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Opportunities and challenges in applying AI to evolutionary morphology

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Main Title

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Running Title

AI for evolutionary morphology

Abstract

Artificial intelligence (AI) is poised to revolutionise many aspects of science, including the study of evolutionary morphology. While classical AI methods such as principal component analysis and cluster analysis have been commonplace in the study of evolutionary morphology for decades, recent years have seen increasing application of deep learning to ecology and evolutionary biology. As digitised specimen databases become increasingly prevalent and openly available, AI is offering vast new potential to circumvent long standing barriers to rapid, big data analysis of phenotypes. Here, we review the current state of AI methods available for the study of evolutionary morphology, which are most developed in the area of data acquisition and processing. 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 case studies of existing approaches using AI for evolutionary morphology, including image capture and segmentation, feature recognition, morphometrics, and phylogenetics. We then

discuss the prospectus for near-term advances in specific areas of inquiry within this field, including the potential of new AI methods that have not yet been applied to the study of morphological evolution. In particular, we note key areas where AI remains underutilised and could be used to enhance studies of evolutionary morphology. This combination of current methods and potential developments have the capacity to transform the evolutionary analysis of the organismal phenotype into evolutionary phenomics, leading to an era of "Big Data" that aligns the study of phenotypes with genomics and other areas of bioinformatics.

Keywords

Artificial intelligence

Phenomics

Evolutionary morphology

Machine learning

Deep 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). Since the early 2010s, deep learning (DL) has gained significant traction 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), and molecular analysis (Atz et al., 2021; Audagnotto et al., 2022; Korfmann et al., 2023; Kuhn et al., 2021; Kwon et al., 2021), among other broad topics within ecology and evolutionary biology (Borowiec et al., 2022; Lürig et al., 2021; Pichler and Hartig, 2023).

One key area of biological inquiry relevant to diverse topics is the field of evolutionary morphology, which aims to characterise and reconstruct the evolution of organismal phenotypes (e.g., Alberch et al., 1979; Love, 2003). The scope of evolutionary morphology is vast, 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 large datasets (e.g., Goswami and Clavel 2024; Cooney et al., 2017, 2019; Hoyal Cuthill et al., 2024; Price et al., 2019). Comparative evolutionary analyses in particular require large sample sizes for robustness in statistical analysis or evolutionary modelling (e.g., Cardini and Elton, 2007; Guillerme and Cooper, 2016a, 2016b). Researchers commonly 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 or computational

limitations (e.g., Bardua et al., 2019a; Goswami et al., 2019; Rummel, 2024). 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 morphology. By making large-scale 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 recently developed 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 in deep learning 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, and (iv) evolutionary analysis. We also focus on ten 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 the areas where there are potential, but limited current, applications of AI to key areas in evolutionary morphology.

Evolution of AI Methods

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 (e.g., Samoili et al., 2020). Further methodological definitions are provided where required in the main text.

Artificial intelligence, or AI, is particularly challenging to define, 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) provide a more operative definition of AI, as a system that can either 'reason', act human-like, or act rationally.

Machine learning, or ML, is a subset of AI that 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).

Neural networks are ML models consisting of layers of interconnected nodes (neurons). Each neuron receives the input, processes it using mathematical functions with parameters, and passes the output to the next layer, enabling the network to learn patterns and make decisions based on data.

Deep learning, or DL, is a branch of ML wherein learning is achieved through complex neural networks with many layers and parameters. With a large number of parameters, DL models are able to make predictions on difficult tasks or extract features with data that have complex structures.

Computer vision is a multidisciplinary field of computer science that enables machines to interpret, analyse, and understand visual information from the world, through image and video processing algorithms. It refers to using computers for pattern recognition 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.

