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ORIGINAL ARTICLE

Emerging Topics and New Directions in Statistical Ecology

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Abstract

Ecological science relies on robust estimates of the abundance, diversity, and spatial distribution of individuals and species, but these quantities are notoriously difficult to observe directly. Data collected on these quantities not only reflect the ecological processes giving rise to them but also the observation process, which is often biased by factors such as uneven sampling effort or imperfect detection. Furthermore, collecting data according to standard sampling designs is often not possible. Statistical ecology as a research field specialises in developing statistical methods for analysing such complex ecological data. Here, we apply text analysis tools to the abstracts submitted to eight International Statistical Ecology Conferences between 2008 and 2022 to guide a review of recent topics in statistical ecology. Results show that estimating various aspects of demography (including survival, recruitment, abundance, density and movement) and spatial distribution remain key areas of research. The field has benefited from and embraced new data collection methods such as automated recorders and rapidly developing remote sensing techniques. How to integrate data from different sources is a central challenge that spans multiple areas of statistical ecology. The statistical ecology community strives to be more inclusive, and to promote rigorous data analysis practices that support reproducible research and transparent conservation decisions. As human pressures on nature intensify, statistical ecology is becoming an increasingly vital area of research.

Keywords Data integration · Ecological statistics · International Statistical Ecology Conference · Quantitative ecology · Statistical Ecology · Structural Topic Model

1 Introduction

We live in a data-rich world. Increasing data streams from unmanned aerial vehicles, camera traps, genetic sampling, acoustic recorders, satellites and other rapidly devel-

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oping data collection tools are adding to data streams from more traditional sources such as citizen science projects, environmental monitoring programmes and long-term studies [1–8]. These data have enormous potential to help scale up from traditional site-specific studies, better understand the natural world around us and to make better conservation decisions. However, it is often difficult to extract the relevant information from all these diverse data streams, for several reasons. First, complex sources of variability affect the data at various levels (across space and time, between individuals, populations and communities, across taxonomic levels) [9, 10]. Second, the data are often not collected according to a probabilistic sampling or experimental design, or even in a standardized way [11]. Third, the process of interest can often not be directly observed and needs to be estimated while taking into account the observation process [12].

Statistical ecology is a growing field of research with the aim of developing statistical methods designed to extract signals from layered and noisy ecological data streams [13, 14]. Statistical ecology has broadly been defined as the study of ecological systems using mathematical equations, probability, and empirical data [15]. Ecologists, conservationists, and managers have long recognised the need for robust quantitative methods to address some of their most fundamental questions [15]. These questions often boil down to "how many individuals are there?" (abundance), "where are they and how do they move?" (spatial population processes / animal movement / species distributions), "how many species are there?" (biodiversity), and "how many individuals survived?" (demography). Methods for estimating abundance and demographic parameters, such as capture-mark-recapture [16] and distance sampling [17], have long been central themes in statistical ecology [14]. More recently, however, the statistical ecologist's field of activity has grown enormously, developing more flexible statistical tools – multi-level models and machine learning algorithms are two examples – and making use of increased computing power to analyse the growing streams of ecological data that are available [18].

Here, we give an overview of the field of statistical ecology as it is reflected by the International Statistical Ecology Conferences (ISEC), the largest gathering dedicated to the field of statistical ecology. ISEC has been held every two years since 2008. We used text analysis tools to analyse the abstracts of contributed talks and posters presented at ISEC (we include abstracts from the conferences held over the period 2008 - 2022) to structure our review. While the analysis of ISEC abstracts provides the structure of our review, we do not restrict ourselves to papers that have been presented at ISEC. We acknowledge that ISEC does not necessarily reflect all research conducted in the field of statistical ecology and that research presented at ISEC probably is not a proportional reflection of the research of the entire field. However, the ISEC conference organisers have made efforts to be inclusive through their choice of invited speakers and special sessions, and we feel that the conferences do reflect the main trends in the field statistical ecology as a whole.

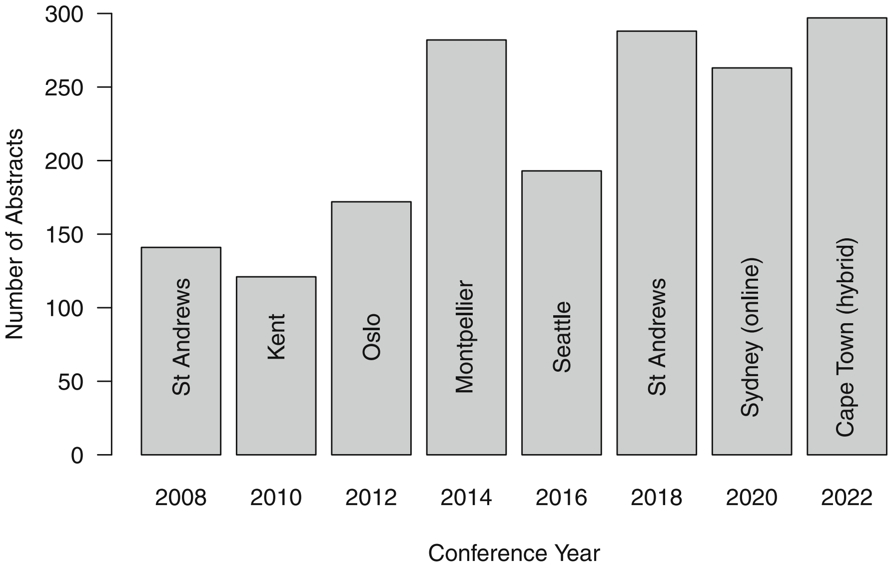

Fig. 1 Number of abstracts used in this analysis for each International Statistical Ecology Conference (ISEC). ISEC was held every second year since 2008. The location where each conference took place is written on the bars

2 Text Analysis of Conference Abstracts

We analysed the abstracts of talks and posters presented at ISEC, which are condensed summaries of the main techniques and messages conveyed in the papers. They carry useful information that can help identify key or latent topics. Calls for abstracts for previous conferences emphasised criteria such as relevance, significance, innovation, and accessibility of the submitted papers with focus on fields that interface between statistics, ecology and related disciplines.

