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Challenges and opportunities in applying AI to evolutionary morphology

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Main Title

Challenges and opportunities in applying AI to evolutionary morphology

Running Title

AI for evolutionary morphology

Abstract

Artificial intelligence (AI) is poised to transform many aspects of society, and the study of evolutionary morphology is no exception. Classical AI methods such as Principal Component Analysis (PCA) and Cluster Analysis have been commonplace in evolutionary morphology for decades, but the last decade has seen increasing application of Deep Learning to ecology and evolutionary biology, opening up the potential to circumvent long standing barriers to rapid, big data analysis of phenotype. Here we review the current state of AI methods available for the study of evolutionary morphology and discuss the prospectus for near-term advances in specific subfields of this research area, including the potential of new AI methods that have not yet been applied to the study of morphological evolution. We introduce the main available AI techniques, categorising them into three stages based on their order of appearance: (i) Machine Learning, (ii) Deep Learning and (iii) the most recent advancements in large-scale models and multimodal learning. Next, we present existing AI approaches and case studies using AI for evolutionary morphology, including image capture and segmentation, feature recognition, morphometrics, phylogenetics, and biomechanics. Finally, we discuss areas where there is potential, but a lack of current applications of AI to key areas in evolutionary morphology. Combined, these advancements and potential developments have the capacity to transform the evolutionary analysis of the organismal phenotype into evolutionary phenomics, launch it fully in the “Big Data'' sphere, and align it with genomics and other areas of bioinformatics.

Keywords

Artificial Intelligence

Phenomics

Evolutionary Morphology

Machine Learning

Introduction

The rapid proliferation of tools using artificial intelligence (AI) has highlighted both its immense potential and the numerous challenges its implementation faces in biological sciences. Traditional AI methods (i.e., Machine Learning) have been widely used in biology for decades; indeed, common analytical methods such as Principal Component Analysis (PCA) and Cluster Analysis are both types of Machine Learning (ML). Deep Learning (DL) has gained significant traction since the early 2010s and is increasingly applied to biological problems, including image analysis (Akçakaya et al., 2022; Angermueller et al., 2016; Hallou et al., 2021; Li et al., 2023; Zhichao Liu et al., 2021; Moen et al., 2019; Pratapa et al., 2021; Ravindran, 2022; “What’s next for bioimage analysis?,” 2023), molecular analysis (Atz et al., 2021; Audagnotto et al., 2022; Korfmann et al., 2023; Kuhn et al., 2021; Kwon et al., 2021), and a broad range of topics in ecology and evolutionary biology (Borowiec et al., 2022; Lürig et al., 2021; Pichler and Hartig, 2023).

One key area overlapping with many topics in evolutionary biology is the field of evolutionary morphology, which aims to characterise and reconstruct the evolution of organismal phenotypes. The scope of evolutionary morphology is huge, encompassing pattern, process, and mechanism, from cellular to macroevolutionary levels, across the entire 3.7-billion-year history of life on Earth and, consequently, often involves massive datasets. Due to the sheer quantity of potentially informative data, some of the most significant challenges evolutionary morphologists face are the ability to collect, process and analyse this data in a reasonable time frame whilst limiting computational cost. Researchers often face a trade-off between the breadth and depth of their study, as, typically, high-resolution morphological datasets must sacrifice taxonomic, ecological, or chronological coverage owing to time- and computational limitations.

AI offers an unparalleled opportunity to bridge this breadth-depth gap and thus transform the field into “Big Data” science, thereby supporting the development of *evolutionary phenomics*. By making big data analysis more feasible, integrating AI into this field will ultimately allow a better understanding of the drivers and mechanisms of morphological evolution.

Here, we focus on the applications of AI to the study of evolutionary morphology, exploring not only pre-existing uses but also the potential of recent AI methods that have not yet been applied to the study of morphological evolution. We introduce the main available AI techniques, categorising them into three groups based on their order of appearance: (i) Machine Learning, (ii) Deep Learning, and (iii) Recent advancements from Transformers to large-scale models. Next, we present existing AI approaches in the order of a common lifecycle of evolutionary morphological studies: (i) Data Acquisition, (ii) Image Data Processing, (iii) Phenomics, (iv) Evolutionary applications. We also focus on six case studies in which AI can benefit evolutionary morphological studies, and provide a table of AI tools already available that can be integrated into evolutionary morphology research. Finally, we discuss areas where there is potential but no current application of AI to key areas in evolutionary morphology.

Evolution of AI methods

Here, we outline the major stages in the evolution of AI relevant to the study of evolutionary morphology. We categorise them into three imperfect groupings based on their order of appearance: (i) Machine Learning, (ii) Deep Learning with Neural Networks, and (iii) Recent advancements from Transformers to large-scale models.

We begin by providing the key definitions necessary for a base-level understanding of this review. These primarily centre on the nested relationships of AI, ML, and DL (Figure 1), but also include the adjacent and overlapping field of computer vision. Because AI applications for evolutionary morphology primarily involve the analysis of images or text, computer vision is often an integral part of AI applications to evolutionary morphology, including most of those discussed here. However, it is worth noting that computer vision is not limited to AI but also present in numerous applications for image data that do not involve AI (Samoili et al., 2020). Further methodological definitions are provided where required in the main text.

Artificial intelligence, or AI, concerns intelligent machines capable of mimicking human-like cognitive functions. It is, however, particularly challenging to specifically define AI as its scope is extremely broad. The European AI strategy (European Commission, 2018) provides a definition as follows: "Artificial Intelligence refers to systems that display intelligent behaviour by analysing their environment and taking action — with some degree of autonomy — to achieve specific goals", leaving the interpretation of *intelligent behaviour* open to the reader. Russel and Norvig (2021) try to provide a more operative definition of AI, as a system that can either ‘reason’ or act human-like, or reason or act rationally.

Machine learning, or ML, is a subset of AI, and can be defined as "the ability of systems to automatically learn, decide, predict, adapt, and react to changes, improving from experience and data, without being explicitly programmed" (Amalfitano et al., 2024).

Deep learning, or DL, is, in turn, a subset of ML wherein learning is achieved through complex neural networks designed to simulate the cognitive architecture of the brain. Fine-grained tasks on complex data can be achieved using vast amounts of data and with limited human intervention.

Computer vision is a multidisciplinary field of computer science that enables machines to interpret, analyse, and understand visual information from the world, mimicking human vision capabilities through image and video processing algorithms. It refers to using computers for object-class recognition, where objects or individuals can be identified in 2D and 3D digital media. While many applications of computer vision for evolutionary morphology involve AI, it is not limited to AI and is applied in diverse fields.

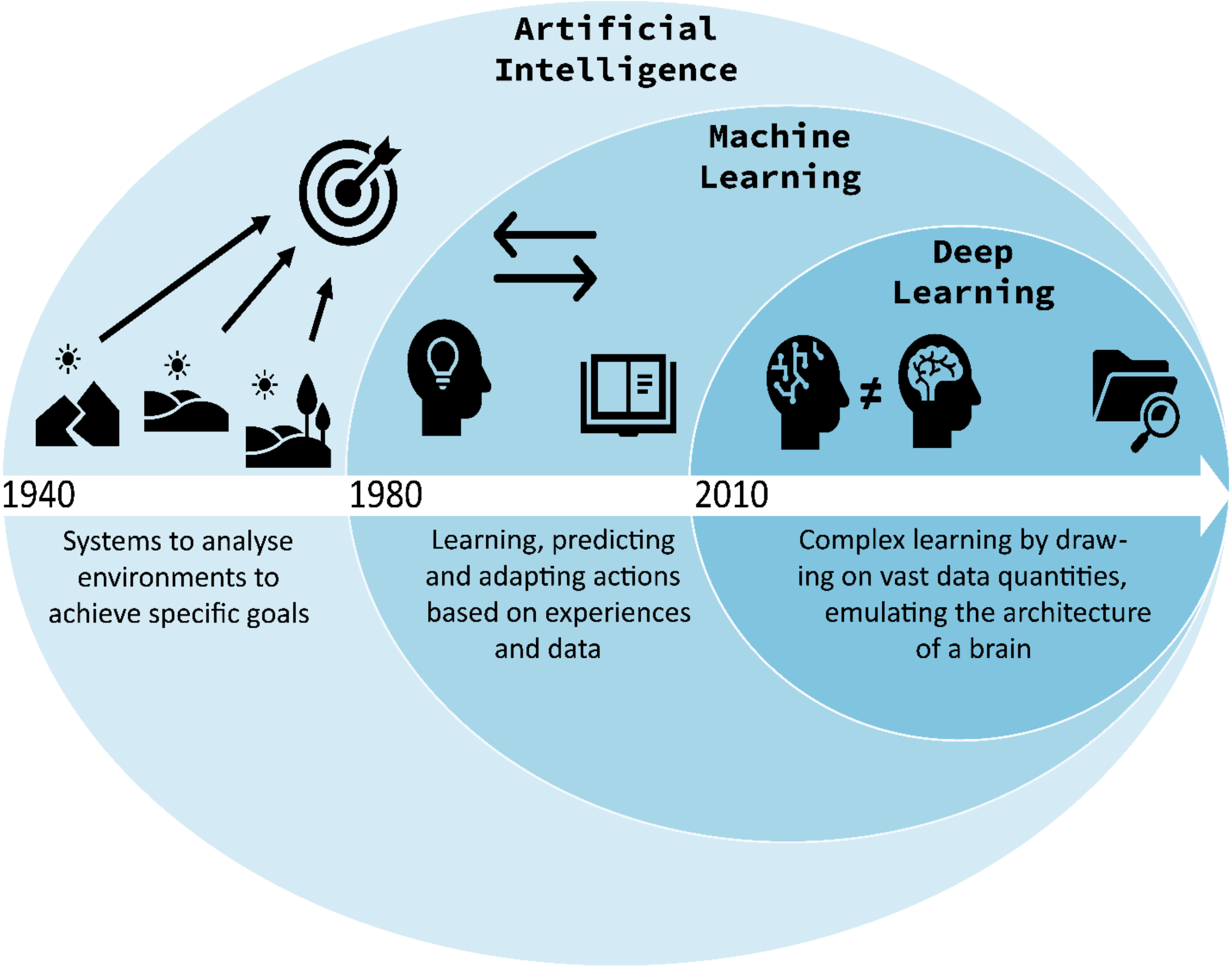

Figure 1: Broad definitions, relationships, and differences between artificial intelligence (AI), Machine Learning (ML) and Deep Learning (DL), the sequential development of each successive subset, and their broad introductions over time (Carbonell et al., 1983; Goodfellow et al., 2016).

Classical Machine Learning

Prior to the development of Deep Learning, AI methods had been successfully used for classifying, clustering, and predicting structured data, such as tabular data. Techniques like Random Forests (Breiman, 2001) and K-means clustering (MacQueen, 1967) have been widely utilised in evolutionary morphology studies (Dhanachandra et al., 2015; Pinheiro et al., 2022). These methods are typically end-to-end, whereby data is inputted, and the methods learn patterns to generate results.

Meanwhile, when it comes to image data, classical (prior to DL) computer vision pipelines were composed of two separate computational steps. The first involved the extraction of local or global characteristics (features) that were deemed useful for a task from images. This meant that, for example, the borders and edges of an image needed to be identified, and subsequently, an object could be detected based on the edges, as in the active contours (Kass et al., 1988) and level sets methods (Chan and Vese, 1999; Osher and Sethian, 1988). The extracted features were then used as inputs to ML algorithms that were optimised for structured data.

Subsequent efforts were then devoted to the design of methods to extract relevant features, i.e., features that were able to capture the relevant structures within an image, such as Haar features (Papageorgiou et al., 1998), Scale-Invariant Feature Transform (SIFT) (Lowe, 2004), Histogram of Oriented Gradients (HOG) (Dalal and Triggs, 2005), Fisher kernels (Perronnin et al., 2010; Perronnin and Dance, 2007), and curvelets (Candès et al., 2006). These engineered (or hand-crafted, or heuristic) features were then often used as inputs for ML methods, which can be broadly classified into the following approaches: predictive methods, classification, clustering, and dimension reduction (Breiman, 2001; Cortes and Vapnik, 1995; Jolliffe and

Cadima, 2016; Lloyd, 1982). Although DL architectures and convolutional neural networks (CNNs) had already been proposed in the early 1990s (LeCun et al., 1989), their success was limited due to a lack of computational power and the availability of large datasets needed to fully exploit their capabilities. However, there were some attempts to design ML systems that could learn the extraction of optimal linear features for downstream tasks (classification, detection, clustering, reduction) within a boosting framework (Vedaldi et al., 2007).

Deep Learning

Although artificial neurons (McCulloch and Pitts, 1943) and then artificial neural networks were introduced several decades ago (Rosenblatt, 1958), they were often outperformed by other methods, especially ensembles of decision trees like Random Forests (Breiman, 2001) or boosted trees (Chen and Guestrin, 2016) across a variety of tasks. This failure was mainly due to the difficulty in training fully connected networks (networks in which the neurons of each layer are connected to all neurons in the following layer) with more than a few layers. Even when shared-weights approaches, and CNNs were introduced (Fukushima, 1980; LeCun et al., 1989), they remained on the fringe of the computer vision community, with the primary bottlenecks being the computational power required to build networks with multiple layers and the amount of data needed to train such systems.

As the availability of data and the performance of computer hardware improved, especially with the advent of graphics processing units (GPUs), deep CNNs rose to prominence in the field of computer vision. The year 2012 represents a key turning point when a deep CNN achieved the best result in the ImageNet Large Scale Visual Recognition Challenge (classifying millions of images into 1000 classes) (Krizhevsky et al., 2012). Ever since, computer vision tasks have been dominated by solutions using deep artificial neural networks, to the extent that learning with deep neural networks (DNN; a key DL technique) is now generally referred to as AI, a name formerly used only for methods trying to solve general intelligence tasks, rather than specific tasks. In recent years, DL has undergone significant expansion into diverse domains, demonstrating its adaptability and offering promising solutions to challenges in various fields such as physics, medicine, and even gaming (Poon et al., 2023; Raissi et al., 2019; Shallue and Vanderburg, 2018; Silver et al., 2016).

Around the same time, neural network-based methods such as recurrent neural network (RNN) (Graves et al., 2013) and Long-Short-Term-Memory (LSTM) (Hochreiter and Schmidhuber, 1996) have been applied to sequential data and have shown great results for handling text and time series data. These methods have then been widely used in natural language processing (NLP) tasks.

The difficulty of gathering a large enough dataset to fully train a DL model for a specific task can be mitigated by the assumption that many low-level features learned by large models are generally enough for most tasks. Under this assumption, the features learnt for a task can also be used (transferred) for a different task. A technique frequently used in DL is the use of pre-trained models that are then fine-tuned (the entire model adapts to the new task) or used for transfer learning (only the final layers of the models are trained). Using pre-trained models reduces the need for large datasets, often improves model performance, and saves training time and resources. A common example is the use of models pre-trained with the ImageNet dataset for downstream tasks (Chen et al., 2017; Ren et al., 2016), such as in Sun *et al.* (2018), where the ImageNet-based model was used for object detection from underwater videos in marine ecology.

Transformer, large-scale AI models, and Multimodal Learning

In 2017, a model architecture known as Transformer was developed to address many NLP tasks, such as translation (Vaswani et al., 2017; Vydana et al., 2021). Transformer uses a self-attention mechanism, allowing each token (i.e., words, phrases, sentences, etc.) to interact with other tokens during training. Transformer can handle more information than RNNs and LSTM, can analyse contextual information, and is also better at parallelisation. Since Transformer's introduction, it has become state-of-the-art for many NLP tasks (Ahmed et al., 2017; Baevski and Auli, 2019).

By 2020, most vision models were using CNN-based methods. Transformers have been implemented as the backbone architecture for vision models (Dosovitskiy et al., 2021; Ze Liu et al., 2021). A common method is to divide an image into patches, which are treated as sequential inputs similar to tokens in NLP tasks. When Transformer is applied, models can recognise patterns and relationships between different image parts.

Research has shown that having large and diverse datasets allows models to generalise well and perform more accurately (Goodfellow et al., 2016; Russakovsky et al., 2015). Supervised learning is a common learning strategy that requires all training data to be manually labelled. However, gathering a large amount of labelled data is extremely labour-intensive. Different training strategies are applied to tackle this problem (Figure 2). Semi-supervised learning uses both labelled and unlabelled data for training (Zhu and Goldberg, 2022). Weakly-supervised learning uses less accurately labelled data for training (Lin et al., 2016). Self-supervised learning only uses unlabelled data. These strategies allow DL models to leverage as much data as possible without the need for extensive manual work.