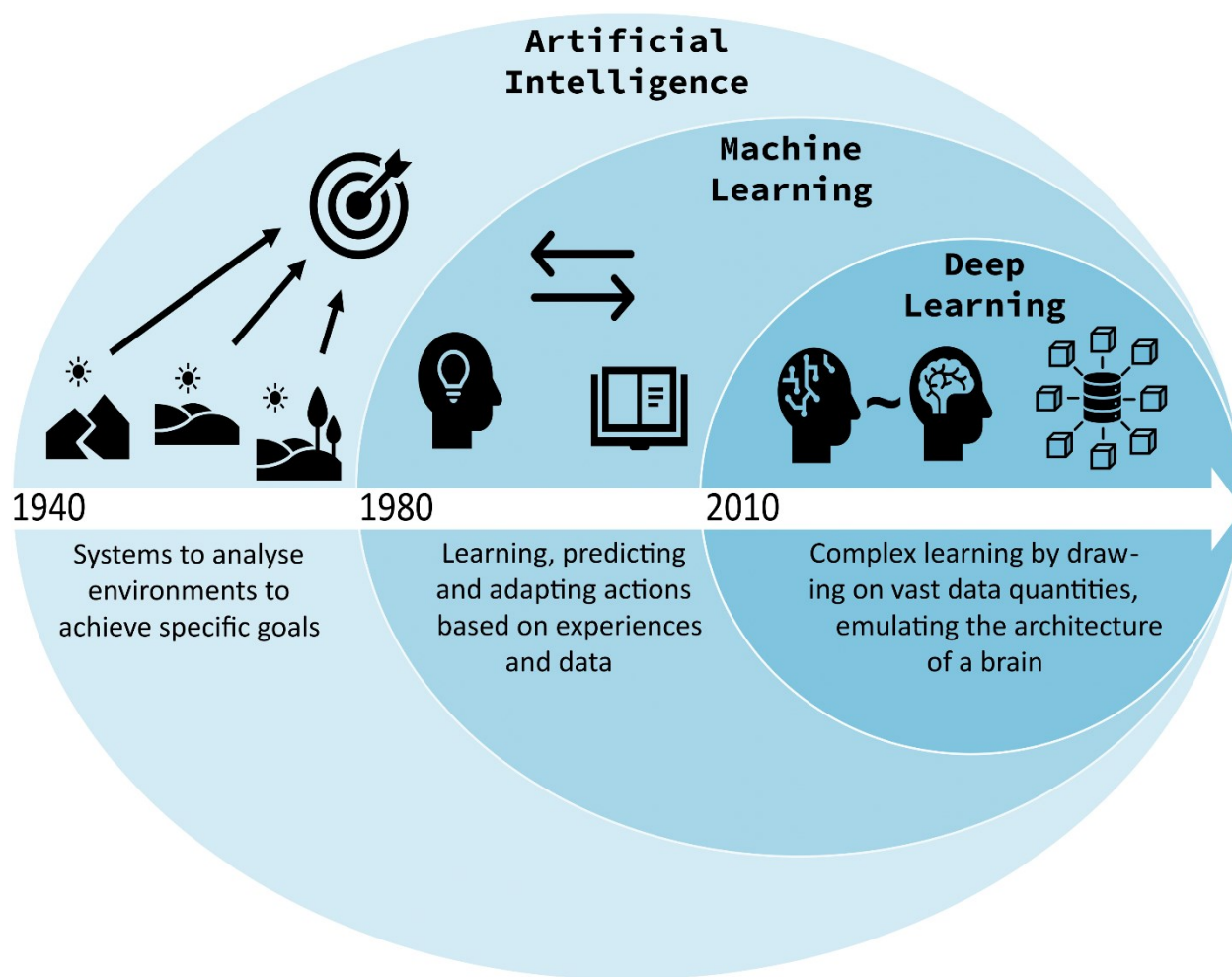


Figure 1. Broad definitions, relationships, and differences between artificial intelligence (AI), machine learning (ML), and deep learning (DL), the sequential development of each successive subset, and their broad introductions over time (Carbonell et al., 1983; Goodfellow et al., 2016).

Classical Machine Learning

Prior to the development of deep learning, ML 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 used 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 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 devoted to the design of methods to extract relevant structures within an image, such as Haar features (Papageorgiou et al., 1998), scale-invariant feature transform (Lowe, 2004), histogram of oriented gradients (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: 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 (e.g., classification, detection, and clustering) within a boosting framework (Vedaldi et al., 2007).