Using the `pdftools` [19] and `quanteda` [20] packages in the R statistical programming environment [21], we extracted abstracts from the abstract book for each ISEC conference held from 2008 to 2022. In total, we collected 1757 abstracts from eight conferences, with the number of abstracts increasing over time as conference participation grew (Fig. 1).

Data preparation involved converting all the text in the abstracts to lowercase. The combined dataset of abstracts was then checked for duplicates and extensively cleaned, removing numbers, punctuation, special characters, and stopwords (most common and low information words e.g., "a," "and," "the"). The text was used to generate individual word tokens. Each token underwent stemming, which reduces words to their root forms by removing prefixes or suffixes. For example, "analysing," "analysed," and "analysis" would be stemmed to "analys". N-gram analysis explores sequences of words or characters in a text to uncover patterns and frequent pairings. It groups words into units of size n, such as unigrams (single words), bigrams (pairs of consecutive words), or trigrams (three-word sequences). In this study, we focused on extracting bigrams to balance simplicity with meaningful contextual insights, enabling

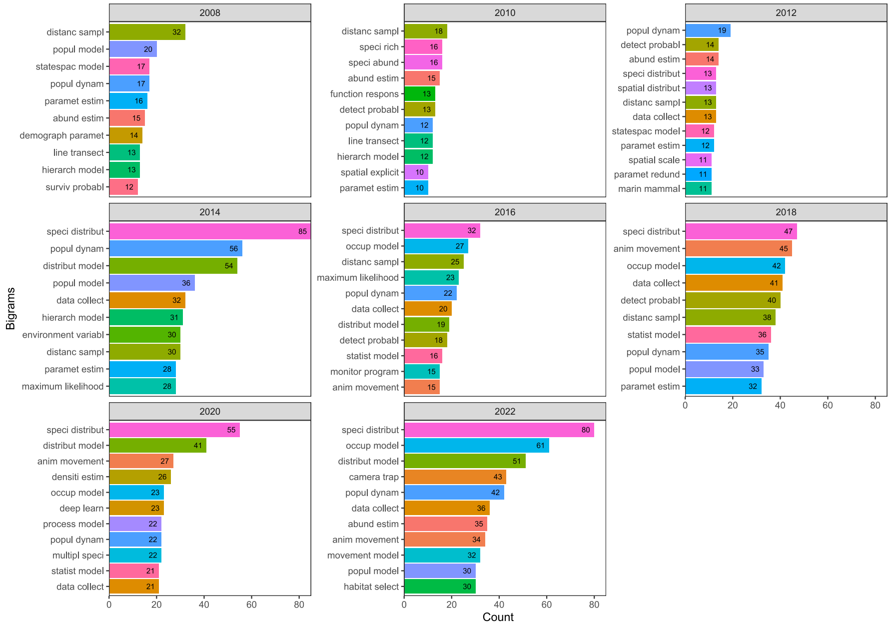

Fig. 2 Frequencies of the most common two-word phrases (bigrams) appearing in the abstracts presented at the International Statistical Ecology Conference (ISEC) held every two years from 2008 to 2022. Individual phrases are colour coded to facilitate comparison among years

the identification of commonly co-occurring words and shedding light on how the context of abstracts has evolved across different conferences.

The most frequent bigrams suggest that at the first two ISEC conferences, in 2008 and 2010, the work presented was dominated by areas that had a strong history of collaboration between ecologists and statisticians. These include abundance estimation by distance sampling and estimation of demographic parameters from capture-mark-recapture data. Bigrams related to these fields – such as ‘distanc sampl’, ‘abund estim’, ‘line transect’, ‘detect function’, ‘surviv probabl’, and ‘popul model’, among others – were the ones most frequently found in ISEC2008 and ISEC2010 abstracts (Fig. 2). Abundance estimation, population demography, and modelling of population dynamics (bigrams ‘popul dynam’ and ‘popul model’) remained important themes throughout the entire period. A theme that became more common at ISEC over time was modelling where species occur. Species distribution models (reflected by the bigrams ‘speci distribut’ and ‘distribut model’) and occupancy models (bigram ‘occup model’) became common tools that the community helped develop and apply. Another theme that became popular is animal movement (‘anim movement’ and ‘movement model’), reflecting the need for developing methods to analyse increasingly available animal tracking data [22, 23].

The bigrams only hint at topics that were discussed at ISEC and we used topic models to identify such topics more formally. Topic models are techniques used to uncover hidden themes or topics in text data by grouping related words and documents

[24–28]. Structural Topic Models [26–28] can quantify the influence of document metadata (e.g., conference year, location) on topic prevalence. This method is ideal for unstructured data like abstracts, allowing us to identify topics and examine their prevalence in the ISEC abstracts.

The models were fitted using the `STM` package [29] in R [21]. We selected the appropriate number of topics based on exclusivity (words unique to specific topics) and semantic coherence (representative words for coherent concepts). The number of topics has to be specified by the analyst and there is no single correct way to do so. Specifying too few topics can lead to different themes becoming amalgamated and the identified topics are hard to interpret. However, with an increasing number of topics, semantic coherence tends to decline, meaning that semantically related words tend to be split across several topics until the same theme appears in several topics, again making the topics hard to interpret. After considering a range of models ranging from 1 to 45 topics, we determined a 15-topic model as the most helpful for our analysis of the research covered in the ISEC abstracts.

We characterised the topics by looking at the words in each topic with the highest likelihood (Probability, Table 1). FREX (frequent and exclusive) words are those that are both common in a topic and unique to the topic. They identify words that differentiate topics. We also studied sample texts that the model identified as being representative for each topic, keeping in mind that individual abstracts can contain a mix of topics.

