, this study showcases the value of DNA barcoding in food web ecology. Another study on species interactions is explicitly investigating interactions among three major taxonomic groups representing multiple trophic levels (Garcia-Robledo et al.; abstract entitled “Reconstructing interactions among plants, insect herbivores, and phoretic mites using DNA barcodes: modeling coextinctions under projected climate change”). This presentation underscores the complex and novel ecological research

that can be facilitated by DNA barcoding. As a final example, Fofanov et al. are exploring species interactions across domains of life, studying bats, arthropods, and guano-associated bacterial communities in subterranean habitats.

Up to three interacting trophic levels are also being investigated in the context of medically important studies. For example, Brugman et al. elucidate three interacting levels: mosquito species identities (vectors), host species identities (vertebrates which comprised the mosquito blood meals), and the presence/absence of the Myxoma virus (pathogen). Similarly, Lutomiah et al. analyze the blood meal source and viral status associated with mosquitoes collected during a Rift Valley Fever outbreak in Kenya. To better understand the role of birds as reservoirs of three avian-transmitted viruses, Tseren-Ochir et al. analyze bird fecal samples to identify the bird species as well as screen for viral status. These studies demonstrate that simultaneously considering the pathogen and hosts is possible, and broader adoption of such methods may provide substantial public health benefits through monitoring and possibly mitigating vector and pathogen distributions.

#### Concluding remarks

In just 12 years since it was formally proposed as a standardized, large-scale endeavour, DNA barcoding has matured into a broad-ranging international research program. In August 2015, the 6th International Barcode of Life Conference is hosted in Guelph, Canada, and is currently set to include 470 contributed presentations by presenting authors representing 54 nations. The breadth of research topics ranges from reference barcode library building for select taxa to food web studies spanning three or more trophic levels. Barcoding-enabled research is also providing new insights into the origins and distribution of humans as well as our shared history and associations with other species with whom we share the planet (Davies et al.; Stoeckle and Thaler). Diverse socio-economically important applications of DNA barcoding are maturing, including multiple studies highlighting quarantine/regulatory applications of DNA barcoding and marketplace surveys of seafoods, medicinal plants, and mushrooms.

Important questions for biology and for society are becoming tractable. “What is this specimen on an agricultural shipment?”, “Who eats whom in this whole food web?”, and even “How many species are there?” are questions that can be answered in time periods ranging from a few years to one or a few decades. The presentation by Hebert outlines a vision for the “Planetary Biodiversity Project”, a mega-science project that will run from 2020–2040. Beyond elucidating the number and distributions of species, the next phases of DNA barcoding may expand yet further into predicting community shifts with climate change and improving the management of biological resources.

Research agendas enabled by DNA barcoding and meta-barcoding are reflective of varied personal, institutional, national, and international research interests relating to biodiversity. Interestingly, standardization of genetic markers is also permitting substantial creativity—with scientifically novel projects showcased in these conference proceedings as well as socio-economically important studies, such as those on medicinal species and vectors. As attested by the diverse abstracts presented in this special volume, DNA barcoding is enabling new research avenues and new ways of accessing information about biodiversity. This tool links a highly diverse community of researchers, and the 6th Conference represents an opportunity for inspiration, sharing of ideas, discussion, and planning of the next exciting research endeavours.

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