Deep Learning

Although artificial neurons (McCulloch and Pitts, 1943) and then artificial neural networks (Rosenblatt, 1958) were introduced several decades ago, 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 at that time. This was mainly due to the difficulty in training fully connected networks (wherein 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 AI 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. A key turning point was reached in 2012, when a deep CNN achieved the best result in the ImageNet Large Scale Visual Recognition Challenge (classifying millions of images into 1000's of classes) (Krizhevsky et al., 2012). Ever since, computer vision tasks have been dominated by solutions using deep neural networks (DNNs; a key DL technique), to the extent that learning with DNNs 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). Concurrently, neural network-based methods such as long-short-term-memory (LSTM) (Hochreiter and Schmidhuber, 1996) and recurrent neural networks (RNNs) (Graves et al., 2013) have been applied to sequential data and have shown great results for handling text and time series data, which has led to them being widely used in natural language processing (NLP) tasks (Canizo et al., 2019; Zhou et al., 2015).

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 (Tan et al., 2018). Under this assumption, the features learnt for a task can also be 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) (e.g., Mathis et al., 2018). Using pre-trained models reduces the need for large datasets, often improves model performance, and saves training time and resources (Devlin et al., 2019; Dosovitskiy et al., 2021). 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 computer vision models were using CNN-based methods. Transformers have been implemented as the backbone architecture for computer 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 (Dosovitskiy et al., 2021). 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 sufficient quantity of labelled data is often extremely labour-intensive, as most applications require relatively large training datasets. 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), and self-supervised learning only uses unlabelled data (He et al., 2021). These strategies allow DL models to leverage as much data as possible without the need for extensive manual work.

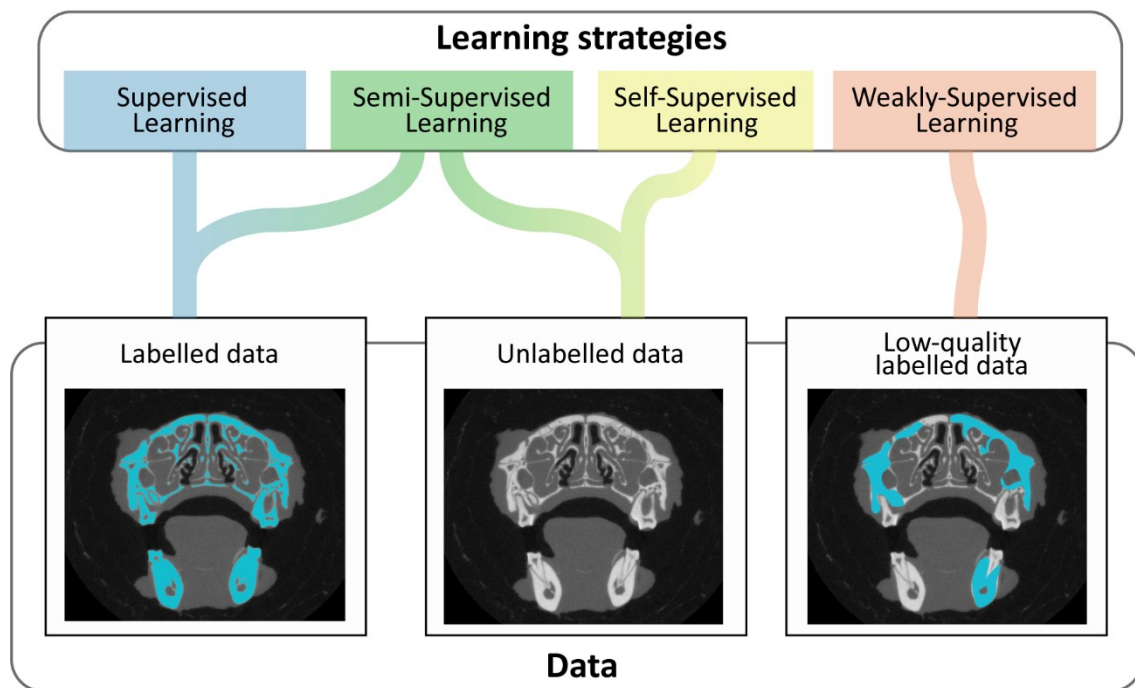


Figure 2. An overview of existing learning strategies and the levels of labelling used in these strategies.

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., 2018, 2019). 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 (e.g., Brown et al., 2020).