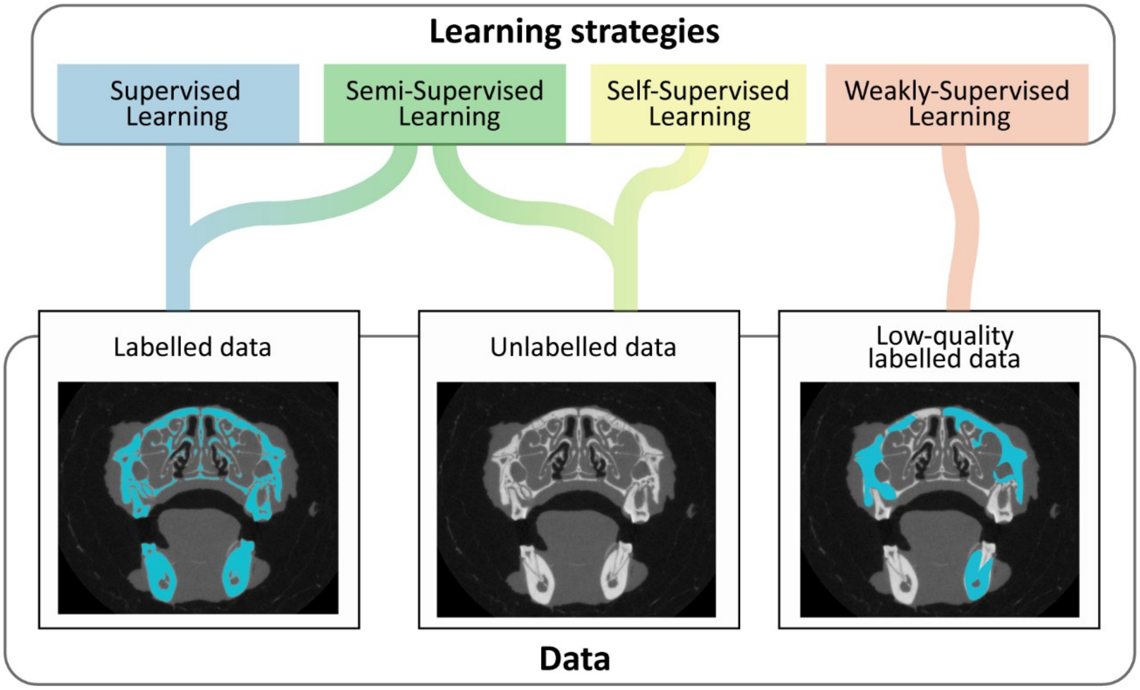

Figure 2: An overview of existing learning strategies and the levels of labelling used in these strategies.

Self-supervised learning has been widely used in NLP studies. One example uses parts of sentences as input data to predict entire sentences, thereby allowing all the unlabelled text to be considered as training data (Devlin et al., 2019). Models trained with masked sentences can be used as powerful pre-trained models for fine-tuning downstream tasks. With access to more training data and larger model architectures, generative models like the Generative Pre-trained Transformer (GPT) family were developed (Brown et al., 2020; Radford et al., 2019, 2018). Recent GPT models (e.g., GPT-3.5 and GPT-4) are capable of performing exceptionally well on many NLP tasks, even when doing zero-shot (no training needed for new tasks) or few-shot (only a few training samples needed) learning.

Contrastive learning is one of the self-supervised learning strategies that is widely used in computer vision (Oord et al., 2019; Wu et al., 2018). The idea of contrastive learning is to train a model to map similar instances (e.g., a different view of the same image) close together while mapping dissimilar images farther apart in the feature space. Although different ways have been designed to map similar/dissimilar instances (Chen et al., 2020; He et al., 2020), the fundamental concept remains the same. As a result, contrastive learning enables models to capture intricate visual patterns and semantics from data without the need for labelled data, thereby improving performance on downstream tasks. Later, masked images (where parts of images are obscured) have been used to predict original images and have been shown to achieve promising results (He et al., 2021).

These learning strategies have opened new avenues for training models, which enable the training of large models using unlabelled or a small set of labelled data, which is particularly applicable to biological sciences, given the wealth of data available in natural history collections. Additionally, AI has been successfully applied to process various data modalities, including text, images, and videos. Multimodal learning can be implemented by combining features extracted from different data modalities into one feature space. Multimodal learning enables tasks such as generating images with text descriptions or generating descriptions for images (Radford et al., 2021). With more data available (e.g., through self-supervised learning) and the advancement of AI models (e.g., Transformer), the field of multimodal learning is rapidly evolving. In evolutionary morphology, multimodal learning can effectively process diverse data modalities, such as photographs, micro-computed tomography (micro-CT) scans, and 3D mesh models (Figure 3).

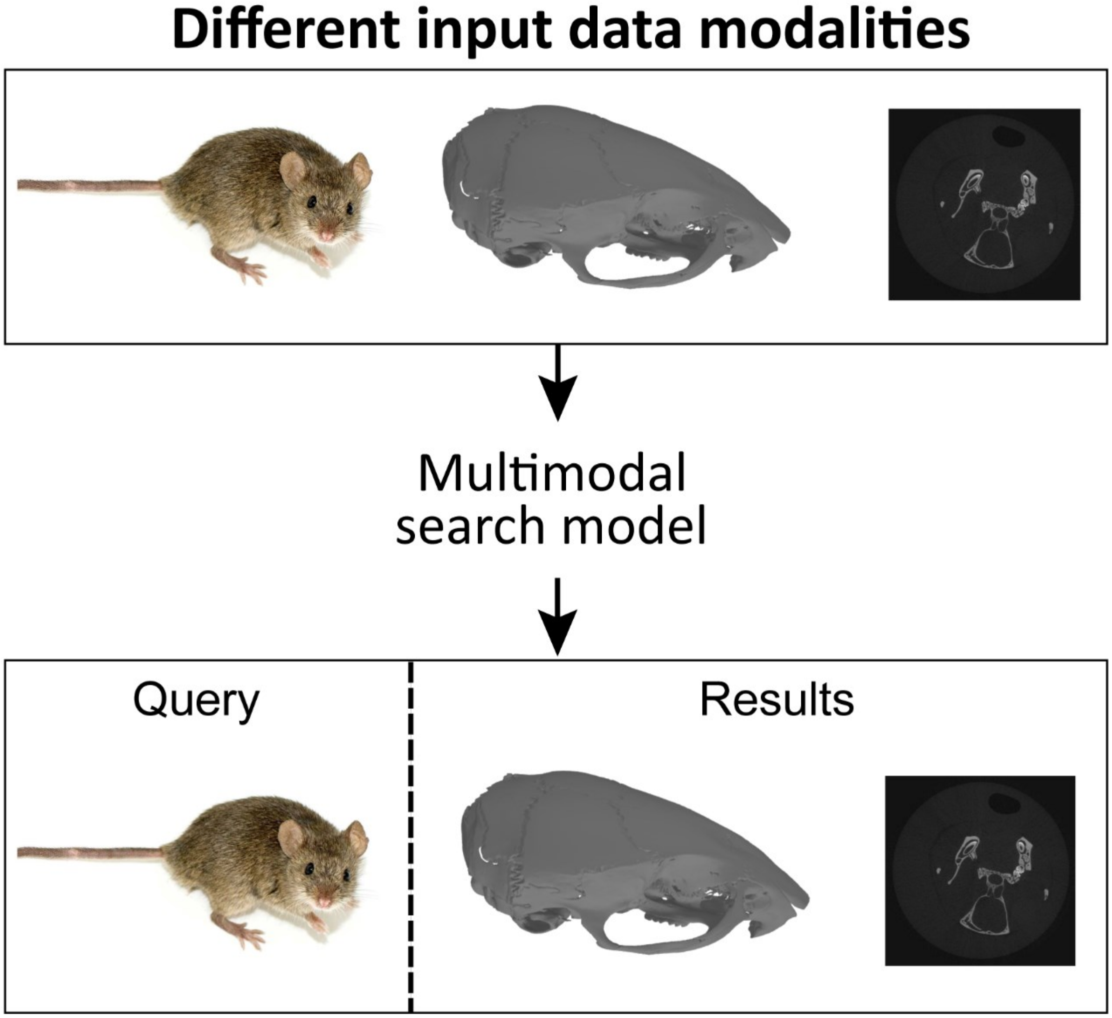

Figure 3: An example of a multimodal search. Upon inputting a photograph, the multimodal search model will find the mesh models and micro-CT scans that share similar features with the input photograph.

Here, we have only briefly reviewed three major stages in the development of AI. A full review is beyond the scope of this paper, and there are numerous other subfields of AI not explicitly reviewed in this section, such as robotics and graph neural networks. Nonetheless, these methods hold substantial potential for the study of evolutionary morphology and, where appropriate, will be noted in the subsequent sections focused on current usage and future applications in this field.

AI for Evolutionary Morphology

In this next section, we pivot towards a goal-oriented review and prospectus of applications of AI in evolutionary morphology, with accompanying case studies. We present the overview of currently available AI tools for evolutionary morphology studies in four sections: Data Acquisition, Image Data Processing, Phenomics, and Applications to Research in Evolutionary Morphology. We introduce these methods with a schematic of generalised AI workflows (Figure 4), which are expanded in the following sections.

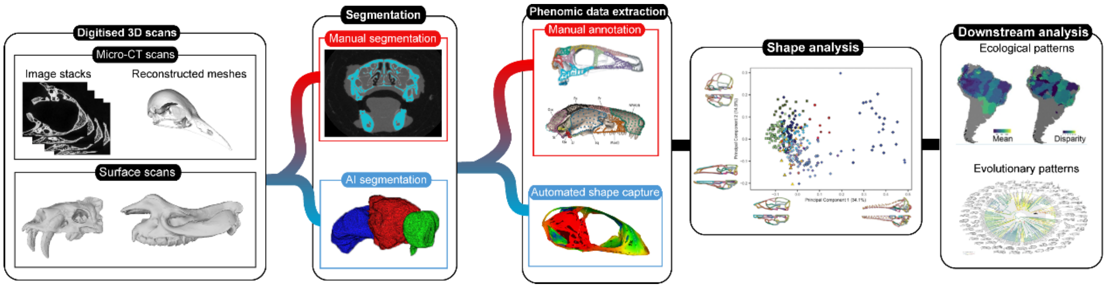

Figure 4: Schematic of a common workflow using manual and AI approaches for evolutionary morphological analysis involving 3D images and meshes. This includes manually annotated caecilian and theropod skulls from Bardua et al. (2019) and Felice et al. (2020), shape information and evolutionary patterns figures from Goswami et al. (2022). Ecological analysis figure from Foister and Felice (2021).

Data Acquisition

The first step of acquiring data is to collect the relevant samples, which are to be used appropriately and ethically in the subsequent investigation. For analysis of evolutionary morphology, this includes obtaining not only the data that is being measured but also the corresponding metadata such as details about museum collections. The suitability, quality, and quantity of data are of critical importance to the development and implementation of AI models. Data should be diverse and clean; fulfilling these requirements can make a larger difference than model choice, and without data that conforms to these requirements, good models will perform badly (Whang et al., 2023). The diversity of data refers to including enough examples of each class of interest. Cleaning data is the process of minimising errors from training datasets. Preprocessing a dataset increases the suitability of the data for training and can include contrast enhancement, noise reduction and masking, where a portion of the image is designated for further analysis (Lürig et al., 2021). Determining how much data is enough depends on the specific problem at hand. Scarce data can be expanded using existing databases or by employing pre-trained networks for transfer learning (Sharif Razavian et al., 2014). However, DL models can be successful on small training sets. Few-shot learning is a form of transfer learning that uses training data where 1-20 examples of each class are available (Y. Wang et al., 2021). Scarce data for a small number of classes is commonly referred to as the long-tail problem. Where there is an imbalance between the presence of classes in the dataset, the model may find it difficult to discriminate the scarcely represented classes and perform unreliably (Schneider et al., 2020).

Data scarcity and imbalance can be improved by additional data collection or artificial data expansion, e.g. augmentation. Alternatively, an imbalance can be tackled by explicitly accounting for biases in the training algorithm (Buda et al., 2018). Augmentation effectively increases the size of the training set without new data collection by manipulating images to create ‘new’ images from the existing data. This can be achieved by rotating, mirroring, scaling or by altering the pixel values (Shorten and Khoshgoftaar, 2019). This process must be controlled with the aim of the model in mind. For example, for planktonic foraminifera, the chirality of a species can be important in species classification, meaning augmentation by mirroring (i.e., horizontally flip) makes the labelled image into a facsimile of a different species (Hsiang et al., 2019).

Identifying and cataloguing specimen data

Many, perhaps even most, studies of evolutionary morphology are based primarily on data housed within museum collections. However, museum collections are rarely fully catalogued and even then it is difficult to search for a specific specimen or representatives of specific groups. This difficulty is because data is often inconsistent in quality and structure, particularly in large collections (Dutia and Stack, 2021). AI can play a key role in this, particularly when it comes to tasks of identifying, cataloguing, and locating specimens within collections. Some of the key challenges to solve within that topic include recognising species and extracting taxonomic and metadata to enable effective searches.

DL has recently been applied to many types of biological specimens and collections (e.g. Soltis et al., 2020). These methods have been developed and applied extensively for recognising species, metadata, traits, and even life history stages of digitised specimens (Case Study 1). This is most established in the botanical sciences, where flat herbarium sheets are easily digitised in large numbers, likely due to their relative ease of digitisation. In some instances, albeit to a lesser degree, species identification methods have also been applied to digitised photographs of animal collections (e.g., Ling et al 2023; Macleod 2017). Applications to species identification of both plants and animals from photographs have been greatly enhanced by citizen science, resulting in useful online tools such as iNaturalist and Pl@ntNet (Goëau et al., 2013; Unger et al., 2021). CNN algorithms have borne promising results and can correctly distinguish morphologically similar species (Feng et al., 2021; Hollister et al., 2023). Other machine-learning methods, such as those described by Wilson et al. (2023), have also been applied to rescaling and increasing the quality of and extracting metadata from images of museum specimens, allowing for automatic feeding of this information into databases.

Beyond images of the specimens themselves, AI approaches to capturing information of specimen labels are a critical aspect of cataloguing specimens and making key data searchable. Case Study 1b outlines the approach by which ML can be used to identify labels and transcribe them for databases, saving vast amounts of manual effort. Together, species identification and taxonomic and meta-data extraction methods from images represent a powerful tool for unlocking the full potential of natural history collections. These approaches can make data more discoverable and usable for documenting biodiversity both in collections and in the field (Karnani et al., 2022; Schuettpelz et al., 2017; Wäldchen and Mäder, 2018; White et al., 2020).

Information on specimens is not limited to museum catalogues but is also available in the wealth of scientific publications detailing and imaging specimens for varied purposes. However, extracting taxonomic data from the literature to describe or identify living and fossil species is a time-consuming task. Often it is also difficult to find the first appearance of a species name and correctly identify all synonyms for a taxon, as well as accounting for more recent taxonomic reclassifications. Recently, a few research groups have attempted to tackle this problem using ML, with both NLP and other DNN algorithms having been successfully applied to extract scientific terms and taxonomic names from scientific articles. This is a relatively new application of ML, and more work is required to train models on a variety of sources, including articles in different languages and historic publications (Le Guillarme and Thuiller, 2022).

Once these data are captured, we need effective tools to search for connected specimens. ML has not yet been adopted on a large enough scale to allow searching global natural history collections and connecting specimens. Dutia and Stack (2021) recommend ‘Heritage Connector’, a framework and software for using ML to allow better connecting specimens in collections and publications. This software achieved a precision score of greater than 85% with science museum group records. If refined or applied on a wider scale to natural history collections, it will certainly ease access to the vast specimen data available in global collections.

Case Study 1: Machine Learning within Museum Digitisation and data collection

The digitisation of museum specimens is vital for the future of collections, and their datasets undoubtedly play a significant role in scientific research in many fields, such as evolutionary morphology. In recent years, institutions have increasingly begun to incorporate recent technologies and recent ML tools within their digitisation pipelines. These implementations have led to a range of advances from speeding up digitisation processes, enabling the digitisation of items that were once difficult to digitise, to unlocking novel data from post-processing digitised items.