In the following section, we use the topics identified by the bi-grams and STM to guide our overview of the field of statistical ecology. Rather than discussing the topics in order of their frequency (as presented in Table 1), we discuss them in a sequence that allows for a more logical flow. Using ISEC abstracts as a guide for the topics covered in the general field of statistical ecology, we do not restrict the discussion of these topics to papers that were actually presented at ISEC. However, we note that our approach might lead us to emphasize topics that are overrepresented at ISEC compared to the broader research field.

3 Key Topics in Statistical Ecology

3.1 Statistical Models for Ecological Data (Topics 1, 5 and 9)

Most ISEC abstracts contain elements from the broader field of statistics and the text analysis has grouped these into three related topics that we discuss together here.

Statistical ecologists embrace a strong modelling philosophy and due to the often complex processes that generate ecological data, hierarchical models are key tools [9, 10, 30, 31]. Ecological data usually not only reflect the underlying ecological process we are interested in but also the observation process, which can add extra variance to the data (e.g. [32]) and bias estimators that don’t account for the observation process (e.g. [33]). Developing models that separate the ecological process from the observation process has therefore received much attention and is a theme that we will come back to in later sections. For example, state-space models have proven useful for the analysis of ecological time series [34].

Table 1 Topics identified through probabilistic topic modelling of abstracts presented at the International Statistical Ecology Conference (ISEC) between 2008 and 2022. We list the words in each topic that have the highest likelihood (Probability). FREX (frequent and exclusive) words are those that are both common in a topic and unique to the topic. The column headed 'Percent' gives the prevalence of each topic in the corpus

Topic	Percent	Highest Probability and FREX Words
Topic 1	12.20%	Probability: model, fit, distribut, data, covari, process, predict, bayesian, variabl, ecolog
		FREX: fit, covari, model, latent, flexibl, randomeffect, hierarch, posterior, distribut, linear
Topic 2	8.40%	Probability: speci, communiti, distribut, interact, divers, occup, bird, environment, predict, model
		FREX: speci, communiti, divers, interact, occup, rich, occurr, multispeci, distribut, trait
Topic 3	7.80%	Probability: sampl, detect, survey, estim, abund, distanc, design, site, probabl, observ
		FREX: sampl, survey, distanc, detect, transect, design, abund, site, line, effort
Topic 4	7.80%	Probability: spatial, chang, forest, dynam, landscap, scale, process, model, plant, pattern
		FREX: forest, landscap, plant, tree, dispers, land, chang, diseas, cover, scale
Topic 5	7.70%	Probability: method, data, likelihood, estim, paramet, simul, comput, analysi, exampl, illustr
		FREX: likelihood, method, comput, approxim, real, illustr, exampl, maximum, mcmc, miss
Topic 6	7.40%	Probability: habitat, variabl, effect, season, environment, site, area, water, year, temperatur
		FREX: habitat, season, water, temperatur, predat, variabl, prey, river, period, factor
Topic 7	7.30%	Probability: statist, ecolog, manag, network, test, develop, tool, research, packag, analysi
		FREX: network, statist, learn, ecolog, packag, tool, test, softwar, decis, ecologist

Table 1 continued

Topic	Percent	Highest Probability and FREX Words
Topic 8	6.90%	Probability: data, inform, collect, monitor, integr, dataset, sourc, differ, process, citizensci
		FREX: sourc, citizensci, collect, map, project, data, monitor, program, integr, dataset
Topic 9	5.90%	Probability: estim, error, measur, rate, bias, model, uncertainti, growth, paramet, simul
		FREX: error, interv, measur, bias, uncertainti, negat, binomi, growth, proport, confid
Topic 10	5.80%	Probability: movement, anim, behaviour, state, time, model, behavior, data, forag, observ
		FREX: movement, behavior, behaviour, forag, state, hidden, markov, anim, gps, track
Topic 11	5.70%	Probability: popul, dynam, data, demograph, estim, rate, trend, integr, paramet, genet
		FREX: popul, demograph, dynam, genet, trend, declin, stochast, integr, timeseri, rate
Topic 12	5.20%	Probability: surviv, individu, breed, model, year, age, rate, reproduct, bird, migrat
		FREX: breed, surviv, reproduct, age, migrat, nest, mortal, life, femal, year
Topic 13	4.70%	Probability: densiti, model, individu, estim, spatial, captur, capturerecaptur, anim, trap, camera
		FREX: densiti, captur, capturerecaptur, trap, camera, individu, recaptur, mark, explicit, spatial
Topic 14	4.20%	Probability: fish, model, fisheri, manag, assess, stock, marin, data, estim, sea
		FREX: fish, fisheri, stock, catch, assess, manag, marin, sea, atlant, sustain
Topic 15	3.00%	Probability: record, acoust, whale, tag, estim, detect, data, call, anim, method
		FREX: acoust, whale, tag, record, call, deploy, mammal, marin, visual, depth

Note: We set the number of topics to 15. Key words for the identified topics

Ecological data often contain dependencies that violate the assumption of independent observations made by many statistical methods. Species are related to each other through their evolutionary history and data analyses may need to account for such phylogenetic dependencies [35, 36]. Ecological data are also often correlated across space and time, and spatiotemporal models have been useful for describing ecological processes like the expansion of a species' range [37]. Hierarchical models are also useful tools for fitting ecological process models to experimental data [31]. Mixture models have been used to deal with the often-present hidden heterogeneity in ecological data [38].

The field has embraced Bayesian approaches [9, 39–43], and developed methods for model selection [44–47] and multi-model inference [48]. Parameter redundancy is a common problem in models that statistical ecologists use [49]. While Bayesian methods and flexible software like WinBUGS [50],Stan [51] and NIMBLE [52] have made it easier to fit complex hierarchical models to data, Bayesian methods also offer a systematic way of incorporating existing knowledge through informative priors [53]. Eliciting expert knowledge has been an important theme [54].

Ecological data often consist of counts (e.g. number of individuals or species detected at a site), proportions (e.g. proportion of sites that are occupied by a species, proportion of a population surviving, proportion of area covered by vegetation) and binary outcomes (e.g. survived vs died, occupied vs not occupied). Models that can handle non-normally distributed outcomes and mean-variance relationships are therefore important in our field [55–57]. Ecological data often contain a large proportion of zeros and there are a number of modelling strategies to accommodate these [58].