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 approaches 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 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 (Johnson et al., 2023). Additionally, AI has been successfully applied to process various data modalities, including text, images, and videos (Radford et al., 2021). Multimodal learning can be implemented by combining features extracted from different data modalities into one feature space. This 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. There have been a few implementations of multimodal models on biological data (Stevens et al., 2024). In evolutionary morphology, multimodal learning can effectively process diverse data modalities, such as photographs, micro-computed tomography (micro-CT) scans, and 3D mesh models.

A full review of the above three major stages in the development of AI is beyond the scope of this paper, and there are numerous other subfields of AI not explicitly reviewed in this section,

such as robotics (Dumiak, 2008) and graph neural networks (Dettmers et al., 2018).

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 evolutionary analysis. We introduce these methods with a schematic of generalised AI workflows (Figure 3), which are expanded in the following sections.

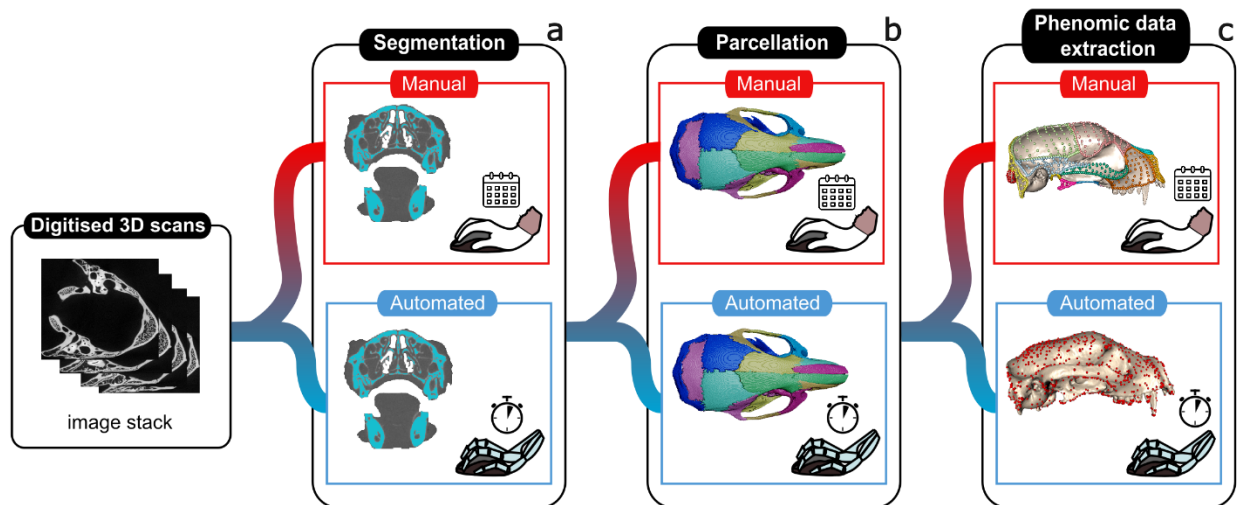


Figure 3. Schematic of a common workflow using manual and AI approaches for evolutionary morphological analysis involving 3D images and meshes. The main steps are: (a) segmenting

the specimen from the background; (b) isolating the scan into target regions; and (c) extracting phenomic data from the isolated regions.

Data Acquisition

The first step of acquiring data is to collect the relevant samples which are to be used in the subsequent investigation under appropriate best practices (e.g., Parham et al., 2012). 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 specimens (e.g., Davies et al., 2017, Ioannides et al., 2017, Johnson et al 2023, Smith and Blagoderov, 2012). 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). Diverse data includes enough examples of each class of interest. 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 tends to have 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). Clean data minimises errors from training datasets. Pre-processing 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).

Data scarcity and imbalance can also be improved by additional data collection or artificial data expansion, e.g., data 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 (Mulqueeney et al., 2024a; 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 searching for a specific specimen or representatives of specific groups can be challenging. This difficulty is because data is often inconsistent in quality and structure, particularly in large collections (Dutia and Stack, 2021). Some of the key challenges to address in cataloguing museum specimens include recognising species and extracting taxonomic and metadata to enable effective searches. AI can play a key role in this, particularly when it comes to tasks of digitising, identifying, cataloguing, and locating specimens within collections.