Example 1a: Machine Learning & Robotics for Specimen Digitisation

At its most basic definition, digitisation involves the creation of digital objects from physical items, and within museums, this is often attributed to the photographing, scanning, or filming of physical specimens. However, traditional ways of digitising artefacts, such as digitising each specimen individually, can undoubtedly be invasive to the specimen, highly time-consuming and not very cost-effective. This has led to a series of innovations that can help advance museum digitisation, from drawer scanning (Schmidt et al., 2012), which enables multiple specimens to be digitised at once, to special rotating platforms that, when combined with photogrammetry techniques, allow for the 3D scanning of specimens, whilst avoiding the use of more expensive or time-consuming scanning techniques (Medina et al., 2020). ML can lend a hand to these innovations to advance digitisation even more, such as the use of computer vision techniques and CNNs to segment individual specimens from whole-drawer scans (Blagoderov et al., 2012; Hansen et al., 2020; Hudson et al., 2015).

Another technological advancement that can aid digitisation is robotics. Robots are indeed already in use in other sectors, such as book scanning at libraries (Dumiak, 2008). Though usually highly expensive, the prices of robotic arms have been decreasing, and one can now purchase a robotic arm for less than £20,000 (Stanford University, 2022). This has enabled digitisation teams within museums such as the Natural History Museum, London, to start exploring robotics for digitisation research (Scott et al., 2023). Here, the goal is to have a collaborative robot (cobot) aid a digitiser in the mass digitisation of certain specimens (Figure 5). By implementing CNN algorithms and/or turning to reinforcement learning (RL), a robotic arm can lead to a pipeline that can enable digitisation teams to mass digitise multitudes of specimens, even possibly overnight, revolutionising museum digitisation work.

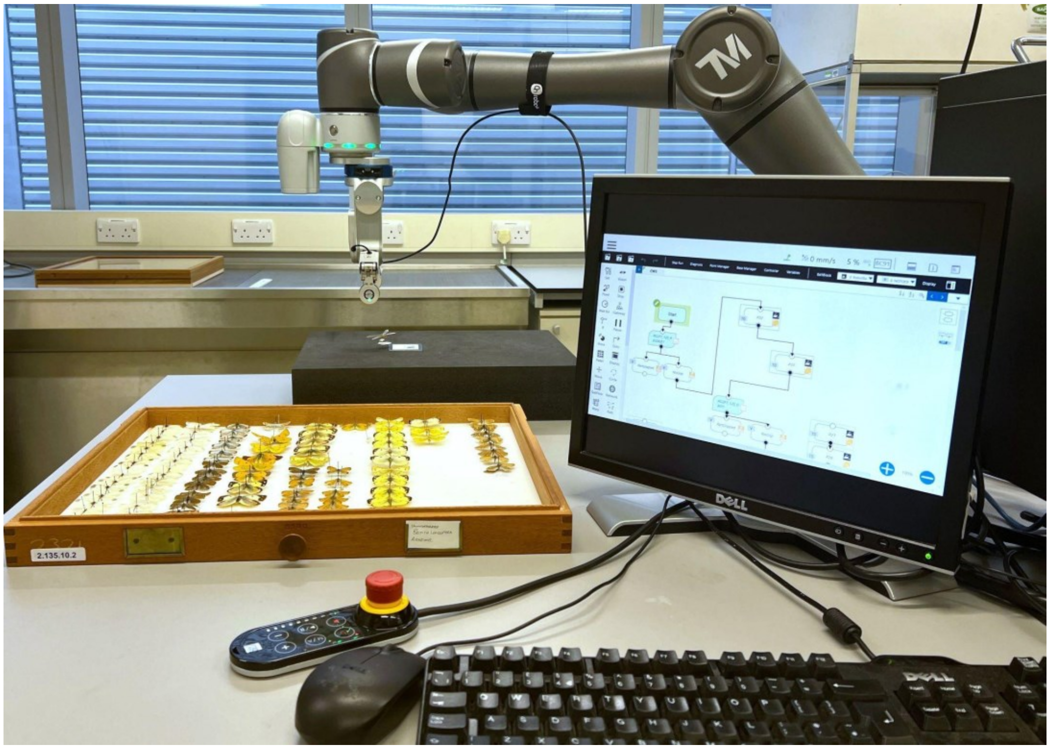

Figure 5: A Techman 500 robotic arm in action at the Natural History Museum, London, placing down a sample pinned specimen from a Lepidoptera collection. Here, the robotic arm has been trained to locate the specimen from the drawer, and then pick it up and place it on a board in order to scan the specimen.

Example 1b: Label Extraction within Digitisation Pipelines

There is a wealth of data contained within or alongside museum specimens. Specimen labels are a good example of an attribute that is often just as vital in digitisation as the specimen itself. ML tools, along with the latest digitisation innovations, have allowed for the development of techniques that enable digitisers to extract information from labels automatically whilst digitising specimens. For example, a cost-effective and efficient pinned insect digitisation process was introduced by Price et al. (2018), which involved placing the specimen within a light box and capturing a handful of photographs simultaneously with multiple cameras from varying angles. The framework described there and in Salili-James et al. (2022b) shows how one can turn to ML to merge labels together from the differently angled images to obtain clean, unobstructed images of labels and hence automatically extract textual information from them for digitisation purposes (Figure 6). The first step in this process is reliant on DL tools such as CNNs to locate labels from the multiple images of the specimen. Next, various mathematical and computer vision tools are used to *stitch* the found labels together to have one clear image of each label. These labels can then be fed into an Optical Character Recognition (OCR) and then an NLP algorithm to transcribe the text and to automatically obtain trait information. This leads to a streamlined, automated pipeline to extract label information that helps speed up digitisation efforts.

In general, ML allows for trait extraction to be more easily embedded within digitisation pipelines. One area where this is proving highly effective is in automatic trait extraction from digitised herbarium specimens (Walker et al., 2022), with pilot studies have shown promising results on different types of plants. For example, in LeafMachine (Weaver et al., 2020; Weaver and Smith, 2023), a CNN algorithm was trained to measure leaf area and perimeter from low-quality images, with a success rate of 60%. In another study, a different CNN algorithm was shown to be capable of discriminating between growth shoots and vegetative structures in tropical plants from French Guiana (Goëau et al., 2022). While this study showed a high false positive rate of 20% when identifying growth shoots, it performed well, given the complexity and variability of these structures. Overall, these methods have been shown to be able to quickly identify important ecological and evolutionary parameters from herbarium specimens, while still holding a large potential for improvement by expanding the training dataset and refining the algorithms.

As well as the actual plant specimen, herbarium sheets can contain multitudes of data including textual information about the specimen such as location, collector, date, and morphological and colour information if scale and colour bars are included. Text data extraction, in particular, can be very helpful for digitisation, as the information is embedded with the photograph when digitised onto the database - and this is often done by a digitiser performing manual transcriptions. ML methods can now be used to help speed up the digitisation process of herbarium sheets, for example, by using a combination of different models to extract and categorise textual information during the digitisation process automatically. Another example of ML related to herbarium sheet digitisation involves knowledge graphs. Knowledge graphs are an exciting tool in DL that broadly enables a representation of data structured in a graph with interlinking entities. This allows users to define relationships between different items in datasets. Furthermore, knowledge graphs can then be used to form knowledge bases, which can help model large datasets and hopefully one day allow for the creation of a planetary knowledge base (Gu et al., 2023). Beginning with datasets of herbarium sheets, one can build on knowledge graphs (Gu et al., 2022) and create a knowledge base as seen in Gu *et al.* (2023) that can help the digitisation of Herbarium sheets from filling-in missing textual data and correcting data to automating transcription tasks.

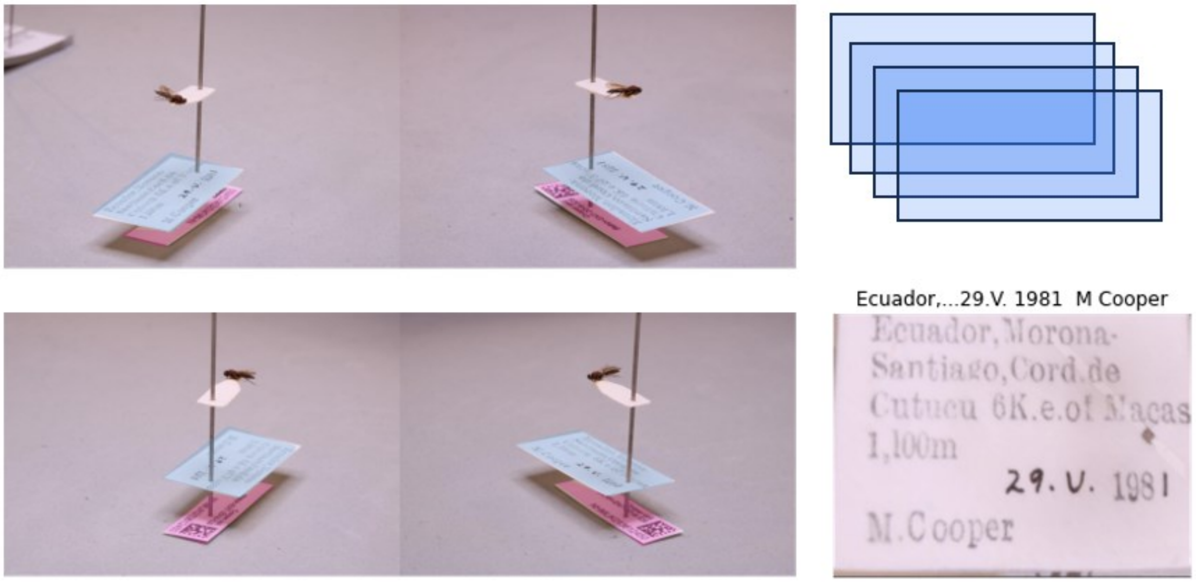

Figure 6: An example of the workflow described in Salili-James *et al.* (2022b). With the setup introduced in Price *et al.* (2018), the algorithm uses a CNN model to segment all labels found on each of the four images of the specimen. For each label, it then merges the four layers together in order to have one version of each label, which can be fed into an automatic transcription algorithm using OCR. On the bottom right, we see an example of a merged label, with a sample of the automatically transcripted text above it.

Image & scan data collection

While we refer to the use of images for specimen cataloguing above, here we focus on the details of image data collection and analysis. The use of images is central to the study of evolutionary morphology, from simple drawings and photographs to 3D computed tomography (CT) scans (Cunningham et al., 2014). The ability to generate high-resolution images has increased exponentially in recent years, particularly with initiatives for mass-scanning of collections and databases for open sharing of image data (e.g. Phenome10K: Goswami, 2015; MorphoSource: Boyer et al., 2016; and DigiMorph: Rowe, 2002). Two-dimensional digitisation of collections often involves photographing collections (i.e., specimens, drawers, etc.) to create digital copies of the data. These photographic images can then undergo segmentation or region identification and extraction, where specific components are identified and separated from the image for further processing or evaluation.

Present-day efforts to digitise specimens with two-dimensional images for large-scale data acquisition and utilisation often involve some automated processes, which can streamline both digitisation and the interpretation of data overall. Recent studies (Salili-James et al., 2022b; Scott and Livermore, 2021) describe software that uses ML models to identify regions of interest in two-dimensional images. Once trained, ML and DL software can capture photographs, segment regions of interest (ROIs), and complete other tasks for large collections datasets. This streamlines the overall acquisition and processing of digital data. Over time, ML software becomes more accurate as it learns through training datasets. This means that efficiency and accuracy can increase as the software is exposed to more data.

The use of automated robotics for digitisation and high-throughput data collection has historically been applied to two-dimensional methods such as photography (e.g., Case Study 1). Three-dimensional data, such as micro-CT data, can also be collected with new robotic technologies like autoloaders (Rau et al., 2021). Autoloaders allow users to set up multiple specimens for micro-CT and synchrotron scanning, set distinct parameters for each scan, and subsequently run the autoloader without supervision. The autoloader processes specimens in a queue, pulling each from the stand using a robotic arm, and setting up distinct parameters for each (Rau et al., 2021). This fully automated process results in greater efficiency of acquisition, as the number of specimens digitised via this method increases when digitisation can occur without technician supervision. Whilst the use of robotic technology to digitise collections could greatly increase the efficiency of image collection, the improvements are more than mechanical. Robots can learn behaviours through Reinforcement Learning (trial and error, as well as rewarding and/or punishing). By interacting with the environment (e.g., the digitisation room), robots can learn optimal actions that maximise rewards (e.g., successfully imaging a specimen).

Novel and potentially more efficient scanning methods are continuously emerging. For instance, Neural Radiance Fields (NeRF) is a fully connected neural network that can generate a 3D scan of an object by inputting photos of it from different viewpoints (Martin-Brualla et al., 2021). Compared with traditional photogrammetry and CT scanning, this method is able to compute three-dimensional scans based only on sparse images (Yu et al., 2021). While the resolution and accuracy are typically inferior to a full 3D scan, it can make 3D data capture more accessible and faster for some objects (e.g., extremely large specimens).

Image Data Processing

Image data capture has become increasingly available in recent years, with large programmes focused on mass scanning of natural history collections (Hedrick et al., 2020). The bottleneck has now shifted to processing images in order to obtain usable data on phenotype. Here, we focus on the two major aspects of image data processing: segmentation for feature extraction and element isolation and expanding segmentation for 3D volumetric data. We note that segmentation is used for a wide range of image processing operations from separating objects of interest from background to selecting regions of interest within a larger object or isolating multiple specimens in a single image.

Segmentation: 2D Image Data

Image segmentation refers to dividing an image into meaningful areas or objects and extracting ROIs, allowing for targeted analysis, and understanding of visual content (Yu et al., 2023). Segmentation facilitates numerous computer vision tasks, including object recognition by isolating objects or regions within an image (Garcia-Garcia et al., 2018; Jin et al., 2022), object tracking (Zhao et al., 2021), and interpreting a scene with multiple objects (Byeon et al., 2015). This process has traditionally been performed manually; however, it remains subjective (Schmelzle et al., 2017) and time-intensive (Hughes et al., 2022). ML techniques offer a useful way of overcoming these issues.

Numerous automated image segmentation algorithms have been developed in the past decades that do not require DL (Boykov et al., 1999; Dhanachandra et al., 2015; Minaee and Wang, 2019; Najman and Schmitt, 1994; Nock and Nielsen, 2004; Otsu, 1979). Yet, in recent years, DL has introduced novel methods linked to high-performing models able to achieve high accuracy rates on common benchmarks (Kale and Thorat, 2021; LeCun et al., 2015; Luo et al., 2021; Yu et al., 2022; Zhao et al., 2021). DL-based segmentation methods are the state-of-the-art for many image segmentation challenges and often outcompete other automated methods.

For example, Sashimi, a toolkit developed by Schwartz & Alfaro (2021), was introduced to simplify high-throughput organismal image segmentation using DL. The toolkit underwent testing by automatically segmenting the target fish images from photos with both standardised and complex, noisy backgrounds. By utilising advanced DL techniques, it aims to improve the efficiency and precision of image segmentation, ultimately leading to significant progress in image analysis and classification.

Beyond extracting a complete representation of a specimen from an image, most biological applications will need to identify specific features, whether individual traits or entire elements. Perhaps more than any other aspect, this step is overwhelmingly manual at present and as such represents the primary bottleneck for big data phenomic analyses from comparative datasets. Automated approaches to identifying and isolating features, traits, and elements, however, is perhaps the most important area to develop, as it would potentially allow for continuity of information on biological homology in large-scale comparative analyses and for removal of subjective decisions in trait descriptions. For example, methods that could extract individual elements of a larger structure could then allow one to conduct quantitative analyses of just those isolated structures or analyses of the relationships among structures (i.e., phenotypic integration and modularity (Zelditch and Goswami, 2021)), where existing automated morphometric methods typically are homology-free and capture overall shape but cannot identify which elements are actually changing in a multi-element structure.