Ecologists often need to analyse multivariate data, e.g. counts of individuals of a set of species with the goal to test whether these differ across a set of sites or points in time. Popular analysis tools are multivariate analysis of variance that can be used to partition variance using any distance metric and in any multifactorial ANOVA design [59, 60]. However, distance-based multivariate analyses make unrealistic assumptions about the mean-variance relationship typically found in ecological data [61] and there is a trend towards using generalised linear models and their recent multivariate generalisations [62].

Many of the large ecological data sets are observational, rather than obtained through manipulative experiments. Structural equation modelling [63–65] and causal analysis principles [66] are increasingly used to establish causal relationships in ecological analyses.

3.2 Modelling the Distribution of Species and Communities (Topic 2)

Many ecological questions require us to know where species occur in a given area. These questions range from focusing on the spatial distribution of a single species, to questions about co-occurrence of groups of species and the composition of communities, to local species richness. At the level of a single species, we often want to know which factors limit a species' distribution, which habitat is suitable for a species, which new areas an invasive species can colonise, how a species shifts its range in response to climate change, etc. The most common data type used to address these questions consists of species occurrence records, also known as presence-only data. Presence-only data can be used with traditional Species Distribution Models (SDMs) [67] to predict where species occur, based on associations between observed species occurrences and environmental variables [68]. However, with this type of data, we have incomplete information on where species occur, locations are generally not sampled in a probabilistic way and information on sampling effort is usually not available [69]. There has been considerable interest in identifying best practices and developing novel approaches for dealing with issues associated with presence-only SDMs [69–71], including how to deal with observer and sampling bias [72], choice of pseudo-absence or background data [73], model evaluation [74], model uncertainty [75] and modelling method [76]. Presence-only data cannot inform us about a species' prevalence because the sampling intensity is generally not known. Models fitted to presence-only data therefore yield a measure of relative habitat suitability, rather than what we often would like to know, i.e. the probability that a species occurs at a site [77]. If we have absence records in addition to occurrence records, i.e. presence-absence data, we can estimate prevalence and occurrence probability [77]. However, true absence is often difficult to establish because species can go undetected during surveys, in which case, we are dealing with detection / non-detection data.

Occupancy models estimate the probability that a species occupies a site [78]. They account for incomplete detection by modelling the observation process using repeated detection / non-detection data [79] or time-to-detection data [80, 81]. Occupancy models have been used to address ecological questions at a wide range of spatial scales, from local patch occupancy to species ranges [82, 83]. They have been extended to examine occupancy dynamics (dynamic occupancy models [84]), describing breeding range vs non-breeding range (multi-state occupancy models [85]), to account for spatial effects [86, 87], etc. The models have been adapted to address data issues like mis-identified individuals [88, 89], and variable observer effort and skills [90]. Efficient algorithms and software exist for fitting occupancy models to large data sets [91, 92].

Community ecology and macroecology deal with groups of species and the processes that allow species to co-exist or not. While community ecology focuses more on the processes that shape local communities, macroecology deals with patterns and processes at larger spatial scales. Both fields depend on a good understanding of where groups of species occur. Multi-species occupancy models estimate the occupancy probability of groups of species across collections of sites while accounting for the observation process [93–95]. Joint species distribution models combine species distribution modelling with multivariate techniques to gain insights into the processes that structure communities [96, 97].

Estimating biodiversity is a thorny problem because samples are typically incomplete and rare species, in particular, tend to go undetected. Occupancy models have been extended to estimate species richness from detection / non-detection data [98]. Other data types that are also common in biodiversity studies are samples of individuals and species lists collected at specific locations. These are also usually incomplete samples of the target community but species richness and other biodiversity metrics can be estimated from these data using rarefaction and extrapolation [99, 100].

3.3 Monitoring, Citizen Science and Integrated Species Distribution Modelling (Topic 8)

Monitoring programmes are used to assess trends in biodiversity across space and time. These programmes often supply critical data for evaluating the efficiency of management and conservation policies, or to measure our progress towards conservation targets. Statistical ecologists have helped develop monitoring protocols and corresponding analysis methods that yield statistically robust results [11] and are most effective at yielding the necessary information [101].

Monitoring programmes sometimes rely on data collected through citizen-science projects, which tend to have a large spatial extent and yield a lot of data [102]. Designing survey protocols and data analysis methods for citizen science projects is an important theme in statistical ecology [103]. Some citizen science data are used in species distribution models [69, 104]. Citizen science data are often collected in a fairly unstructured way and explicitly accounting for the observation process seems particularly important for this type of data [7, 105, 106].

Where citizen science data exist alongside data collected through more structured monitoring programmes, we would like to combine the advantages of the former (typically large spatial extents and large amounts of data) with the latter (typically more rigorous survey designs and data collection protocols, but see [107]). This can be achieved through statistical data integration, which has received a lot of attention in the field of species distribution modelling. Integrated species distribution models tend to have a higher predictive accuracy than models built on a single data set [108, 109]. Also, by combining data collected from different areas one can develop large area SDMs which allow for effective study of species distributions over large spatial scales [110, 111]. Integrated SDMs are generally built on integrated data models with joint likelihoods and are underpinned by theory based on point processes [112]. Integrated modelling with joint likelihoods can account for sampling issues, variation in spatial and temporal support, as well as account for uncertainty in the data sources [113]. Although data integration can be used to combine a variety of data types, combining presence-only data with presence-absence data remains the most common type of spatial data integration [114–119].

3.4 Spatial Ecology (Topic 4)

Spatial ecology examines the role of space in shaping ecological processes and patterns, covering aspects such as species distribution, diversity, and ecological interactions [120]. These phenomena are studied using spatial data collected at various scales, including points, regions, or networks. Such data are often visualised on maps to identify hotspots or highlight conservation priorities among other uses. A key challenge in spatial ecology is spatial autocorrelation, where data collected at nearby locations are not independent, thus violating the assumptions of many statistical methods [121]. Methods for dealing with spatial autocorrelation are therefore an important area of research in spatial ecology [122].