At its most basic definition, digitisation involves the creation of digital objects from physical items. Within museums, this is often attributed to the photographing, scanning, or filming of physical specimens (Blagoderov et al., 2012). However, traditional ways of digitising artefacts, such as digitising each specimen individually, can be invasive to the specimen, time-consuming,

and not very cost-effective (Price et al., 2018). 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, as seen in Ströbel et al., (2018) and 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).

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 to recognise species, metadata, traits, and even life history stages of digitised specimens. This is most established in the botanical sciences, where flat herbarium sheets are easily digitised in large numbers as 2D photographs (Gehan et al., 2017; Goëau et al., 2022). This has also led to advances in DL-based classification and segmentation tasks of traits within digitised herbarium sheets (e.g., Walker et al., 2022; Weaver et al., 2020), such as with LeafMachine (Weaver and Smith, 2023), which is a tool for automatic plant trait extraction, from flowers and leaves to rulers and plant label detection. 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 of DL 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 (Unger et al., 2021) and Pl@ntNet (Goëau et al., 2013). 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 for capturing information from specimen labels can save vast amounts of manual effort for cataloguing specimens and making key data searchable (Case Study 1). Together, species identification and taxonomic and metadata 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; Schuettpeitz 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. It may also be 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 successfully applied to extract scientific terms and taxonomic names from scientific articles (e.g., Le Guillarme and Thuiller, 2022). 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.

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. For instance, Dutia and Stack (2021) created 'Heritage

Connector', a toolkit for using ML to allow better connectivity of specimens in collections and publications. This software achieved a precision score of greater than 85% with science museum records of 282,259 objects from 7,743 organisations. Further development of software such as this, applied on a global scale, will improve access to the vast specimen data held in natural history collections worldwide.

Case Study 1: Machine Learning within Museum Digitisation and Data Collection

A) Label Extraction within Digitisation Pipelines

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 4). 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.

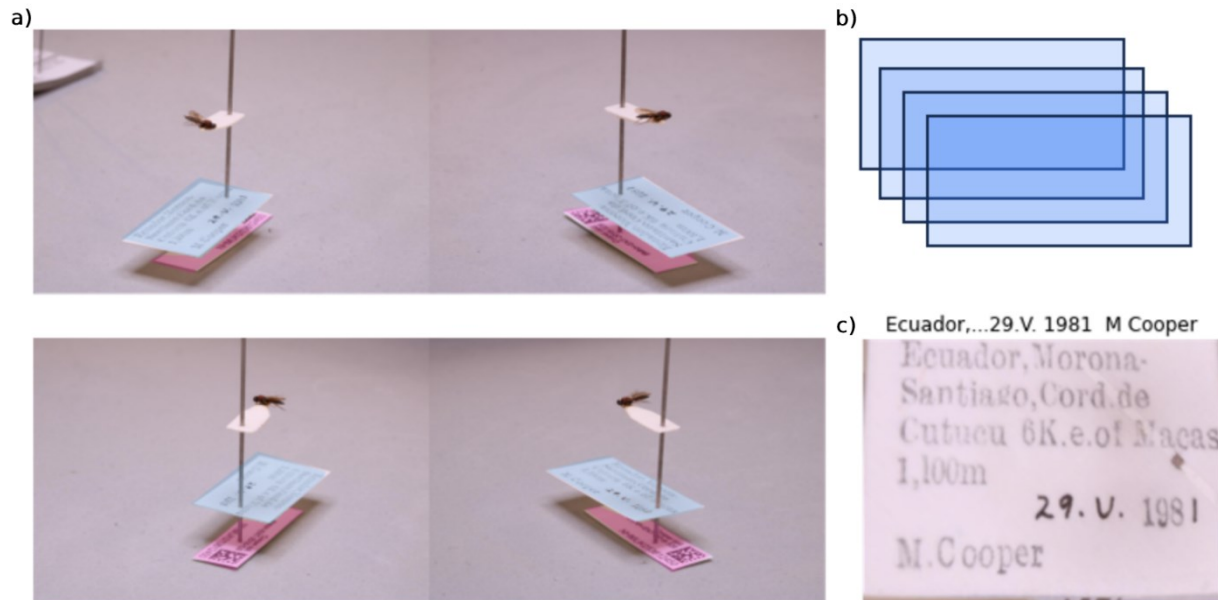


Figure 4. An example of the workflow described in Salili-James et al., (2022b); (a) using a setup introduced in Price et al., (2018), the algorithm uses a CNN model to segment all labels found on each of the four images of the specimen, (b) for each label, it then merges the four layers together in order to have one version of each label, which can be fed into an automatic transcription algorithm using OCR, (c) an example of a merged label, with a sample of the automatically transcribed text above it.