For image data, most efforts at feature extraction have focused on 2D images, extracting features such as size and shape or using pixel intensity and edge characteristics to extract a plurality of features that are then subjected to dimensionality reduction by identifying those that are most relevant for the task. This reduction can select features based on the impact of downstream results (e.g., classification), or by using PCA or similar approaches to identify the major components of variation across a dataset (Grys et al., 2017). Along these lines, there are established applications of AI approaches to the recognition of phenotypes and phenomics in medical research, for instance, in mining health records (Frey, 2018). These approaches have also been used to identify known phenotypes associated with specific genetic variants (Zhang et al., 2022) or experimental treatments, as in Latent Space Phenotyping, a novel image analysis method that allows the automated recognition of the response to treatments from sequences of images, e.g. different growing conditions of crops (Ubbens et al., 2020). DL has also been applied to feature recognition relating to movement, such as in human foot bone morphology (Ma and Zhi, 2022). These approaches are less common for interspecific datasets; however, they have been applied to recognize and categorise fossil samples. Elsayed (2023) developed an automated approach for identifying and classifying tooth fossils from various animals, including sharks, elephants, hyrax, and primates. Deep-learning algorithms, such as CNN, were trained to recognise, classify, and extract pertinent details from 2D images of teeth fossils. The proposed methods were verified and can be used in various morphology and palaeontology research settings.

Segmentation: 3D volumetric data

ML and DL approaches to image segmentation are also routinely applied to images forming a 3D stack and achieve accurate results with processing scans from CT (Ait Skourt et al., 2018) and magnetic resonance imaging (MRI) (Lösel and Heuveline, 2017) (Case Study 2). Due to the special characteristics of these types of imaging, such as greyscale and volumetric images with depth information, specific ML and DL models have been developed, particularly for medical images (Milletari et al., 2016; Ronneberger et al., 2015). These methods allow for greater consistency amongst measurements and allow for scalable studies (Willers et al., 2021). In addition, user-friendly tools for segmenting medical images have been developed that offer built-in features for automatic image segmentation such as Dragonfly (Comet Technologies Canada Inc., 2022) and Biomedisa (Lösel et al., 2020). These have since been applied to biological systems (Lösel et al., 2023; Mulqueeney et al., 2024).

Case study 2: Image segmentation for volume rendering

DL tools such as Biomedisa (Lösel et al., 2020) have emerged as powerful solutions for automating feature extraction from 3D images (Figure 7). Additionally, the semi-automated batch-processing pipeline MiTiSegmenter can bulk segment and label around 200 samples from microCT data (Kendrick et al., 2022). They offer an efficient alternative to labour-intensive and potentially biased manual image segmentation methods. In the study by Mulqueeney et al. (2024) the efficacy of these neural networks is shown to be influenced by the quality of input data and the size of the selected training set. In the context of this case study, this is reflected in the ability for different networks to extract specific traits. In the smaller training sets, predicting the volumetric and shape measurements for internal structures presents a greater challenge compared to the external structure, primarily due to sediment infill (Zarkogiannis et al., 2020b, 2020a). However, by increasing the training set and applying data augmentation, this problem is mitigated. This reaffirms the principle that expanding the training set leads to the production of better DL models (Bardis et al., 2020; Narayana et al., 2020), albeit with diminishing returns as accuracy approaches 100% (Kavzoglu, 2009). These findings help to highlight how training sets can be designed for optimal use in precise image segmentation that is applicable for obtaining a wide range of traits.

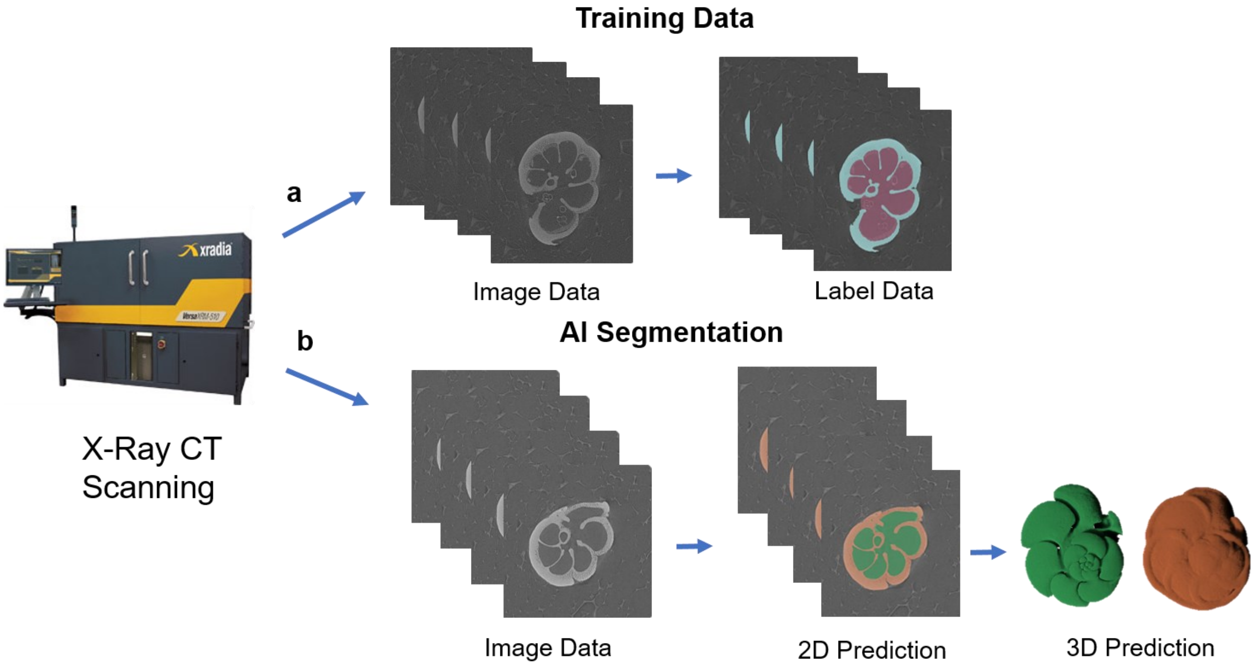

Figure 7: Workflow from Mulqueeney et al. (2024) for producing training data and applying a deep convolutional neural network (CNN) to perform automated image segmentation. The workflow includes (a) the creation of training data for the input into Biomedisa and (b) an example application of the trained CNN to automate the process of generating segmentation (label) data.

Beyond increasing efficiency of segmentation over manual thresholding, DL-assisted segmentation may be beneficial whenever thresholding ROIs is not possible. For example, when specimens being scanned are very dense, scans may not have a consistent perceived density (e.g. Alathari, 2015; Furat et al., 2019). Objects of similar densities may not be displayed at the same greyscale value through the scan, though the structural properties of the material will be evident. Scans like these are often also very noisy as a result of the high power of the beam needed to penetrate them, this frequently results in artefacts and irregularities within images (Das et al., 2022). Hence, thresholding cannot always obtain a clear segmentation, leaving manual segmentation as the only recourse prior to these models being implemented. A DL segmentation model however can be trained to segment scans based on visual patterns when a minimal number of slices are pre-labelled (Tuladhar et al., 2020). Noteworthy uses of this approach include distinguishing fossils from rock matrices with a comparable composition within CT images (Edie et al., 2023; Yu et al., 2022), a common problem when imaging palaeontological specimens. In their recent study, Yu et al. (2022) addressed the difficulties of labelling and segmenting CT images, specifically in dinosaur fossils. Traditional manual segmentation methods can be time-consuming and prone to errors due to subjective judgments. To overcome these limitations, the authors employed DL techniques, specifically CNNs, to automate and improve the accuracy of CT image segmentation.

Another case where DL segmentation may be useful for CT data is when attempting to segment regions of an object made of the same material (i.e., if an object of a single material ossifies as a single structure but has varying patterns of ossification along the structure) or when multiple objects have similar densities. DL segmentation models have also shown to accurately segment these objects into different ROIs based purely on pattern. Improvements in the quality of image data acquisition (Withers et al., 2021) alongside the increasing selection of good models (L. Wang et al., 2021) and training sets (Nikolados et al., 2022) for biological data are further assisting in mitigating these common issues in image segmentation with DL approaches.

The ability to easily separate discrete modules has the potential to greatly simplify workflows that are currently mostly manual. An application of these automated or semi-automated segmentation procedures is the isolation of complex biological features or structures that are both time-consuming and difficult to extract manually, such as vertebrate skeletal systems. For instance, skulls are made up of several distinct, overlapping bones–sometimes including other elements such as horns and teeth–the challenge of efficiently separating these elements would be greatly simplified by applying these methods (Case Study 3). Additionally, this would allow the segmentation of morphological features enclosed within or defined by the interaction between bones, such as endocasts and closed cavities within bones, as well as open-ended sutures. More work in this area will be critical for AI approaches to evolutionary morphology.

Beyond file types, most current methods use human-sculpted 3D elements as benchmarks (Chen et al., 2009). These 3D models are generally very low polygon count and manifold, and as a result do not reflect the majority of real-world examples. Work by Schneider *et al*. (2021) attempted to address this by developing a segmentation pipeline able to process higher-polygon and non-manifold meshes. This is ideal for geometric morphometrics, where variations in morphology of focal specimens are only discernible when meshes have sufficient polygons to properly map their topology.

Finally, while identifying known phenotypes from supervised learning is relatively straightforward, although practical limitations of computational power can hinder 3D image data analyses, it is less clear whether unknown or novel phenotypes are similarly recognisable or if trained models can accommodate large amounts of variation, both of which will be common in analyses of evolutionary morphology. Nonetheless, employing AI to identify new or cryptic features and, by extension, new species has great potential, particularly in light of promising applications of unsupervised learning to discover unknown phenotypes, for example in cell morphology (Choi et al., 2021).

Case Study 3: Feature extraction and region isolation via Parcellation

Employing automated shape analysis tools often requires one to extract features of interest from the entire image or mesh. As in image segmentation, one of the foremost challenges in feature or trait extraction emerges when differentiating tissues or objects exhibiting low contrast disparities, often arising from either similar material densities or the specific imaging techniques employed (Tuladhar et al., 2020). As noted above, conventional methods such as thresholding or region-growing face difficulties in precisely discerning objects under such conditions. To address these limitations, contemporary solutions harness the power of DL. Similarly, DL also finds application in extracting distinct parts of biological anatomy, utilising either semantic segmentation techniques (Hou et al., 2021) or well-crafted training sets (Lösel et al., 2023), even in scenarios where density values closely resemble each other (Case Study 4). Although these methods currently require some manual intervention, they undeniably reduce processing times substantially. Challenges may still arise, particularly in the presence of artefacts or irregularities in images (Das et al., 2022) or when dealing with damaged samples (Zhang et al., 2022). Nevertheless, ongoing advancements in these techniques indicate a trend of continual improvement and broader application.

In an example from our own work, we sought to conduct a landmark-free 3D morphometric study of skull shape in mammals but needed to isolate structures such as cranial ornaments (i.e. antlers and horns) and teeth from the specimen. This is common in analyses using landmarks, as these structures can dominate the variation in an analysis or may have more non-biological variation due to preservation (i.e. missing teeth). These structures may also warrant their own shape analysis, independent from the skull. To accomplish this, we applied an existing application for accomplishing this task, MedMeshCNN (Schneider et al. 2021), which uses Blender, an open-source 3D software. To segregate regions, edges of a mesh are assigned to a specific class (e.g. horns/antlers, teeth, skull in Figure 8), resulting in meshes annotated with the regions of interest. A model is then trained on the annotated meshes and can then be applied to other specimens.

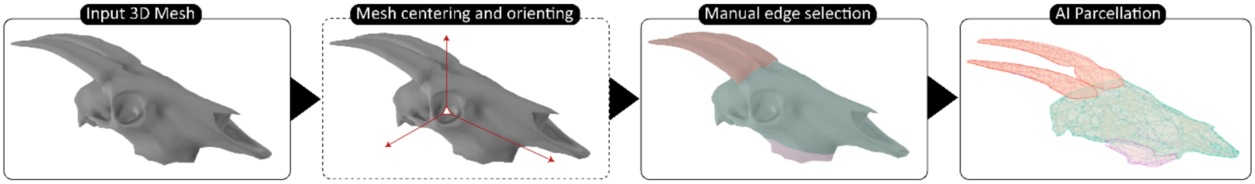

Figure 8: Workflow for segmenting horns/antlers and teeth from a skull using Blender.

As noted above, parcellation of segmented elements allows for more in-depth analysis of specific areas of focus. In 2D analysis, these methods are present in behavioural ecology and neuroscience, where limb tracking of segmented species in video footage is used to infer behaviour of individuals (Marks et al., 2022; Mathis et al., 2018). Similar to 2D, 3D semantic segmentation using CNNs has started gaining traction, notably in the field of pathology (Rezaeitaleshmahalleh et al., 2023; Schneider et al., 2021), engineering (Bhowmick et al., 2020; Kong and Li, 2018) and materials science (Holm et al., 2020; Zhu et al., 2020), and is similarly useful for evolutionary morphology. For example, extracting individual structures, such as sutures, from micro-CT scans of whole crania allows detailed analysis of their morphology and the factors driving their evolution (Case Study 4).

This approach, however, comes with some important challenges when applied to 3D data. First, the high diversity of data types and extensions in which 3D reconstructions can be stored (e.g., .ply, .vol) poses problems to the homogenisation of automated segmentation procedures. Second, the quality of 3D data can also be an issue. Current methods normally employ human-sculpted 3D elements as benchmarks (Chen et al., 2009), which tend to have low polygon counts and thus do not reflect most biological datasets. As a result, semantic segmentation of 3D reconstructions has proven challenging, with various methods attempting to overcome quality issues in the CT data (Schneider et al., 2021; Shu et al., 2022; Sun et al., 2023).

Case study 4: Image segmentation for feature recognition and automatic trait extraction

Instead of parcellating scans, segmentation can be used directly as phenotypic features. This section focuses on a use case of the segmentation of cranial sutures for phenotypic analysis.

Cranial sutures are fibrous bands of connective tissue that form the joints between the cranial bones of vertebrates (White et al., 2021). These features are bounded on two sides by the bones that connect, but unless fused, they are open-ended dorsally and ventrally (Lenton et al., 2005). This presents an issue in that their digital isolation (segmentation) is a highly time-consuming and skill-intensive task, which makes building large datasets for biological comparisons very challenging. We developed a pipeline to address this methodological challenge using supervised DL (Figure 9), as follows. First, as sutures are difficult and time-consuming to label, we created a training set by segmenting only a specified number of slices (e.g., one out of every 100 slices) from a set of scans, thereby prioritising inclusion of a diverse range of scans over dense sampling of each scan. Additionally, a test set is created with sutures segmented throughout the entire stack for a few scans, which can ensure the evaluation is more robust. We then use the training set to train DL models. To address the class imbalance issue, which is caused by sutures normally being small regions, we implemented specific sampling and weighting techniques. We then evaluate the model performance on the test set. Finally, sutures for the rest of the scans can be predicted using a well-performing model from the training. Experts can review these predictions to generate high-quality suture segmentation. The resulting segmentations can be used as a new training set to enhance model performance or used for downstream analysis.

This pipeline allows efficient segmentation of sutures from skull CT-scans. Subsequently, we can use computational methods such as Fourier transform and alpha-shape analysis and landmark-free geometric morphometrics to quantify characteristics of the sutures. Beyond sutures, such a pipeline would be applicable to segmenting (both in 2D and 3D) any open- or close-ended structure, biological or not, that is defined by the interactions between other structures (i.e., cranial endocasts, chambers in mollusc shells, cracks in bones and other materials, junctions between cells).

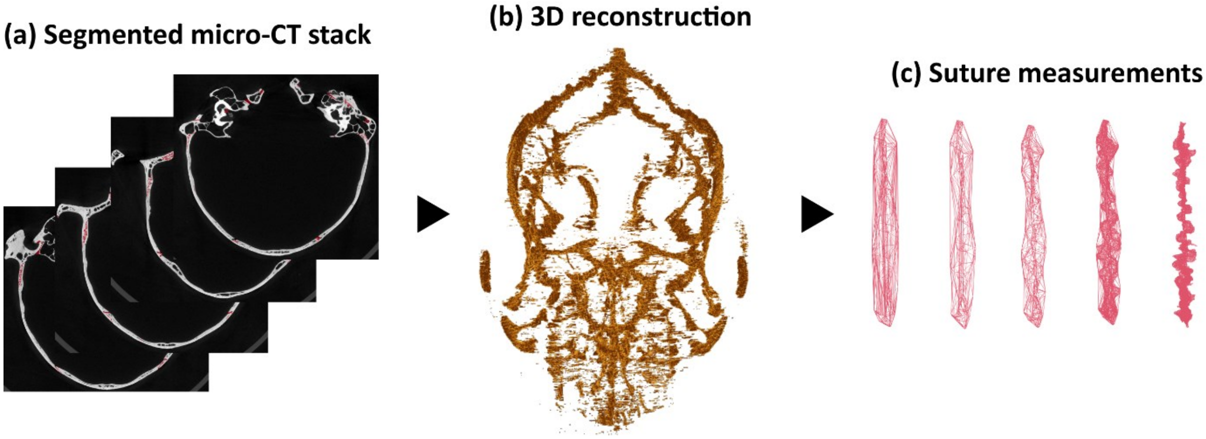

Figure 9: A workflow for extracting sutures on micro-CT scans. This workflow includes (a) segmenting sutures on micro-CT scans of mammal skulls. Segmented sutures are used to generate (b) 3D reconstructions, which can then be used to calculate (c) suture measurements.