The availability of spatial data at various scales (global and local) or level of granularity necessitates careful consideration of scale effects as the modifiable areal unit problem can distort ecological inferences if not properly accounted for [123, 124]. Advances in spatio-temporal modelling have improved the study of ecological processes by integrating space-time interactions [125]. As spatial data sources continue to expand, addressing issues related to data quality, accuracy assessment, error propagation and incorporating robust spatial statistical methods remain essential for addressing pressing ecological and conservation challenges [120, 126].

3.5 Abundance and Density Estimation (Topic 3)

Abundance (number of individuals in a population or some other frame of reference, e.g. site or colony) and density (the number of individuals per spatial unit) are two closely related ecological state variables that have received a lot of attention from statistical ecologists. At face value, it seems like abundance could be easily observed by counting the number of individuals. However, especially with animals, some individuals usually escape detection and abundance therefore needs to be estimated from incomplete observations. Various methods have been designed to estimate abundance, including capture-mark-recapture experiments [127, 128], close-kin capture-recapture [129, 130], removal sampling and methods that use the distance between the observer and the detected animal to account for the observation process [131, 132]. These can be formulated as hierarchical models where the state model describes the distribution of animals and the observation model the detection process that generates the observed data [133].

Density is often a more useful metric than abundance because it can be more easily compared across space and time. However, converting abundance to density is not straightforward because animals move around and it is usually not clear what the size of the area is that has effectively been sampled [134–136]. The effective sampling area – and thus density – can be estimated directly with distance sampling methods, where the information on detection probabilities comes from the observed distances between the observer and detected individuals, rather than from re-encounters of marked individuals like in capture-mark-recapture experiments [17]. Developing distance sampling into a mature set of tools that can be applied in many situations [137, 138] and developing the necessary software [139] to analyse this data type has been a dominant theme at ISEC. Distance sampling has been extended to estimating trends in density in open populations (i.e. populations that change in size due to birth, immigration, death and emigration [140]) and to estimate abundance of multiple species in communities [141].

3.6 Population Dynamics (Topic 11)

A key problem in ecology is to understand how and why abundance (or density) changes over time, i.e. the dynamics of populations [142, 143]. Population dynamics are the result of gains and losses of individuals in the population due to demographic processes (e.g., birth, immigration, death, emigration) [144]. Population dynamics have been studied using a variety of approaches. Building on estimates of demographic processes (Topic 12, Sect. 3.7), matrix population models can be used to examine the dynamics of populations in stationary and non-stationary environments [145, 146]. These models offer a flexible tool to study dynamics of groups of individuals of a single species distinguished by different factors (e.g., age, sex, site, genotype) as well as interacting species [147]. Where time series of population abundances are available, state-space models are a powerful tool for studying population dynamics [34]. Where demographic data (typically capture-recapture data) and time series of abundance are available, integrated population models (IPMs) can estimate demographic rates and population trends, and identify drivers of population dynamics [148–150].

3.7 Demography (Topic 12)

Demographic rates (including survival, age at first reproduction, recruitment and related quantities like dispersal and population growth rates) are usually not directly observable but can be estimated from capture-recapture data [14, 151]. Capture-recapture methods deal with the problem of imperfect detectability of individuals that can be identified, either because they were marked or through unique features such as spots, stripes or genetic material. The Cormack-Jolly-Seber (CJS) approach was a major landmark because it offers a flexible tool for estimating survival from capture-mark-recapture data collected under natural conditions [33]. A more recent milestone is the recognition that CJS models are hidden process models, where the demographic process is represented by a Markov process that is only partially observed [152]. By formulating capture-recapture models as Hidden Markow Models (HMMs), the process model can easily be adapted to study hidden states such as lifetime reproductive success, disease incidence, and hybrid prevalence [152]. Further, the HMM framework allows us to cope with uncertainty in state assignment, thereby facilitating greater use of observational data where misidentification of individuals or states is possible [153]. Capture-recapture methods have long been embedded in freely available software (e.g., MARK [154], E-SURGE [155], R package `marked`[156]) that allow practitioners to fit models using both maximum likelihood and Bayesian approaches. These programmes have been instrumental in laying the foundation for robust inference using capture-recapture data. High computational cost is one of the major drawbacks of fitting increasingly complex capture-recapture models, such as random effects models that account for individual (continuous) heterogeneity, to large empirical data sets. However, new programming systems such as NIMBLE (R package `nimble`; [52]) and Stan [51] help to significantly reduce such computational burdens by improvement in MCMC sampling efficiency [157]. Assessment of goodness-of-fit [158] of complex capture-recapture models and model diagnostics remain a key challenge requiring further work (e.g., [159]).

3.8 Spatial Capture-Recapture (Topic 13)

By combining features of capture-recapture and distance sampling methods, Spatial Capture Recapture (SCR) models can estimate the effective sampling area and density of animals by including spatial information on where individuals are caught [134].

SCR models incorporate a spatial point process as the state component and a suitable detection model for the observation process (driven by the type of data being analysed). Individual heterogeneity stemming from differential space use is accommodated by the detection model depending on the distance from an individual's activity centre to a particular detector [135, 136, 160].

In early applications, the detectors tended to be physical traps but the use of SCR models quickly extended to studies that use other means of detection such as microphones, hydrophones, camera traps, hair snares, human observers, aerial surveys, line transects and area searches (e.g. [161–163]). For example, standard models can be used to estimate animal density from acoustic data when the calls can be uniquely identified (as in the case of bottlenose dolphin signature whistles [164]) or to estimate call density when individual identification is not possible (as for minke whales [165, 166] and calling gibbons [167]). In addition, much effort has gone into the development of new SCR model types that are better suited for these new data streams such as models for line transects or area searches [168], acoustic SCR models that can be used to simultaneously estimate call density and cue rate (as with Cape Peninsula moss frogs [162]), continuous-time models that can be used for individually identifiable data generated by camera trap arrays (see [169] for an application to jaguars), and models for spatially referenced genetic samples [163]. Furthermore, there has been a realisation that while SCR models were developed primarily to model density they can also be used to make other kinds of inference. For example, there have been models developed that link SCR with landscape ecology by integrating resource selection information with SCR models [170] or by using a non-Euclidean distance metric to learn about landscape resistance and connectivity [171–173], and continuous-time models can estimate animal activity patterns [174]. Merging movement models with spatial capture recapture models, animal movement and space use can also be studied from data collected by stationary recorders [175–177].