B) Knowledge Graphs within Digitisation Pipelines

Transcribing text from labels is one step of the data extraction process, but understanding the textual data and conceptualising the data and specimen within a larger picture is another, much bigger goal, which may one day be accomplished with knowledge graphs (Dettmers et al., 2018). Knowledge graphs are structured and contextual data models that represent semantic

information about concepts, entities, relationships, and events (Figure 5). Broadly, this can lead to representations of data structured in graphs with interlinking entities, allowing users to define relationships between different items within large datasets. The Natural History Museum, London has recently begun developing knowledge graphs, with an initial focus on herbarium sheets (Gu et al., 2022). Herbarium sheets contain a wealth of information from hand-written and printed labels appended to the sheet, to hand-written text containing trait and specimen information written directly on the herbarium sheet. Knowledge graphs can help determine links between herbarium sheet specimens, and subsequently, combined with other machine learning techniques, can be embedded into digitisation workflows (Gu et al., 2023). For example, with integrated OCR tools, incorrect or missing information can be corrected and filled in, by analysing the relationships present in the graphs. Knowledge graphs can be used to identify data outliers, find historical errors, and to clean data, making them a great tool for digitisation.

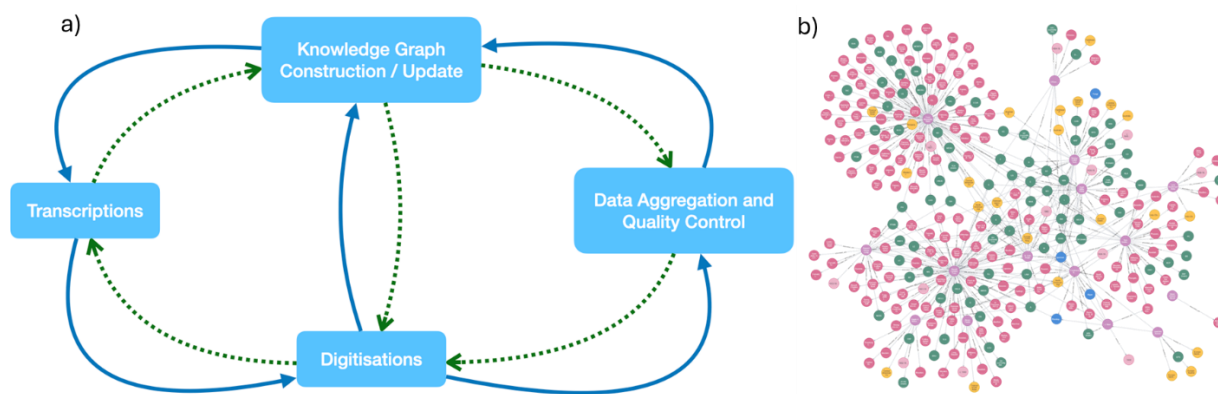


Figure 5. An example of (a) the facets of natural history collection data making up a node of a knowledge graph, and (b) a whole knowledge graph showing interconnectivity between nodes.

Image and 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 for analysis. The use of images is central to the study of evolutionary morphology, from simple drawings and photographs to computed tomography (CT) scans (Cunningham et al., 2014). Two-dimensional digitisation often involves photographing collections (i.e., specimens, drawers, etc.), whereas three-dimensional digitisation involves generating images of specimens using techniques such as photogrammetry, surface scanning, or volumetric scanning.

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 (Case Study 2). 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, AI 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 and efficient as it learns through training datasets and is exposed to more data.

The ability to generate high-resolution 3D images has increased exponentially in recent years, particularly with initiatives for mass-scanning of collections and databases for open sharing of image data, including DigiMorph (Rowe, 2002), Phenome10K (Goswami, 2015), and MorphoSource (Boyer et al., 2016). These images can then undergo segmentation or region identification and data extraction, where specific components are identified and separated from the image for further processing or evaluation.