Phenomics

Phenotypes encompass morphology, behaviour, development, and physiology, all of which mediate an organism’s interactions with other species and its habitat. Phenomics extends phenotype to its genetic, epigenetic, and environmental drivers. Analysis of phenomes thus entails a variety of traits, all of which are essential to be able to understand the dynamics of organismal evolution, yet the resolution as to which we can currently measure is limited. Here, we discuss how AI techniques can be used to more effectively describe phenotypic traits specific to morphology, with sections related to discrete and meristic traits, univariate measures, shape (including linear and geometric morphometrics), colour, and pose estimation.

Discrete and Meristic Traits

Morphological traits underpin the study of phenotypic evolution within phylogenetic systematics (Hennig, 1966). Nonetheless, morphological traits for phylogenetic applications have many limitations (Lee and Palci, 2015). Discrete traits manually scored by each researcher or meristic traits such as element counts collected from specimens have proven time-consuming and difficult to collect due to personal interpretations and potential errors (Wiens, 2001). Despite this, discrete traits are critical for diverse aspects of evolutionary study; for example, they are essential to time-calibrate molecular phylogenies and to reconstruct phylogenetic relations among extinct taxa (Lee and Palci, 2015; Smith and Turner, 2005). Discrete and meristic data are also useful for evolutionary analyses of morphology, evidenced by foundational works of morphological disparity (Foote, 1997, 1993; see Goswami and Clavel, 2024 for a full review).

AI tools have shown potential in recognising and extracting discrete and meristic traits to build morphological matrices for phylogenetic analysis in a quicker and more robust way. AI methods, including CNNs, have been successfully applied on small training datasets to recognise species and extract both discrete and meristic traits (Wäldchen and Mäder, 2018). Other examples include using ML tools to extract, classify and count reproductive structures (Goëau et al., 2022; Love et al., 2021), as well as to produce basic measurements such as leaf size (Hussein et al., 2021; Weaver et al., 2020). These methods have also been shown to work on x-ray scans of fossil leaves (Wilf et al., 2021), including counting stomatal and epidermal cells for palaeoclimatic analysis (Zhang et al., 2023). A similar CNN algorithm has also been successfully applied to classify freshwater fish by genera from the Amazon region using photos of museum specimens, for which traits were recognised with 97% confidence (Robillard et al., 2023). In animal species traits identification, Random Forest algorithms have also shown promising results. For example, they performed better than traditional Linear Discriminant Analysis in delimiting between species of snakes from field photos when given a set of morphological traits (Smart et al., 2021).

Overall, each of these algorithms have the potential to be used in morphological trait extraction and phylogenetic analysis by training them to classify new images for a set of traits and using a training dataset representing the variation in the species or genus for the traits of interest.

Univariate Measures

Morphometrics, the quantification of biological form, allows for direct comparison of size and shape across structures or organisms. Univariate metrics have dominated morphometrics for centuries, but the extraction of univariate traits from a substantial pool of individuals has historically been a laborious and time-consuming process, imposing limitations on available data (Fenberg et al., 2016). Addressing this challenge, AI tools have emerged as effective solutions, streamlining the extraction of univariate traits, including lengths, mass, and size, particularly in

2D images. For instance, neural networks have proven adept at extracting linear measurements, as illustrated by the accurate forewing length extraction of 17,000 specimens of butterflies (Wilson et al., 2023). Moreover, these AI techniques have extended their capabilities beyond simple length measures, such as by measuring plant leaf areas (Kishor Kumar et al., 2017; Mohammadi et al., 2021). Advanced techniques have further facilitated the measurement of length across individual anatomical regions, offering a more nuanced understanding than traditional whole-body length measures (Ariede et al., 2023). These techniques have also enabled the extraction of shape proxies, such as ellipticity (Freitas et al., 2023), and the simultaneous analysis of multiple univariate traits (Fernandes et al., 2020).

AI methodologies have seamlessly extended their proficiency from extracting 2D univariate traits to 3D, by employing analogous methods to obtain linear measurements of both length and width within 3D images (Hu et al., 2020; Lu et al., 2023). Similar to the techniques applied to their 2D counterparts, these methods can concurrently extract multiple traits from individual images (Wu et al., 2021) and tally features across diverse regions in 3D images (Yu et al., 2021). Moreover, they can provide volumetric measures of multiple components through the application of image segmentation (Lösel et al., 2023; Mulqueeney et al., 2024). This advancement represents a notable stride in using AI to extract intricate 3D data.

Shape

Univariate or linear morphometrics has been a tool in evolutionary morphological analysis for centuries, but recent years have seen an explosion of geometric (landmark-based) and surface morphometrics, greatly increasing the scope for capturing and quantifying organismal shape. While surface methods are relatively new, they are expanding rapidly, and geometric methods are well established and offer great potential to increase understanding of evolutionary dynamics (Mitteroecker and Schaefer, 2022). Below we discuss various approaches to multivariate shape analysis and existing AI applications.

Geometric morphometrics

One of the most common ways to quantify and analyse evolutionary morphology at present is by applying geometric morphometrics. This inherently multivariate methodology requires the placement of landmarks that produce two-dimensional or three-dimensional coordinates by labelling homologous anatomical loci to describe biological shapes (Adams et al., 2004; Mitteroecker and Schaefer, 2022). Raw coordinates are then transformed using a superimposition method, commonly Procrustes analysis, which uses scaling, rotation, and transformation to register objects to a common reference frame so that only biological variation remains (Bookstein, 1997). The main advantages of geometric morphometrics include the ability to densely sample complex shapes in three dimensions, the ability to localise variation, the retention of information on biological homology, and the utility of coordinate data for numerous downstream analyses, from macroevolutionary to biomechanical analysis. However, geometric morphometric methods are time-consuming, prone to observer bias, and lack repeatability (Shearer et al., 2017). Moreover, current methods are limited in their scope, in particular because they rely on homologous points of comparison. As a result, they quickly lose explanatory value with increasingly disparate taxa, as homologous points become more difficult to identify and thus fewer in number. As a result, geometric morphometrics is still a largely manual endeavour for comparative datasets, with even semi-automated tools requiring extensive manual effort (Bardua et al., 2019). The introduction of new automated approaches for the analysis of shape may allow us to overcome some of these issues, though the need for grounding in homology will always be a constraint, as well as a critical requirement for maintaining biological meaningfulness, of this approach.

Two distinct groups of approaches have been developed to circumvent the manual effort of geometric morphometrics: automated landmarking and 'landmark-free' or 'homology-free' methods. The former is based on the same principles as geometric morphometrics but seeks to minimise the user's workload by automating placement of homologous landmarks. These methods frequently rely on image registration to propagate landmarks from one set of individuals, or a generic template, to another (Maga et al., 2017; Young and Maga, 2015). These often lack precision in identifying anatomical loci, even in closely related taxa; therefore, to improve the obtained results, others have attempted to use DL and computer vision to the problem of landmark annotation. In 2D images there is the capacity to automatically place landmarks (Porto and Voje, 2020; Case Study 5), while those available for 3D images at present use AI to optimise landmark position after placement, thereby improving accuracy after mapping of landmarks from a template to specimens (Devine et al., 2020). Landmark placement tools are currently only available for 2D images (Porto and Voje, 2020), but these methods have been shown to reduce both data collection time and error and increase repeatability, thereby supporting phenomic-scale data collection for large data sets. Unfortunately, some implementations are computationally demanding to apply, particularly when using 3D data, and all applications at present behave poorly with even a moderate amount of variation, effectively limiting applications to analysis of conspecifics or congeneric species.

Case study 5: Geometric morphometrics - automated landmarking

Geometric morphometrics is a powerful tool for quantifying and comparing morphology across organisms and has become the dominant approach for morphometric analysis over the past few decades. However, identifying and placing landmarks and semilandmarks on 2D or 3D images remains a largely manual and thus time-consuming process, as well as being prone to human error and interuser variation. Thus far, AI has been successfully applied to landmark and semilandmark data to capture shape within species and among congeners, ranging from fruit flies (Porto and Voje, 2020; Salifu et al., 2022), to bryozoan colonies (Porto and Voje, 2020), to mice (Devine et al., 2020; Porto et al., 2021). 3D applications at present use image registration and map landmarks from an atlas onto specimens, and then integrate DL for optimization of landmark placement (Devine et al., 2020). Perhaps the most advanced implementation of DL for landmarks placement at present uses a supervised learning approach combining object detection and shape prediction to annotate landmarks (Figure 10) (Porto and Voje, 2020). Object detection, using a histogram of gradients features rather than the more common but less efficient CNN approach, was used to first identify the structure of interest, followed by shape prediction to annotate landmarks. This approach was successfully applied to three datasets of varying complexity, with object detection in particular performing well for all datasets. While only implemented for 2D images at present, the speed of data collection achieved in that study is remarkable (e.g., >13,000 bryozoan zooids annotated in three minutes, approximately the same needed to manually annotate one zooid; Porto and Voje, 2020) and demonstrates the great potential of AI applications to geometric morphometrics and the need to develop implementations for 3D data.

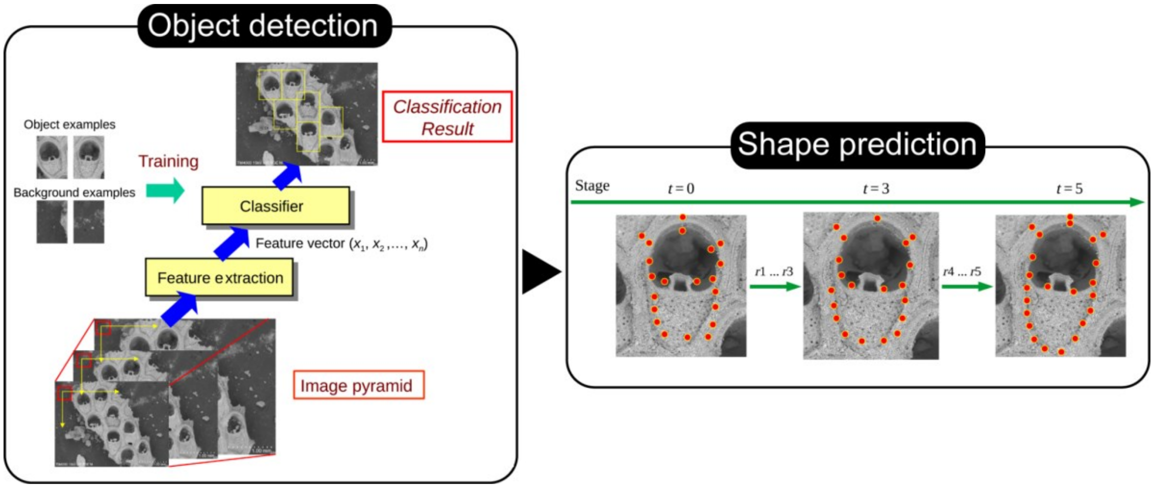

Figure 10: Workflow for automated landmarking in Porto and Voje (2020), showing (a) the object detection framework where a training set is used to first extract features and then perform classification and (b) perform shape prediction using a cascade shape regression model to refine the landmark predictions.

Landmark-free morphometrics

Landmark or homology-free methods seek to remove the placement of landmarks altogether; instead, they focus on describing the entire shape of the selected specimens. There are several methods within this family and most do not directly use AI at present, but we note a few of them as they are promising areas of current development. The most common approaches either decimate a mesh into a large number of pseudolandmarks (i.e., points without any homology) (Boyer et al., 2015; Pomidor et al., 2016) or use an atlas-based diffeomorphic approach (Durrleman et al., 2014; Toussaint et al., 2021). Both of these approaches allow shapes that do not share homology to be compared and limit the loss of geometric information, but they may be prone to sensitivity to factors outside of just shape, including alignment and scaling.

Nonetheless, they offer a potentially rich source of data for AI applications, as we discuss here with particular emphasis on diffeomorphic methods.

Broadly, diffeomorphic methods involve a shape on a deformable grid that can be stretched and compressed, with mathematical tools called *diffeomorphisms*, to resemble other shapes. These methods, often referred to as methods of elastic shape analysis due to the *elastic* nature of them, can be used to quantify dissimilarities between shapes, register (*match*) shapes together, and analyse morphometry, all without requiring landmarking. Techniques that incorporate these methods include Large Deformation Diffeomorphic Metric Mapping (LDDMM) (Beg et al., 2005), the Square Root Velocity Framework (Srivastava et al., 2011), and Currents (Benn et al., 2019). One way *elastic* landmark-free techniques are proving increasingly useful is when analysing morphometry in a two-dimensional sense, for example, when studying the boundaries of objects seen in images. Here, instead of requiring landmarks on the boundaries, the boundary curve is analysed as a whole. Importantly, this also allows for possible invariances to be handled. For example, the metrics within methods can be made to be invariant to shape-preserving transformations, such as scaling, translation, rotation, and/or reparametrisation (i.e., *where* on the boundary the curve starts/ends).

There are some diffeomorphic methods that can be expanded into higher dimensions as seen with open curves (Lahiri et al., 2015) and closed curves (Klassen and Srivastava, 2006) - this can prove particularly useful in the analysis of curves on surfaces in evolutionary datasets. There has also been recent research on elastic methods focused on surfaces (Hartman et al., 2023; Jermyn et al., 2017; Pierson et al., 2021). As described in Hartman *et al*. (2023), the techniques here can be categorised into two sections, those that apply to parameterised surfaces and those on unparameterised surfaces (i.e., containing no known point landmarks).

Methods of elastic shape analysis can play an important role in ML, whether this is with classical methods or combined with the latest DL tools. These applications can broadly be split into the following three categories:

1. **Elastic Shape Analysis as a classical machine learning tool**: One motivation for the use of elastic shape analysis is that it allows us to consider the space of the objects we wish to analyse and define our metrics with respect to this space; therefore, not assuming linearity of spaces (unlike traditional landmark-based methods). This enables us to create a framework to compute statistics, analogous to standard tools on linear spaces. One such analogue is Principal Component Analysis (PCA), which is a standard tool for dimension reduction in classical ML. This can be done in various ways, from defining ways to work directly on the space of objects or a tangent space to that space (as it is often mathematically and computationally simpler, as described in Srivastava *et al*. (2011)), or by transforming the original objects into a linear space, and then performing standard PCA, as can be done with the framework seen in Benn *et al*. (2019).
2. **Elastic methods as a pre-processing technique for machine learning**: In recent years we have seen elastic diffeomorphic methods applied to real-world datasets and then combined with ML algorithms to provide tools to analyse morphological data. This technique is particularly helpful when a distance matrix can simply be incorporated within a ML algorithm. For example, in Salili-James *et al*. (2022a), diffeomorphic metrics were used to quantify differences between the shapes of natural objects such as boundary curves of gastropods and leaves and then combined with a classical supervised ML algorithm (namely, K-Nearest Neighbour) to classify genus and species, based purely on the morphology of the object.

3. **Machine Learning algorithms with elastic metrics**. ML algorithms will often have a *distance metric* embedded within them. These are especially apparent in classical (statistical) methods of classification (such as Support Vector Machine [SVM]) and clustering (such as K-means), where a metric is used to compare the relative position of two points in a dataset. The choice of metric here can sometimes greatly affect the results, and naturally there are times where a landmark-free elastic (e.g., geodesic) metric can be better suited to the algorithm than standard (often linear) metrics. Furthermore, there have recently been studies that have incorporated DL techniques with elastic metrics, such as in Hartman et al. (2021). Here, a Siamese neural network was trained to predict square root velocity distances between curves, such as the boundary curves of leaves from the notable Swedish Leaf Dataset (Söderkvist, 2016, 2001). Thus, it is justifiable to expect more studies showing DL methods combined with elastic metrics in the near future.