3.9 Bioacoustics and Passive Acoustic Monitoring (Topic 15)

Many animals produce sounds that can be used to monitor them using rapidly improving recording equipment (Passive Acoustic Monitoring, PAM [178, 179]), and to study their behaviour, ecology, occurrence, occupancy and density (e.g. [180]). There are many advantages of PAM over traditional survey methods for a wide range of sound producing animals, including the ability to survey continuously over time, being less dependent on weather and environmental conditions, and increasing sample size in particular for species that are difficult to see. Statistical ecologists have developed methods for automatic detection of sounds of interest, as well as occupancy and density estimation, especially through spatial capture recapture (Topic 13, Sect. 3.8). Methodological developments continue to appear and we anticipate additional progress in areas like (1) near continuous-time density estimation (2) the use of machine learning and deep learning for automatic sound detection and classification, to process the ever growing amounts of data being collected (e.g. [181]), and (3) ways to efficiently use the data from such automated methods and associated uncertainty measures – like detection confidence scores – in density estimation pipelines. Data integration approaches (e.g. [182]) where acoustic data is used together with visual data and other observational data streams to make inferences about a common underlying state process are also likely to see further development in coming years.

3.10 Animal Movement (Topic 10)

The advent of miniaturized tracking technology with increasingly advanced sensor types has made it possible to study the movement of animals in more detail, for more diverse species [22]. Movement is a prevalent feature of many organisms, and it is often the result of active decisions that encode interesting aspects related to their ecology, such as dispersal, space use and behavioural traits.

Animal movement data are most commonly geographical locations obtained from animal-attached devices that record or transmit information at some temporal resolution, with a varying degree of spatial error [183, 184]. In addition to locations, tracking devices also now yield other types of movement data, such as vertical movement (depth or elevation) [185] and acceleration [186]. The common feature of all animal movement data is that they are time series of locations of a number of individuals, often observed over the same time window. However, not all movement data are tracking data – capture-recapture and spatial capture-recapture data have also been used to infer movement (Topic 13, Section 3.8).

Analysing movement data required new statistical approaches, a challenge eagerly taken up by statistical ecologists [187]. Since Nathan et al. [188] proposed a movement ecology paradigm, coinciding with the first ISEC in 2008, a wealth of methods for analysing movement data have been developed, ranging from relatively simple, discrete-time analyses to complex, hierarchical models that can be framed in continuous time, in either a frequentist or Bayesian statistical framework. The methods now available for analysing animal movement data are both modifications of existing methods, and new statistical methods developed specifically for making ecological inferences from animal movement data that account for the specific features these data present. One of the biggest recent advances for movement modelling is that it is now standard for data from multiple data streams (e.g., locations, accelerometer data, heart rate) to be modelled simultaneously within the same modelling framework [189]. The emergence of methodological reviews [34, 190, 191] and user friendly packages in `R`, such as `moveHMM` [192], `momentuHMM` [193] and `hmmTMB` [194] (reviewed by [195], see also [196]), has made it easier to answer fundamental and novel questions in movement ecology [197].

3.11 Habitat Selection (Topic 6)

Habitat/resource selection studies investigate how habitat is used by organisms in relation to what is available to them [198]. In this context, movement has been traditionally treated as a nuisance feature of the data that introduces spatial and temporal dependencies, complicating their analyses [197, 199]. Recent approaches acknowledge that in reality, movement is profoundly linked with space use and, in turn, with resource selection [200, 201]. There are important trade-offs between the value of resources and their availability [202], and movement traits allow us to better separate these two components of habitat use – e.g. we can estimate the energy necessary to reach some habitat patch [203]. Most recent developments go one step further and acknowledge that the value of resources might be affected by the behavioural state of the organisms [204–206], who might change their preferences depending on whether they are resting, foraging or commuting, for example. There have been exciting developments in the continuous-time modelling framework with great potential to link individual movement and resource selection with population redistribution, addressing a long-standing question in ecology [207, 208].

3.12 Fisheries (Topic 14)

A main focus in fisheries science has been the development of models to provide management advice (e.g. on catch limits, conservation measures, fishing seasons or gear regulations). To evaluate the health of a stock, it is important to have accurate estimates of biomass, exploitation rates, recruitment rates, population sizes and composition [209, 210]. Those estimations are based on the data that scientists and managers can collect, which can be fishery-dependent (e.g. logbooks, landings declarations, on-board observers data on catch, bycatch and discards) or fishery-independent data (e.g. scientific surveys with catch and acoustic data). Different data types can be integrated using models that account for biases due to preferential sampling – data obtained from areas where fishers chose to fish – and data aggregation (e.g. declaration of catch in spatially aggregated areas) [211, 212]. Stock assessment in data-limited fisheries require special modelling approaches [213–215].

Bayesian approaches admit the full range of uncertainty that often enters stock assessments through various sources [216]. Computational and software solutions like Integrated Nested Laplace Approximation (INLA) [217], Template Model Builder (TMB) [218, 219] and Automatic Differentiation Model Builder (ADMB) [220] have made parameter estimation in complex models of stock, population, depletion and growth dynamics possible. Following open science practices, many R packages have been developed and presented in ISEC to help with processing, modelling and analysis of different types of fisheries data (e.g. `DABOM` [221], `ecomix` [222], `FIMS` [223], `PITcleanr` [224], `Rfishpop` [225], `selfisher` [226], `sspm` [227], `STADEM` [228], `starve` [229], `VAST` [230] and `zoid` [231]).