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).

Case Study 2: Robotics for Digitisation

A) Machine Learning and Robotics for Specimen Digitisation

One 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 (Zhang et al., 2022), 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 was to have a collaborative robot (cobot) aid a digitiser in the mass digitisation of certain specimens (Figure 6). Computer vision can be combined with robotics in order to identify, move, and scan specimens, with synthetic specimens used during the training stages in order to mitigate the risks of specimen damage. Thereafter, by implementing CNN algorithms and/or turning to reinforcement learning, 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 6. 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. Synthetic specimens were used in the training stage for this task.

B) Automation of Specimen Digitisation

The use of automated robotics for digitisation and high-throughput data collection has historically been applied to two-dimensional methods such as photography. 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; van de Kamp et al., 2018). This fully automated process results in greater acquisition efficiency, 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 can 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).

Image Data Processing

Capturing image data has become increasingly widespread 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 phenotypic data. Here, we focus on the major aspects of image data processing: segmentation for feature extraction and element isolation for both 2D and 3D 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).

There are two main parts to segmentation; semantic segmentation, where all objects of a class are grouped as one entity when segmented; and instance segmentation, where objects of the same class are distinguished. These types of segmentation facilitate 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 without DL (Boykov et al., 1999; Dhanachandra et al., 2015; Minaee and Wang, 2019; Najman and Schmitt, 1994; Nock and Nielsen, 2004; Otsu, 1979); however, it remains subjective (Joskowicz et al., 2019) and time-intensive (Hughes et al., 2022). However, in recent years, novel DL methods have facilitated models 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 state-of-the-art for many image segmentation challenges and often outperform other methods.

2D Image Segmentation

There are many applications of automated methods on 2D image datasets for morphological studies. Many studies have aimed to extract features such as size (Al-Kofahi et al., 2018), shape (Lürig, 2022; Schwartz and Alfaro, 2021), and pixel values (He et al., 2022; Van Den Berg et al., 2020) from segmented photographic images, and used the extracted features to quantify organismal morphology. Moreover, due to the properties of 2D radiological images (e.g., MRI and CT), such as distinguishable grayscale values, specific segmentation models have been developed, particularly for applications to medical images (Ronneberger et al., 2015). Some studies have used these models to segment these radiological images and measure morphological features (e.g., Norman et al., 2018; Montagne et al., 2021). As these automated segmentation methods allow for greater consistency amongst measurements they make measurements more repeatable, and, particularly in medical fields, they allow for better longitudinal studies (Willers et al., 2021). These methods applied to 2D images can be adopted

for studying evolutionary morphology, for instance in evo-devo or histology, however, as an increasing number of investigations seek more detailed measurements, 2D images may lack sufficient spatial or internal structure information, making segmentation on 3D cross-section images crucial.

3D Image Segmentation

AI approaches to image segmentation have been adapted for 3D data, being routinely applied to image stacks generated from CT (Ait Skourt et al., 2018, Kendrick et al., 2022) and magnetic resonance imaging (Milletari et al., 2016; Lösel et al., 2020). 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 datasets on biological systems (Lösel et al., 2023; Mulqueeney et al., 2024a; Rolfe et al., 2023) (Case Study 3).

Beyond increasing the 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). Another case where DL segmentation may be useful for CT data is when segmenting 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. Objects with similar densities may be displayed at the same greyscale value through the scan, thus may be difficult to distinguish. Scans such as these are often also very noisy as a result of the high power of the beam needed to penetrate them, frequently resulting in artefacts and irregularities within images (Das et al., 2022). DL segmentation models can be trained to overcome these

issues and 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 (e.g., Edie et al., 2023; Yu et al., 2022), a common problem when imaging palaeontological specimens.

Case Study 3: 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). They offer an efficient alternative to labour-intensive manual image segmentation methods. In the study by Mulqueeney et al., (2024a), a range of different training sets were used to train a CNN in order to segment CT image data of planktic foraminifera, with each of the accuracy of these models then being compared. The results showed that the efficacy of these neural networks was 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 of 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., 2020a, 2020b). However, by increasing the size of the training set through selecting additional specimens or by 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.