Another family of approaches mathematically describe the surface of the selected objects using integral geometry (L. Wang et al., 2021). These surface descriptors can describe the shape of structures independently and may not suffer from issues of invariance and alignment to the same extent as the landmark-free approaches noted above. However, some applications remain limited, and they have not been widely tested with diverse biological datasets; thus, their efficacy remains to be established. Additionally, all these approaches have drawn some concerns over ignoring homology (Mitteroecker and Schaefer, 2022), though there is great potential for reintroducing homology by combining these approaches with AI tools for feature or trait extraction, as described above and demonstrated in Case Study 3. These approaches could potentially be used not only to study the shape of specific homologous elements, but also could accelerate studies of modularity and integration (Zelditch and Goswami, 2022), which rely on large sample sizes to assess the relationships among structures, how those relationships reflect genetic, developmental, and functional associations among traits, and how they influence the evolution of morphology over shallow to deep time scales. Overall, despite the attention being paid to new AI techniques and its great potential for automating the quantification of shape, there are at present few applications to datasets above the species-level.

Colour

Colour and patterning are key evolutionary components in taxa as diverse as insects, fishes, birds, and reptiles because of their importance in crypsis, aposematism, mimicry, communication, and sexual selection (Cuthill et al., 2017). Understanding how these patterns evolve is, therefore, crucial for understanding broader evolutionary themes such as natural and sexual selection, convergence, parallel evolution, and character displacement. Colour patterning can help researchers to recognise and discriminate between species and is commonly used in taxonomic, behavioural, and ecological studies. Traditionally, studies have been limited to qualitative descriptions, which has restricted analyses to relatively small sample sizes due to the difficulty of manually comparing large numbers of diverse and complex patterns and colour combinations. Quantitative analyses of colour patterning have become more common in recent years, with important large-scale studies being carried out in birds (Cooney et al., 2019; Dale et al., 2015) and butterflies (Van Der Bijl et al., 2020). Furthermore, automated and semi-automated methods have been developed to segment colour from images (Weller et al., 2022) and to quantify and analyse colour patterns (Maia et al., 2019).

Such methods have helped address the limitations of manually processing data, but there are limits to automated procedures. Automated methods are much faster and less subjective than manual methods for colour segmentation but are less flexible. Van der Bijl et al. (2020) used a colour profiling approach to assess sexual dimorphism in 369 species of butterflies, using a pixelated image to produce a linear sequence of coordinates containing lightness and colour values. This method is effective but time consuming because each specimen must be photographed, with images manipulated and standardised by hand. As a result, although containing an impressive sample size, the total number of species analysed in this study represents only 2% of the estimated 18,500 extant species of butterflies.

ML offers a potential solution to this bottleneck by combining the capacity to process vast amounts of data and to use large datasets to train and refine its approach. Large image datasets of museum specimens are increasingly being made available for researchers and can act as both training datasets and as comprehensive samples for analysis. ML uses feature extraction and classification to process images in species identification (Wäldchen and Mäder, 2018), and this can be translated into comparing and contrasting colour patterning, by quantifying both spectral (i.e., colour and luminance) and spatial (i.e., the distribution of pattern elements) properties of colour patterns across multiple specimens. With this approach, ML methods can identify individual specimens from photographs, reducing the workload by removing the need to manually process images (Maia et al., 2019). One successful implementation is the analysis of camera trap images, with one study focussing on Serengeti images having a 96% success rate compared with a crowdsourced team of human volunteers (Norouzzadeh et al., 2018). ML has further been used to identify individuals within species of small birds (Ferreira et al., 2020), pandas (Hou et al., 2020), and primates (Guo et al., 2020), based on only minute differences in colour pattern.

Furthermore, the preparation and analysis of data workflows can be greatly improved with the use of AI and some of the most significant progress in this area has been conducted on museum bird specimens. DL methods have been applied to segment and extract plumage from images which greatly enhances the speed at which images can be processed and colour information extracted (He et al., 2022; Case Study 6). This approach has been taken to even higher levels of specificity by applying pose estimation methods to identify specific points of bird anatomy regions to improve the efficiency of the pipeline for extracting colour information from specimens (He et al., 2023).

Case study 6: Colour

Studying macroevolution of morphological traits often requires extensive measurements from digitised specimens. This can become extremely inefficient in large clades such as in the case of birds where there are an estimated 8,000 extant species globally. Understanding the evolution of avian species, therefore, necessitates extensive datasets of specimens even before factors such as sexual dimorphism are considered. Several recent studies have employed DL models to assess plumage in birds on a global scale (Cooney et al., 2022; He et al., 2022). DL was applied to segment the whole plumage area from photographs of over 120,000 bird photos across more than 7,500 bird species (Figure 11). The colour and ultraviolet (UV) reflectance of the plumage were extracted from the segmentations. These measurements were then used to study the signalling traits among Passerine birds (> 4,500 species). Findings revealed that UV reflectance is widespread across Passerine birds and is strongly phylogenetically conserved, and the light environment plays a significant role in the evolution of UV reflection (He et al., 2022). Another observation was that both male and female tropical Passerine species tend to be more colourful than their temperate counterparts (Cooney et al., 2022). These findings highlight the potential of AI-generated predictions in biological analyses, addressing questions and hypotheses that could not have been answered previously due to limitations in the efficiency of manual methods.

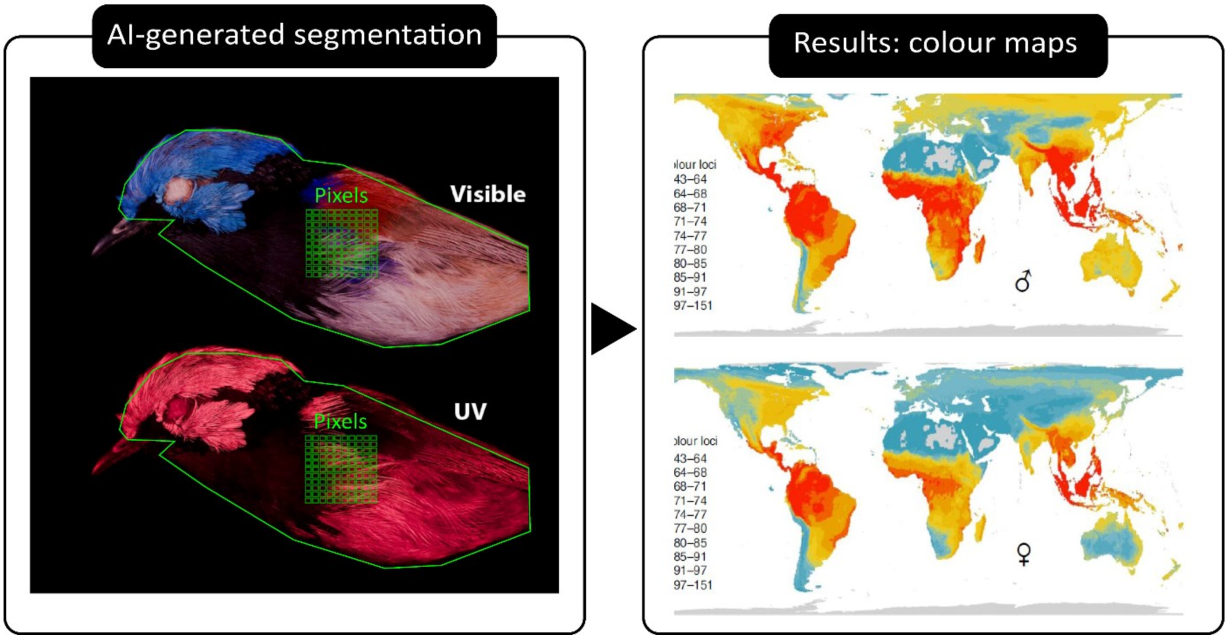

Figure 11: An example of using AI-generated segmentation to study bird plumage colours, modified from Cooney et al. (2022).

Pose estimation

One of the major avenues of the use of ML, particularly computer vision, in the biological sciences has been pose estimation (Pereira et al., 2019). This approach estimates the relative position of body parts to each other and is used to recognise different animal poses and their changes during locomotion. While estimation is usually conducted on static images, these capabilities have also been adapted to recognise and quantify movement. Indeed, parsing kinematic patterns from videos has become the hallmark of locomotion, biomechanics, and behavioural studies, contributing to the rapid transformation of these fields. Pose estimation is a relatively simple computer vision problem, based on the annotation of training sets from images (Mathis et al., 2018). Originally, algorithms were unable to recognise parts that were not sufficiently distinct from the background, an issue called the ‘background problem’ (Diaz et al., 2013), and mitigating this required the placement of markers on the moving parts prior to filming. This problem was amplified in video estimation, as motion blur also constituted a significant challenge, requiring the use of extensive and highly specific training datasets (Nath et al., 2019). In light of these issues, the main element of novelty in the field has been the development of computer vision algorithms able to handle video analyses requiring smaller datasets without markers, such as that offered by the recently introduced DeepLabCut toolbox (Mathis et al., 2018; Nath et al., 2019), which has quickly become the standard tool used for marker-free 3D pose estimation (Figure 12). Its capabilities are based on transfer learning: the neural network it is based upon was pre-trained with large datasets, allowing the application of DL to much smaller supervised datasets (Mathis et al., 2018).

Efforts are being made within the field of pose estimation to bridge gaps between biological and computer science expertise. This is increasingly evident in the games and animation industries where there is a need to model animal behaviours for games and films. Manually editing each keyframe can be a painstaking task for animators, thus physics-based models have been employed for years, such as for automatically animating horse gaits (Huang et al., 2013). In recent years, ML tools have been incorporated to automate the process further, such as in the software, WeightShift, which combines full-body physics-based animation with AI to animate characters (Chapman et al., 2020), or in animating the locomotion of quadrupeds using neural networks (Zhang et al., 2018). Another area of pose estimation which has recently benefited from ML is via natural language. AmadeusGPT is a natural language interface for DeepLabCut, which integrates pose estimation and object segmentation (Kirillov et al., 2023). With this the end-user can describe a query and get outputs without needing to code (Ye et al., 2023).

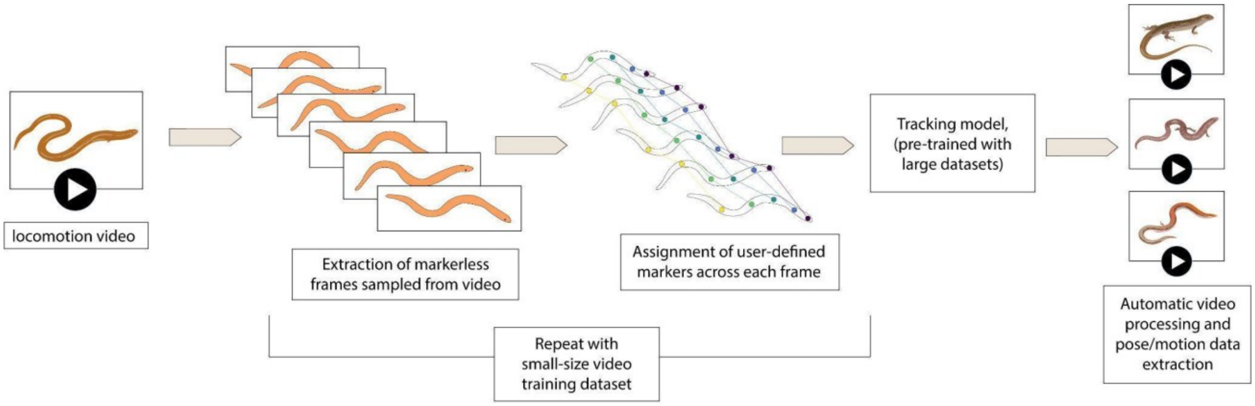

Figure 12: Simplified pipeline for markerless motion tracking and pose estimation from videos using DeepLabCut (Mathis et al., 2018). Limb-reduced skinks (Camaiti et al., 2023) are here used as an example of locomotion tracking.

Applications to Research in Evolutionary Morphology

AI has the capacity to transform our ability to capture morphology for evolutionary analysis, as detailed above. We are already seeing the implementation of AI approaches for diverse questions in evolutionary biology, but these barely scratch the surface of the potential applications of AI across the field. Below we discuss a range of topics within evolutionary morphology that have already benefited from AI applications and identify key areas in evolutionary morphology that are ripe for development. We also provide a table of tools (Table 1) that are already available for applying AI to evolutionary morphology.

Clustering and classification

Classifying individual specimens is an initial step in many evolutionary studies, but is often a time consuming task. Fortunately, ML techniques using image clustering have become widespread in the classification of individuals into distinct species (Punyasena et al., 2012;

Barré et al., 2017; Hsiang et al., 2019; Valan et al., 2019; Wäldchen and Mäder, 2018). Current research predominantly employs CNNs (Krizhevsky et al., 2012), which excel at extracting features from images and providing probability estimates to assign images to specific species classes. For example, Hou et al. (2020) introduced the ADMorph dataset, which trained and evaluated DL models for the morphological analysis of 3D digital microfossils. The study focused on enhancing the accuracy of DL models by testing the segmentation performance of multiview convolutional neural networks, PointNet, and VoxNet. The dataset aims to facilitate developing and evaluating DL algorithms for the precise analysis and classification of microfossil structures. Hou et al. (2021) further expand the prior study by highlighting the potential of DL to automate segmentation and accurately delineate and classify about 500 fish microfossils within CT images.

These methods tend to focus on classifying species and rarely describe the relationships between classes or higher-level classification, though there are some preliminary works in this area. For example, Kiel (2021) describes a method combining DL and computer vision approaches to train a CNN to categorise images of bivalve species into family groupings based on known taxonomy. For images of each species, the algorithm estimates the probability that it belongs to one family rather than another, and the results demonstrate that this approach was robust for family-level classification (and, to a lesser extent, for topology estimation, as detailed below). Morphometric data is also available for use in species identification, and in recent years ML techniques such as Artificial Neural Networks (ANNs) have been employed to accurately classify species using morphometric data (Salifu et al., 2022).

Each of these techniques must identify distinct morphological attributes for grouping, posing challenges for taxa with few specimens, such as many fossil taxa. Despite these constraints, the ability to use ML algorithms to differentiate, cluster, and classify taxa based on morphology has vast potential for fields from species delimitation and detection to phylogenetics. New work along these lines is detailed in the next sections.

Species delimitation

Species delimitation, opposed to classification, requires the ability to identify whether individuals belong to a population, which in some cases may lead to assignation of individuals as new taxonomic entities. The limitations of image clustering methods make them ill-suited for this task. Instead, emerging techniques in one-class classification systems (Perera and Patel, 2019) or open set recognition (Geng et al., 2021) offer promising avenues for extending species identification beyond initial classifications done through image analysis. However, inherent challenges remain; these techniques are currently used for outlier detection and would need to be adapted to establish species.

An alternative approach would be to use phenotypic traits as a basis for delimitation. Individuals can be grouped into self-similar clusters by analysing phenotypic traits, forming the basis for delineating populations and species (Ezard et al., 2010). Traditionally, Gaussian mixture models (GMMs) employing a Maximum Likelihood approach have been utilised (Fraley and Raftery, 2002). However, the advent of deep Gaussian mixture models (Viroli and McLachlan, 2019), which incorporate ML techniques, may be more suitable. These models show heightened levels of complexity, enabling them to capture intricate relationships within data. These approaches, combined with the increasing ability to acquire image or trait data rapidly, may allow for a more nuanced and comprehensive understanding of taxonomy.

Several genomic species delimitation methods have been extensively used in the last decade, including Bayesian species delimitation (BPP) (Yang, 2015). In addition, unsupervised ML algorithms have been employed on genomic data to predict clusters of individuals

(Derkarabetian et al., 2019). More recently, CNNs have been utilised to build a morphology-molecule network (MMNet) that integrates morphological and molecular data for species identification (Yang et al., 2022). Despite their widespread adoption and increasing applications in taxonomy, these methods cannot deal with taxa that are not present in the training set, rendering them ineffective for identifying novel or undiscovered species.

AI tools can certainly be used to detect anomalies from images in such a way that can be useful for identifying species and discovering new ones. One possible place for such application is during the digitisations of museum specimens. For example, in Hansen *et al.* (2020), a CNN-based model was trained to classify beetles from images of digitised museum specimens. A model can then be built upon to flag missing species. These models, particularly when combined with further classification and clustering tools, such as with heatmap analysis (Hollister et al., 2023), can one day be used to identify new species by simply scanning digitised museum collections.

Similar to the accumulation of image data, many more genomic markers and whole genomes are being sequenced today. Consequently, unsupervised or semi-supervised AI-based integrative taxonomic tools have the potential to play a key role in furthering species discovery. In addition to phenotypic traits and genomes, researchers are obtaining additional suites of organismal data such as acoustics, behaviour, and ecology. AI will be key to bringing these complex datasets together for a biologically meaningful interpretation of a species.