An ecosystem-based approach to management [232] does not only include the assessment of the target populations, but all the others that could be affected by fishing pressure. The development of active and passive tagging devices and the growth of movement science (Topic 10, Section 3.10) allowed investigating interactions between animal movement and fishing activity, to assess potential effects of fishing pressure on target and non-target species (including seabird, seal, turtle and whales), their populations, habitats and bycatch risk [233–235].

The assessment of the effect of management measures on the fisheries and the ecosystem – such as different thresholds for harvest level and bycatch – and other anthropogenic factors such as climate change and offshore wind farms have also been topics of interest at ISEC [236–240]. Interactions between fishing vessels have been studied via graph theory and network analysis [241].

3.13 Management and Conservation; Developing Statistical Ecology Skills (Topic 7)

Two important themes in statistical ecology seem to have ended up in a single topic in the text analysis of ISEC abstracts. One of these themes is around supporting the management and conservation of nature. The other theme is around statistical ecology training and promoting reproducible research.

3.13.1 Management and Conservation

Environmental managers have to make decisions under uncertainty [242] in its various forms [243]. Not all uncertainty matters for decision making [244] and Value of Information theory helps decide what information is needed to reduce important uncertainty [101, 245]. Reducing important uncertainty while managing an ecological system is one of the goals of adaptive management where uncertainty is captured by a set of alternative models and the expected outcome of alternative management options is evaluated using structured decision making [246–248]. Modelling [249] and decision science [250] have become key tools for biodiversity conservation [251]. Decision science has also proven useful for optimising surveys for threatened species [252], spatial or temporal allocation of conservation resources [253, 254] and for managing ecosystems in a changing environment [255].

3.13.2 Reproducible Research and Statistical Ecology Training

Questionable research practices occur in ecology and can often be traced back to inappropriate use of statistical methods [256, 257]. There is a need for clear analysis protocols [258, 259] and broadly agreed principles of good statistical ecology [260]. Effective data exploration and visualisation tools are indispensable [261].

The statistical ecology community addresses the gap in statistical training available in some life sciences degree programmes responsible for training of ecologists [262] by providing dedicated statistical training to ecology graduate students, researchers, and practitioners. This typically takes the form of technical training workshops centered around specific statistical methods or software and ISEC has been part of this provision.

Through surveys and round table discussions, the ISEC community has defined important aspects of the discussion around embedding statistics into undergraduate ecological curricula [263] and the following messages have emerged:

1. We should teach concepts before tools – many statistical tools used by ecologists arise from modelling the processes that generate the data. Therefore, teaching should focus on the common concepts that underpin statistical tools which will develop broad transferable knowledge that can be applied beyond specific tools.

2. Teaching should be motivated by ecological problems and context – the perceived abstract and irrelevant nature of statistics is a critical barrier to learning and can be avoided by using context-rich real-world problems.

ISEC would also be an opportunity to train statisticians in ecological concepts but so far, this has not received the same level of attention as training ecologists in statistical methods.

4 Inclusivity and Accessibility

Statistical ecology addresses questions that are globally relevant [13] calling for a diversity of approaches that are based on a diverse community of statistical ecologists. We assessed the efforts to render participation in ISEC accessible and welcoming to people from different backgrounds through nine indicators: the existence of a bursary or financial aid programme, a code of conduct, a diversity and inclusion statement, accessibility guidelines, the disparity in the number of members of the scientific committee per region, the disparity in the number of plenary speakers per region and gender and the disparity in the number of delegates per region. We gathered data from books of abstracts, conference websites with active URLs and local organizers.

Over time, ISEC has applied several measures to promote diversity, equity and inclusion (DEI). Most ISEC editions (2008, 2010, 2014, 2018, 2020, 2022, 2024) had some form of bursary programme to help people with financial constraints attend the conference. A code of conduct was introduced at ISEC 2018 and this practice continued in the 2020 and 2022 editions. The code of conduct aims to keep the participants safe by stating behaviors that are deemed unacceptable in the conference, the consequences of engaging in those behaviors and how to report violations [264, 265]. ISEC 2022 produced an inclusivity statement, which stated the vision of the organizers and their commitment towards DEI and integrated the culture of the hosting country. None of the editions of ISEC had guidelines or a statement on accessibility. Accessibility guidelines not only show the commitment of organizers on this matter but also show people with disabilities that the conference could include them. The inclusion of people with disabilities is often overlooked in both in-person and online events [266, 267].

The ISEC scientific planning committee decides on plenary speakers and reviews abstracts submitted by prospective delegates. During the first editions of ISEC (2008 and 2012) the scientific planning committee members were all men but this shifted to similar proportions of men and women in the last editions (2020, 2022 and 2024) (Fig. 3; top left). Regarding regions, there was a higher representation of European researchers during the first editions (2008, 2010, 2012, 2014; Fig. 3; top right) but then the scientific committee diversified and included large proportions of members from Canada-USA and Oceania, and a minority from Latin America and Africa. No edition has included researchers based in Asia.

Inviting someone to give a plenary talk means special and public recognition of their career and a greater opportunity to showcase their work to those attending the conference. While the earlier editions had more men than women among the plenary speakers, later editions had slightly more women than men (Fig. 3; middle left). Most