Phylogenies - Building Trees

Evolutionary studies frequently require data structures on the relatedness between taxa in the form of phylogenetic trees. Estimating phylogenetic trees is often computationally heavy and thus would benefit from the use of machine learning (ML) methods; however, ML remains relatively uncommon in phylogenetic inference, and research into this area is still in its infancy. Despite recent progress in addressing the limitations of traditional methods, the extent of the accuracy and scalability of ML methods remains uncertain. ML algorithms can mitigate the computational costs associated with Maximum Likelihood and Bayesian approaches, being flexible and not necessarily requiring explicit model specification. However, a significant obstacle for supervised methods is the scarcity of training data for tree inference. Due to the uncertainty associated with phylogenetic inference, the ‘ground truth’ of phylogenies is fundamentally unknowable, leading to a reliance on simulated data that may not accurately reflect evolutionary relationships.

In recent decades, genetic data has dominated phylogenetic studies of extant species (although these data are not available for the vast majority of extinct taxa). It is thus unsurprising that much of the early work on ML in phylogenetics focused on molecular rather than morphological data, and recent reviews of ML approaches for tree building (Mo et al., 2023; Sapoval et al., 2022) have correspondingly focused on molecular phylogenetics instead of morphology-based phylogenetics. This mirrors traditional phylogenetics, where molecular methods, due to sheer quantity of data that can be extracted with relative ease, are often prioritised over morphological data. However, a number of approaches being tested using sequence data may have potential for future application to morphological data. CNNs and RNNs have been employed to infer quartet (4 taxa) topologies using simulated sequence alignments and protein data (Suvorov et al., 2020; Zou et al., 2020). These methods can be trained to deal with instances of extreme model violation where traditional statistical methods such as Maximum Likelihood might fall short, and once trained, allowing faster tree estimation (Zaharias et al., 2022). Simulated quartet experiments outperform methods like Maximum Likelihood, especially in scenarios of high substitution heterogeneities, which many standard models struggle to account for (Zou et al., 2020). However, more recent analyses contest this, and traditional methods have outperformed neural network methods when the taxon number is increased above four (Zaharias et al., 2022).

These methods have mostly been applied to individual sequences, but applying them to species trees involves further complexities such as incomplete lineage sorting and introgression (Degnan and Rosenberg, 2009; Maddison and Knowles, 2006; Suvorov et al., 2020). Restrictions of limited taxa and the complexity of species tree inference are emerging areas of research, such as in a recent study applying generative adversarial networks (GANs) to simulated data and seven species of fungi (Goodfellow et al., 2014; Smith and Hahn, 2023). The phyloGAN model uses two networks: a generator that suggests new topologies, and a discriminator trained to differentiate real and generated data, estimating the fit of proposed topologies and alignments. This method imitates the heuristic search employed by many traditional methods to explore tree space for more optimal trees. PhyloGAN shows an improvement in the number of taxa that can be considered compared to previously mentioned methods, but is still limited compared to traditional methods, and hampered by lengthy computational times (Smith and Hahn, 2023).

Another molecular ML tree building approach is Phyloformer, which computes distances between molecular sequences in a multiple sequence alignment (MSA) (Nesterenko et al., 2022). This method simulates trees, then uses probabilistic models of sequence evolution, working backwards to simulate MSAs. Supervised learning is used to train a Transformer-based model to reverse-engineer the phylogeny based on an associated MSA. For Phyloformer, the algorithm estimates pairs of evolutionary distances between sequences that can then be used to infer a tree, using traditional methods such as Neighbour Joining (NJ). Phyloformer outperforms standard distance-based methods, as well as Maximum Likelihood due to its higher computational speed.

The methods described here use ML to estimate evolutionary relationships, either by approximating distances between taxa or by directly inferring topologies, but their applicability to morphological data remains unclear. Methods such as Phyloformer still rely on models of sequence evolution, which are lacking in the field of morphometrics due to increased complexity and the lack of clearly defined smallest units of change across the tree of life. This presents a potential challenge to the application of this framework of methods, though morphological data could be coded into such analyses as matrices.

In contrast to advances in ML for molecular phylogenetics, tools for AI-based phylogenetics focused specifically on morphology are a relatively recent development. Whilst several studies used ML for clustering purposes, as noted above, very few have done so in an explicitly phylogenetic framework. As mentioned previously, Kiel (2021) used feature extraction to estimate family-level classifications of bivalves. They then used the degree of certainty in clustering as a proxy for morphological similarity between families of bivalves. These probability scores are used as a proxy for morphological similarity and to construct a distance matrix, which was in turn used to cluster the families and infer a topology. Whilst this method did find significantly more bivalve families clustering with members of their known subclasses than expected by chance, the resulting phylogeny did indicate many unlikely placements. When multiple CNNs trained at different taxonomic levels were combined, the resulting phylogeny more closely matched the expected clustering based on existing taxonomic standing.

Without explicit models of morphological evolution or an ability to discern homology, such methods may be prone to the confounding effects of homoplasy and convergent evolution. Whilst, even without an explicit model, phenotypic trees from ML-extracted morphological features can still closely match phylogenies based on genetic models (Cuthill et al., 2019), the comparison between the two remains difficult. Adaïmé et al. (2024) present a novel method incorporating pre-existing phylogenetic information into ML training. Multiple CNNs were trained to classify pollen grains using various aspects of morphology (shape, internal structure, and texture). Pollen specimens were then classified into “known” taxa or, if classification uncertainty overcame a certain threshold, they were instead considered novel taxa. The morphological features of these taxa were then fed into a phylogenetic embedding model, which uses a pre-existing molecular phylogeny as the ground truth. The model is trained to transform morphological data so that when phylogeny is inferred, it is as close to the “ground-truth” molecular phylogeny as possible. Thus, the model uses “known” phylogenetic positions of taxa as a template to guide how the morphological characters are used to estimate phylogeny. The model is considered accurate if it can use morphological characters of known taxa to infer a phylogeny closely matching the molecular phylogeny, and subsequently to place novel and fossil taxa (where genetic data has not or cannot be obtained) into the topology. Adaïmé et al., (2024) used this pipeline to infer and date a phylogenetic tree of extant and fossil pollen species. By taking taxa that had “known” phylogenetic placements and treating them as if they were novel, they tested the accuracy of the method, with these pseudonovel taxa being placed in their “correct” respective subclades with high support. By transforming morphological characters based on pre-existing phylogenetic information, this method improves upon clustering based on morphological similarity alone. Evolutionary history is incorporated in the estimation of species relatedness, but concerns could be raised over the assumption of a “ground truth” in phylogenetics. Simulation studies can help avoid this issue but of course, come with the issue that they may not fully replicate the complexities of empirical data.

As noted above, an important consideration for phylogenetics is the type of model used, but identifying the optimal model can be challenging. ML algorithms have been applied to improve model selection methods. ModelTeller (Abadi et al., 2020) and ModelRevelator (Burgstaller-

Muehlbacher et al., 2023) are two such approaches that focus specifically on identifying the most appropriate substitution models for a particular analysis or dataset. Whilst both focus on molecular substitution models, their existence opens the possibility of developing new systems for selecting morphological evolutionary models. Currently available models of morphological evolution are generally more simplistic than those of molecular evolution (Lee and Palci, 2015), though are likely more complex in reality. However, ML could be applied to morphological models of evolution through automated assessment of trait covariations, studies of modularity and integration, changes through time using existing phylogenies, and probabilities of key innovations versus gradual variations. This is a key area for development; at present there are few models available for morphological data that can aid in building phylogenies.

One common issue for several phylogenetic methods (including Maximum Likelihood, Bayesian, and Maximum Parsimony) regardless of data type is the use of heuristic searches, where model parameters (e.g., tree topology, branch length) are adjusted and the likelihood or tree length of each adjustment is then estimated and compared. This approach explores tree space for a set number of iterations, aiming to identify more optimal parameter combinations, but it is limited by the extent of tree search which makes it computationally expensive. Recently, ML methods have been being applied to improve efficiency of heuristic searches, by predicting which neighbouring trees will increase the likelihood without actually calculating the value, thereby reducing computational load (Azouri et al., 2023, 2021).

Another major challenge in both molecular and morphological phylogenetic studies is the impact of missing data, especially for distance-based methods where calculating a distance matrix is complicated by the presence of missing data in the alignments. In the case of molecular phylogenetic studies, this refers to missing bases in sequences. For morphological data this could be a result of incomplete specimens where certain traits or biological structures are missing or difficult to measure or score. Previous studies have shown that missing data negatively affects the accuracy of tree inference methods (Roure et al., 2013; Wiens, 2006). ML methods such as PhyloMissForest (Pinheiro et al., 2022), which is a method based on Random Forest approach, and two methods proposed by Bhattacharjee & Bayzid (2020), use ML to estimate missing distance values within a distance matrix and may outperform traditional statistical methods. Overall, while there are numerous areas in which ML can improve phylogenetic inferences for diverse data types and methodological approaches, it is at present very poorly developed, particularly for morphological data.

Phylogenetic comparative methods and evolutionary modelling

Using a phylogenetic framework to estimate the evolution of clades and traits has become a core part of evolutionary morphology over the past few decades (Adams and Collyer 2019; Felsenstein 1985). Analysis of trait variation across phylogenies and through time relies on the availability of well-supported topologies and time calibration. Recent advances in genome sequencing and big-data approaches to taxonomic sampling and trait data collection have increased the availability of time-calibrated phylogenies. In turn, this has enhanced our ability to reliably map the evolution of traits on phylogenies and consider phylogenetic relations when examining relationships between traits across multiple taxa.

The potential applications of AI in reconstructing trait evolution using a phylogenetic framework have been documented theoretically. These applications include character evolution model choice and the reliable and efficient encoding of phylogenetic information. For example, Ho et al. (2019) demonstrated the theoretical application of ML to ancestral estimation of phenotypic traits using a multi-task learning approach applied to Brownian Motion models of continuous biological traits. A multi-task learning approach is an ML framework that pools data from different tasks (Ruder, 2017). This takes the form of an algorithm able to reduce the variance of estimators, using a penalty term that draws models closer to each other, allowing the estimation of ancestral states of multiple characters simultaneously. This approach improved ancestral estimations compared with Maximum Likelihood models at the expense of a slight bias introduced in the phylogenetic estimates (Ho et al., 2019).

Despite theoretical advances, there are currently few practical applications of ML approaches to estimate trait evolution. A known issue that would benefit from an AI-based modelling approach is the assignment of distinct rates of character evolution to different parts of a given phylogenetic tree (i.e., King and Lee, 2015). ML would enable the simultaneous pooling of multiple data sources, including distributions of states at the tips of phylogenetic trees, branch lengths, node ages, uncertainty in node resolution, and hidden states, and consideration of a wide variety of complex models that may better reflect phenomic datasets (Goswami and Clavel, 2024). ML approaches could also facilitate the comparison of simulations across trees. Furthermore, AI methods could account for phylogenetic relatedness in analyses of trait correlations. In the field of bioinformatics, using DNN and Convolutional Graph Network (CGN) architectures in phylogenetic profiling for protein interactions improved predictions (Moi and Dessimoz, 2022). In particular, combining CGN with a graphical representation of tree topology allowed for prediction across multiple species and could be used to predict pairwise interaction across time. Using these deep neural network algorithms in conjunction with phylogenetic information is currently exploratory but could potentially streamline and improve multiple aspects of estimating trait evolution and ancestral states, allowing better modelling of the complex factors underlying evolution on a phenomic scale.

Function and Adaptive landscapes

In evolutionary biology, adaptive landscapes are conceptual frameworks that illustrate the relationship between the phenotype of an organism and its fitness within a specific ecological context (Arnold, 2003; McGhee, 1999, 1980; Simpson, 1984). They provide a visual representation of natural selection-driven trait space across the blanket of an adaptive landscape, where peaks of specific traits reflect higher fitness compared to putative trait space across the landscape. Over evolutionary time, genetic variation, mutation, recombination, and natural selection drive the population towards regions of higher fitness. Utilising models of trait diversification can be helpful in tracing adaptive peaks of species through time, adapting to different ecological niches or responding to environmental shifts. The study of adaptive landscapes is key both to understanding the evolutionary adaptive mechanisms giving rise to biodiversity and predicting the future adaptive potential of species in light of anthropogenic-driven habitat loss and climate change.

Functional adaptive landscape analysis uses the morphology and function of skeletal elements to model landscapes (Dickson and Pierce, 2019; Jones et al., 2021; Polly et al., 2016; Tseng et al., 2023). In palaeontology, functional adaptive landscapes commonly employ finite element analysis (FEA) as a functional metric (Deakin et al., 2022; Polly et al., 2016). ML algorithms can replace FEA to predict the behaviour of a beam in a one-dimensional system if the algorithms are first trained on initial FEA. ANNs have been suggested to provide more accurate FEA results than boosting regression trees or Random Forest ML algorithms (Vurtur Badarinath et al., 2021). Furthermore, ML algorithms could assist in the morphometrics (Baylac et al., 2003; Punyasena et al., 2012) used in adaptive landscapes in addition to modelling adaptive landscapes through evolutionary time.

Additionally, AI has been increasingly applied to FEA-based biomechanical modelling (Galbusera et al., 2020; Mouloodi et al., 2021). These techniques can be applied to data extracted from static images, 3D-image data (Galbusera et al., 2020), and even motion capture (Mouloodi et al., 2021). The isolation of distinct features (image segmentation) and the capture of locomotory information (e.g. through pose estimation) can both be automated through computer vision, which allows the identification of parts of interest and their spatial relationships to one another. Once features have been extracted, AI can be used to simulate their behaviour in relation to one another under a given set of physical constraints (e.g. Liu, 2019). This is particularly useful for the creation of models of the range of appendicular motion, relationships between internal organs, and even models of cytokinesis (Huiskes and Hollister, 1993; Ross, 2005; Shi et al., 2010).

Phenome-environment and ecometrics

One of the most established areas of phenotypic analysis is quantification of relationships between phenomes of organisms (the sum of their phenotypic traits) and the environmental context in which they evolved. The end goal of many studies using this approach is to assign an ecomorphological characterisation to phenotypic traits and to parse their ecological signal (Barr, 2018). AI has been implemented in this field through the use of algorithms that infer present and past ecomorphologies by reducing the dimensionality of ecomorphological data through ML pipelines such as Random Forest analyses (Mahendiran et al., 2022; Rabinovich, 2021; Sosiak and Barden, 2021; Spradley et al., 2019). Similarly, ML procedures have been used to discriminate and sort phenotypes (especially morphology) based on their belonging to specific ecomorphs or ecological guilds (MacLeod et al., 2022). These studies have highlighted the advantages of AI-based approaches compared to standard procedures used to test the links between morphology and ecology, such as Canonical Variate Analysis (Albrecht, 1980).

The related field of ecometrics is a taxon-free approach to quantifying the distribution of functional traits across space and time (Eronen et al., 2010). Ecometric correspondence between environmental and phenotypic data is used to develop transfer functions which can be used to reconstruct paleoenvironments or incorporate Species Distribution Modelling (SDM) to model future spatial distributions of phenotypes given predicted climatic scenarios (Parker et al., 2023; Vermillion et al., 2018). Existing work uses linear and maximum likelihood approaches to perform ecometric modelling. These approaches have a limit of one or two climate inputs, normally limiting analyses to consider only annual precipitation and mean annual temperature (Parker et al., 2023). However, a Random Forest approach would enable the model to use any number of climatic variables. Similarly, SDMs can be built using CNNs, capturing non-linear transformations across multiple variables (Botella et al., 2018). DL approaches to quantifying phenome-environment would enable models to better approach the complex factors contributing to climate and trait distribution, as in studies of trait evolution.

Niches and Niche Evolution

ML algorithms, including Boosted Regression Tree and Random Forest, have become standard methodologies for modelling the ecological niches of taxa and, by extension, their potential spatial distribution. Over the past decade, research has extensively focussed on predicting the ecological effects of climate change by using ecological niche modelling (Deb et al., 2020; Karuppaiah et al., 2023; Qin et al., 2017; Tang et al., 2021). The most prominent ML model in this area is the ‘maximum entropy modelling method (MaxEnt), which has been applied in thousands of studies since its description in 2006 (Phillips et al., 2006; Merow et al., 2013).