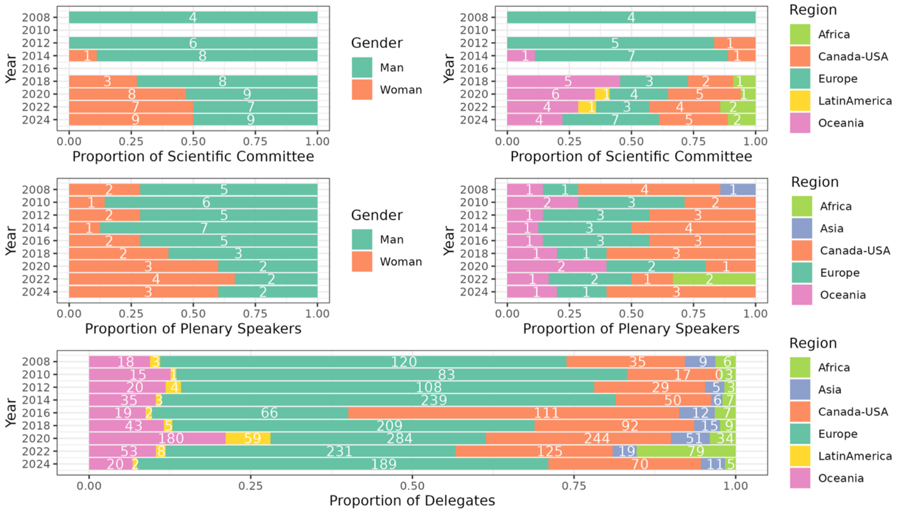

Fig. 3 Barplots showing the composition of the scientific committee (top), plenary speakers (middle) and delegates (bottom) by gender (left) and region (right and center for delegates). The y-axis corresponds to the years of ISEC editions and the x-axis to the proportion of scientific committee members (or plenary speakers or delegates), with the absolute numbers shown as text in the bars. Regions correspond to the affiliation of the people at the time of the ISEC edition and were defined as Africa, Asia, Oceania, Europe, Latin America and Canada-USA. Empty rows represent missing data

plenary speakers were from Europe and Canada-USA and all editions had one or two plenary speakers from Oceania (Fig. 3; middle right). Only the first edition had a plenary speaker based in Asia and the 2022 edition had two speakers from Africa. There have not been any plenary talks from speakers based in Latin America.

We were able to collect data on delegates' participation per country of affiliation of attendees (2014, 2018, 2020, 2022 and 2024) and affiliation of presenters from books of abstracts (2008, 2010, 2012, 2016). In both cases, they were grouped into regions. We were not able to collect comparable data by gender. For this analysis, we assumed that the proportions of presenters and attendees are comparable and that both can be used as proxies of the proportion of delegates. Most delegates came from Europe and Canada-USA (Figure 3; bottom). The conferences held in Europe (2008, 2010, 2012, 2014, 2018 and 2024) attracted a relatively larger proportion of European delegates, while conferences held on other continents (2016: USA, 2020: virtual but organised by an Australian team, 2022: South Africa in person with online option) tended to attract larger numbers of delegates from those areas compared to other editions. Conferences that had online options (2020 and 2022) had larger total numbers of delegates and higher proportions of delegates from otherwise under-represented regions like Latin America.

A round table on diversity and accessibility at the 2022 ISEC discussed the need to make better efforts to make the statistical ecology community aware of ISEC and enable everyone to participate in a meaningful way. The discussion led to recommendations to ensure that all decision-making bodies reflect the diversity of the community, that people in leadership positions in these bodies build a vision about the diversity and inclusion that should be achieved in the community and each particular edition of the conference, to raise funds to provide financial assistance to delegates that cannot afford to attend the conference, to include conference organizers from marginalized regions, to make conferences accessible to people with disabilities and to compensate people for their work on inclusion, especially those from marginalized communities [267].

We encourage statistical ecologists and ecological statisticians to look at the diversity in their areas of work, especially those who are on the scientific committee of ISEC, and develop strategies to make their areas more inclusive and make sure this translates into conference participation and recognition.

5 Future

The needs and opportunities for statistical ecology are evolving rapidly as new data types are becoming available and new questions are being asked. Satellite and aerial remote sensing is being increasingly used by ecologists to address ecological questions, including mapping and monitoring species distributions and ecosystem extents [268, 269]. Associated with this increasing use of remote sensing in ecology is an expanding toolkit of analytical approaches, most notably within the domain of machine learning [270, 271]. Widespread use of earlier techniques such as random forest and boosted regression trees has more recently been superseded by the use of approaches such as artificial neural networks, convolutional neural networks, recurrent neural networks, autoencoders and restricted Boltzmann machines [270]. Machine learning methods are also increasingly used to make various observations (presence of species, number or location of individuals, etc.) from data collected by drones, camera traps, sound recordings, etc [272, 273] that can then be fed into other models.

As observational data are increasingly collected in an automated way, e.g. by satellites, camera traps, microphones, hydrophones, video, etc. and crowd-sourced data increasingly become available, it often feels like we scramble to come up with methods that extract unbiased signals of the process we are interested in, while dealing with ever more complicated distortions introduced by the observation process, and ever-increasing volumes and velocity of data acquisition. There is a need to clarify how the sampling design affects what can be learned from data [274, 275] and a need to develop designs that allow for robust inference while giving the data collectors enough flexibility.

An emerging framework that will force us to test the maturity of our science and confront our shortcomings is that of iterative near-term ecological forecasting [276, 277]. The iterative ecological forecasting cycle mirrors the scientific method, but is aimed at supporting adaptive decision-making and monitoring. Alternative decision scenarios are generated based on assessment of the problem and used to define boundary conditions for which models are run. Forecasts are used to assess the trade-offs and relative merits between alternative decisions, as well as determining monitoring requirements to evaluate the outcomes of different decisions. The problem is then reassessed in the light of new evidence (monitoring data), and the cycle starts again. Key elements of this cycle are assessment and understanding of user needs, quantifying and propagating forecast uncertainties and presenting them in an easily interpretable manner, minimizing data and forecast latency (because a forecast about an event that has already occurred is no longer useful), and iteratively improving the system. Together this requires a broad range of skills, some not traditionally associated with statistical ecologists, including engagement with stakeholders around problem identification and decision support, developing highly efficient informatics pipelines (preferably automated and based on reproducible research principles) and integrating or fusing varied datasets. While the social and ecoinformatics requirements may be onerous to develop and maintain, especially where funding and expertise are limited, some of these challenges may be overcome by working together to develop regionally-focused pipelines that can support multiple ecological forecasts [278]. Using such a system to compare or couple models across spatial, temporal or biological scales may facilitate new fundamental statistical and ecological insights. It will also help us attribute observed changes in ecosystems to drivers like climate and land-use change, and to support conservation decision making in the face of growing pressure on nature.

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Declarations

Conflicts of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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