MaxEnt’s ubiquity in scientific literature is in part due to the algorithm requiring relatively few inputs (only species occurrences and geographic data) and relying on biologically reasonable assumptions. It assumes that a taxon will occupy as large an area as possible (maximum distribution entropy; Elith et al., 2011; Phillips et al., 2006). These limitations have also produced an abundance of literature critiquing and subsequently optimising MaxEnt's statistical assumptions and processes (Campos et al., 2023; Cobos et al., 2019; Low et al., 2021; Sillero and Barbosa, 2021).

Studies that use MaxEnt or other ML methods tend to consider niches as static entities, with many publications 'projecting' the same niche onto environmental rasters representing distinct points in time, sometimes thousands or millions of years ago (Saupe et al., 2019). Niche evolution studies have instead relied on measuring the contemporary niche overlap of different taxa (usually via the methodology of Broennimann et al., 2012), considering the similarities and differences within a phylogenetic context (Doré et al., 2023; Padilla-García et al., 2023; Vasconcelos et al., 2023). While both approaches are useful in understanding ecological evolution across time, they are limited by their discrete temporal sampling – niches change continuously across space and time, and an individual niche of a taxon may also change over time.

ML methods could be developed to identify and accommodate niches changing over time. Taxon occurrences sometimes have associated temporal metadata, which could be used by an AI tool to predict the continuous changes in a niche in the recent past or near future. This could prove especially invaluable in studying the effects of climate change at a higher resolution. Considering a geological timescale, the predicted ecological niches of fossil taxa (modelled with environmental data representing periods in deep time) could be used to calibrate and, thus, further validate continuous niche evolution models across phylogenetic trees.

Prospectus

The scope of evolutionary biology is immense, involving the history of life on Earth over the past >3 billion years. For the vast majority of species that ever lived, the only available data is morphological in nature; thus, studying morphology is crucial for understanding the evolution of organisms. Yet, methods for capturing morphological data remain largely manual, presenting a bottleneck for the study of morphological evolution, particularly in comparison to other biological fields with mature methods for ‘Omics’ level analyses. The use of AI is bringing about a massive transformation in the field of evolutionary morphology, both for data capture and analysis. Integrating AI techniques into this area will become increasingly important as the field continues to move towards larger-scale analyses and bigger data.

As we have discussed, AI has been successfully applied to a range of data acquisition for evolutionary morphology, and AI applications are only increasing in the pace of development and accessibility for non-experts. For example, AI is already making it quicker to generate, refine, and access image data of larger quantities and/or greater resolutions than ever before. Large gaps remain, however, including discriminating features or regions of interest, extracting discrete traits or 3D morphometric data in datasets with large amounts of variation (which are common in comparative evolutionary analysis), and in applying AI for improving evolutionary models for morphological data. These areas should be the focus of efforts over the coming years. While we have detailed applications of AI to several research areas involving morphological evolution, there are many more for which AI has yet to make a significant impact. Below, we note a few subfields of evolutionary morphology that have clear pathways for improvement through AI. Finally, we close with some considerations on the accessibility and environmental effects of AI.

Emerging fields

Retrodeformation - Several studies have demonstrated that fossil data are critical for accurately estimating phenotypic evolution through deep time (Slater et al. 2012; Goswami and Clavel, 2024 and references therein). A common challenge in palaeontology is encountering fossils which have undergone taphonomic distortion via brittle or plastic deformation (Kammerer et al., 2020; Schlager et al., 2018). This can severely hamper attempts to assess and quantify intra- and interspecific shape by introducing non-biological variation, and for this reason, as well as the lack of integration in phylogenetic analyses as noted above, fossil data are often excluded from comparative analyses. Retrodeformation is the process of restoring the original shape of an object by reversing this taphonomic distortion (Herbst et al., 2022; Lautenschlager, 2016). While landmark- and symmetry-based procedures to manually perform these operations are available (e.g. Morpho, Schlager et al., 2018), they are time-consuming and can only be applied to relatively small datasets, restricting the taxonomic breadth of studies. AI provides an opportunity to automate and enhance this process. ML models, such as neural networks, can be trained to recognize and correct specific types of deformations. These models can learn patterns of distortion and apply appropriate corrections. In the future, AI may aid in the reconstruction of 3D objects or scans of distorted or even completely flattened fossils, helping to recover valuable 3D morphology. Once models have been trained on a dataset of naturally distorted fossils and manually performed retrodeformation simulations, they can be integrated into software applications or embedded in hardware systems for real-time correction and analysis. The choice of AI techniques and algorithms will depend on the specific application and the nature of the deformations to be corrected. For instance, de Oliveira Coelho (2015) used logistic model trees to predict the temperature at which human bone was burnt. Likewise, Zeng *et al.* (2021) used a Support Vector Machine (SVM) algorithm to detect small geological faults.

Such methods could be co-opted to estimate the extent of brittle and ductile deformation a fossil has undergone, which then enables evolutionary morphologists to apply the opposite forces to correct the distortion.

Histology - Histology examines the microscopic structure and morphology of tissues, including fossil tissues in palaeohistology. Palaeohistology has historically informed on growth, physiology, and development, but is also increasingly used to investigate the form and function of tissues (e.g. the function of duck-billed dinosaur dental batteries; Bailleul et al., 2019, 2012). AI tools have greatly advanced histology, especially in the sub-field of histo-pathology, to better cancer recognition and clinical oncology (reviewed in Shmatko et al., 2022). AI has been proposed to be a promising avenue to increase throughput for pattern recognition. Some areas where AI pattern recognition has already been explored in biological research are in quality assessment of histological images (Haghighat et al., 2022) and herbivore diet characterisation through micro-histological analysis (Filella et al., 2023). Additionally, DNNs have been used to identify primary and secondary osteon regions and create segmented maps of different osteon regions. This osteon segmentation was combined with phylogenetics to elucidate the developmental pathway towards miniaturisation in the theropod dinosaurs Alvarezsauria (Z. Qin et al., 2022). There is significant potential for the use of AI in histological studies in the context of evolutionary morphology and is therefore an avenue for future exploration.

Genome-phenome mapping - AI has been applied in two main areas of genome phenome association (GPA): the medical sciences, and food production. This is not surprising, as both are umbrella areas of research with high societal impact. Deep matrix factorization (DMF)-based methods developed to handle multi-omics data have been successfully applied to improve genome-wide mapping and genome-wide association studies in the context of molecular phenomes. These include disease susceptibility (Long et al., 2023; Mieth et al., 2021), drug efficiency (Mongia and Majumdar, 2020), crop phenotype prediction (Islam et al., 2023), and microbe-disease association (Y. Liu et al., 2021). More recently, a multi-omics data fusion-based approach (Weighted Deep Matrix Genome Phenome Association) has been proposed to incorporate different kinds of omics data and to predict potential nonlinear GPAs with functional traits (Tan et al., 2022). However, for non-model organisms and evolutionary research, AI is underutilised either through GPAs or genome-wide association studies (GWAS). These fields are rapidly evolving with the increasing amounts of data collected worldwide, and therefore provide promising avenues for implementing new AI algorithms in the near future.

Evo-devo - ML has been successfully applied to the study of gene expression in embryonic development of model organisms (Čapek et al., 2023; Feltes et al., 2018; Naert et al., 2021). Algorithms have also been developed to aid in phenotyping and staging embryos and to recognize diseases and malformations (e.g. Al-Saaidah et al., 2017; Jeanray et al., 2015). In evolutionary developmental biology (evo-devo), phenotype identification is a recent development. A few pilot studies have been conducted using both images and morphometrics data on human cells, model organisms and plants (Cai and Ge, 2017; Chen et al., 2020; Masaeli et al., 2016). CNNs have been used to extract visual patterns from images, to aid embryo staging, and to analyse changes in phenotype during ontogeny (Feltes et al., 2018; Naert et al., 2021).

Data Engineering - Focus should not only be on potential fields and AI methods but also on the morphological data itself. Data engineering involves the preparation of data before any analysis or AI can be applied – this is undoubtedly a crucial aspect of AI as a whole. With the acceleration of data acquisition, along with previously collected data (e.g., Phenome10K: Goswami, 2015; MorphoSource: Boyer et al., 2016), the volume of usable data is increasing. Working towards the “Big Data" analysis in evolutionary morphology, we envision several potential areas of work: (i) Transforming previously collected data into AI-ready formats. There is a substantial amount of data collected before the deep learning era. It would be beneficial to process this data to make it suitable for use in AI models. (ii) Exploring learning strategies such as self-supervised learning. Morphological data, similar to medical data, often requires extensive domain knowledge for labelling, leading to the time-consuming creation of labelled training sets. Therefore, using unlabelled data in training could be a viable option. To have better data and performance evaluation, interdisciplinary collaboration is essential; biologists can help AI experts in tailoring AI methods to better suit the specific data.

Accessibility and Considerations

Until very recently, most AI models were built and applied using Python libraries such as Caffe, TensorFlow, and PyTorch (Jia et al., 2014; Martín Abadi et al., 2015; Paszke et al., 2019), requiring both AI and programming knowledge. Additionally, running these models required specialised, expensive hardware, such as GPUs, which are commonly used in training AI models. Consequently, the required level of expert understanding of AI and costly hardware restricted the accessibility of AI for many researchers in the biological sciences.

As AI continues to advance, it is becoming increasingly accessible to non-experts and more affordable to implement due to several factors. (i) Increasingly user-friendly software has reduced the need for in-depth AI-related knowledge. (ii) The growth of open-source and pre-trained models has significantly reduced the computational resources, data, and time required to develop AI models. (iii) The advent of cloud-based AI services has allowed researchers to access powerful AI without investing in local GPUs. In addition, the cost of robotic arms decreases annually (Zhang et al., 2022), meaning that large datasets capturing phenotype with high resolution are increasingly available.

Despite these advancements, there are certain aspects that require a degree of caution. AI outputs are derived from the data used for training. If the data is biased or unrefined, it could lead to similarly inaccurate and biased results (Mehrabi et al., 2021; Zhang et al., 2022), therefore, attention must be given to data cleaning and preprocessing.

Additionally, the environmental impact of AI cannot be overlooked, particularly as many studies in our fields aim to protect the natural world and limit human-caused climate change and destruction of biodiversity. Evolutionary morphology studies increasingly involve the collection and storage of large quantities of image data. These datasets are currently limited by the hours of manual input required, but will only increase in size as AI approaches allow for more efficient processing and analysis, leading to larger, more complex studies that in turn require increased hardware and energy input. Training large-scale models can consume substantial amounts of energy, contributing to carbon emissions, although admittedly the models trained and used in evolutionary biology are unlikely to be as large as those from tech giants like Google, Meta and OpenAI. Some studies using large scale genetic datasets have estimated the carbon footprint of their computational analyses (Philippe et al., 2019; Y. Qin et al., 2022). More formal approaches to sustainable computer science are being developed in the form of emission calculation tools (Lacoste et al., 2019; Lannelongue et al., 2021), assessments of their suitability for various approaches (Bouza et al., 2023), and proposed principles for greener computational science in the future (Lannelongue et al., 2023). As the scale of AI models and the demand for AI continue to grow, it will be increasingly important for us to evaluate the environmental impact of future studies in evolutionary morphology.

To conclude, we have here provided an introduction and overview of the current and potential future applications of AI to evolutionary morphology. At present, many of these methods remain technical and difficult to apply, due to the need for advanced coding knowledge and access to good hardware such as high-memory GPUs or high-performance computing (HPC) systems. Developments are, therefore, required to make these methods more widely accessible and to allow for greater understanding and addressing of their capabilities and limitations. As AI becomes more accessible and tailored towards applications central to the study of evolutionary biology, we expect that it will transform the study of evolutionary morphology. By accelerating and improving capture and analysis of “Big Data” on phenotype for diverse comparative datasets, AI will allow the realisation of evolutionary phenomics and launch a new phase in the study of past and present biodiversity.

Table 1. Currently available tools using AI that are applicable to research in evolutionary morphology. We include coding libraries, websites, and software, along with their application within evolutionary morphology, the data types they support, and the programming language where applicable. The table is broken into four main sections: acquiring textual data, deep learning, image processing software, and softwares for evolutionary morphology research.

This table will be regularly updated at http://www.phenomeai.org/.

Tool name / Library	Capabilities	Supported Data types	Programming language	Reference
Acquiring Textual Data				
NLTK, spaCy	Natural language processing (NLP). For example, it can be	Text	Python	(Bird et al., 2009)

(python libraries)	used for extracting scientific words/taxonomic names from Journal articles			
TaxoNERD *(python library)*	Extracts scientific names, common names, and name abbreviations. Can link taxa mentioned to a reference taxonomy (e.g. NCBI Taxonomy, GBIF Backbone and TAXREF)	Tabular data, text, images	Python or R	(Le Guillarme and Thuiller, 2022)
pytesseract *(python library)*	Optical character recognition (OCR) to turn images to text. Python wrapper for Google's tesseract engine.	Images	Python	(Dome and Sathe, 2021; "Tesseract documentation," 2021;

				Hoffstaetter, 2022)
Google Vision	Deep Learning Application Programming Interface to perform OCR.	Images	N/A	(Walton et al., 2020; "Vision AI," n.d.)
Deep Learning				
PyTorch, TensorFlow, *(python libraries)*	DL frameworks.	Tabular data (arrays, matrices etc.) Image based data Text Audio	Python	(Martín Abadi et al., 2015; Paszke et al., 2019)
Scikit-learn *(python library)*	Tools for classical ML. Classification methods (e.g. Support Vector Machine [SVM]), clustering methods	A variety of datatypes, from tabular data to image	Python	(Pedregosa et al., 2011)

	(e.g., K-means clustering), dimension reduction (e.g. PCA).	and sound data etc.		
PIL, scikit-image, open-cv-python *(python libraries)*	Image processing and computer vision tools. For example, thresholding, contour extraction with Snakes (Active Contour).	Images	Python	(van der Walt et al., 2014)
Monai, Biomedisa *(python libraries)*	DL tools that are designed for processing medical images	Images, especially medical images	Python	(Cardoso et al., 2022; Lösel et al., 2020)
Image processing software				
ORS Dragonfly, Avizo-Amira,	Softwares for processing and segmenting medical and cross-sectional	Medical images	The software is not open-source; but it	(Dragonfly: Comet Technologies Canada

VGSTUDIO MAX	images. AI-based segmentation methods are also supported.		supports Python scripting.	Inc., 2022; Avizo: Thermo Fisher Scientific, 2021)
3D Slicer, Imagej	Open-source softwares for processing medical and cross-sectional images. Users can add extensions such as SlicerMorph, or build their own extensions	Medical images	C++, Python, Qt	(Kikinis et al., 2013; Rolfe et al., 2021; Schneider et al., 2012)
Tools can be used in evolutionary morphology				
MeshCNN	Mesh classification and segmentation	3D mesh models	Python	(Hanocka et al., 2019)

	Can be used for segmenting 3D mesh models of specimens			
Detectron2 ML library	Object detection Can be used for identifying a specimen in an image.	Images	Python	(Wu and Kirillov, 2019)
Segment Anything	A pre-trained segmentation tool that can generate decent segmentation results	Images	Python	(Kirillov et al., 2023)
DeepLabCut	A tool for placing keypoints on images and videos.	Images and videos	Python	(Mathis et al., 2018; Nath et al., 2019)
Pl@ntNet	Species ID through identification of traits for plants	Images	N/A, input images directly to online tool (identify.plantnet.org)	(“Pl@ntNet IPT,” 2023; “Pl@ntNet,” 2023)

FloraIncognita	Species ID and identification of traits for plants	Images	N/A, input images directly to online tool (floraincognita.com)	(Mäder et al., 2021)
Fishial.ai	Species ID and feature recognition for fish	Images	N/A input images directly to web portal (portal.fishial.ai)	(“Fishial.ai,” 2019)
Merlin Bird ID	Species ID for birds from descriptions, photographs, and sound recordings	Images Audio	N/A, input images directly to mobile app (merlin.allaboutbirds.org)	(Cornell Lab of Ornithology, 2024)
Wolfram Mathematica	Identifying type of specimen in an image Categorising traits of specimens from images	Images	Wolfram Language, C/C++, Java	(Wolfram Research, Inc., 2024) Wolfram Research, 2024
MaxEnt	Modelling taxa’s ecological niches	Species occurrence	Java	(Phillips et al., 2024)

		data, environmental rasters		

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Data availability statement

No new data were generated or analysed in support of this research. The tools table in this paper will be kept updated at http://www.phenomeai.org/.

Competing interests statement

We declare no competing interests.

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