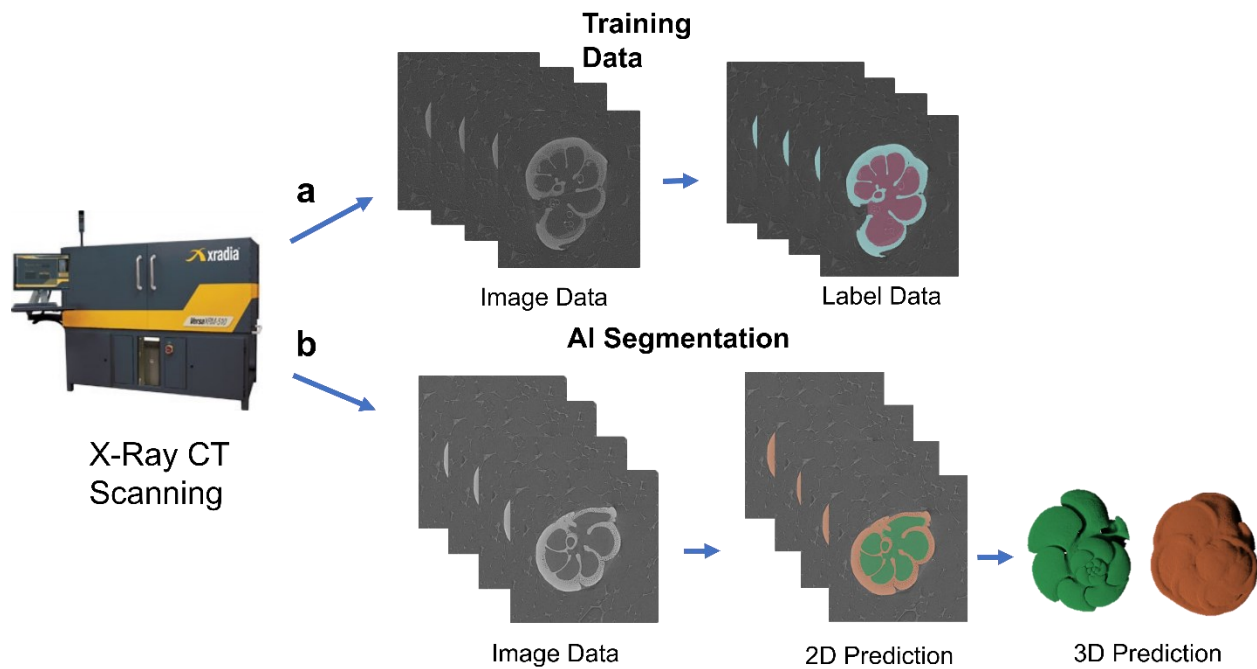


Figure 7. Workflow from Mulqueeny et al., (2024a) for producing training data and applying a CNN to perform automated image segmentation, reproduced under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>). The workflow includes (a) the creation 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.

Isolating Regions

Isolation of regions within a segmented 2D or 3D image 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 (Rezaeitalashmahalleh 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).

Case Study 4: Image Segmentation for Automatic Trait Extraction

Segmentation can also be used to extract phenotypic features directly, such as sutures from their surrounding bones. Cranial sutures are fibrous bands of connective tissue that form the joints between the cranial bones of vertebrates (White et al., 2021). Due to sutures being small regions, measuring them is a highly time-consuming and skill-intensive task. Ongoing work of several authors (MC, AG, EG, YH, and OK-C) addresses this methodological challenge using DL models (Figure 8). Firstly, a dataset was created by segmenting only a specified number of slices (e.g., one out of every 100 slices), which was then split into training and validation sets for model training. Additionally, a test set was created with sutures segmented throughout the entire stack for a few scans, which is used for a robust evaluation of accuracy. As sutures are normally small regions, this creates a class imbalance issue, which can be mitigated through a weighted training approach, with sutures having more weight during training than the surrounding bones. The model performance was evaluated on the test set using the intersection over union for segmented regions. After selecting the best model, sutures for the rest of the scans were predicted and reviewed to generate high-quality suture segmentations. The resulting manually checked and corrected segmentations can be used as a new training set to

enhance model performance or used for downstream analysis. Subsequently, features from the extracted sutures can be quantified. 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).

(a) Segmented micro-CT stack (b) 3D reconstruction (c) Suture measurements

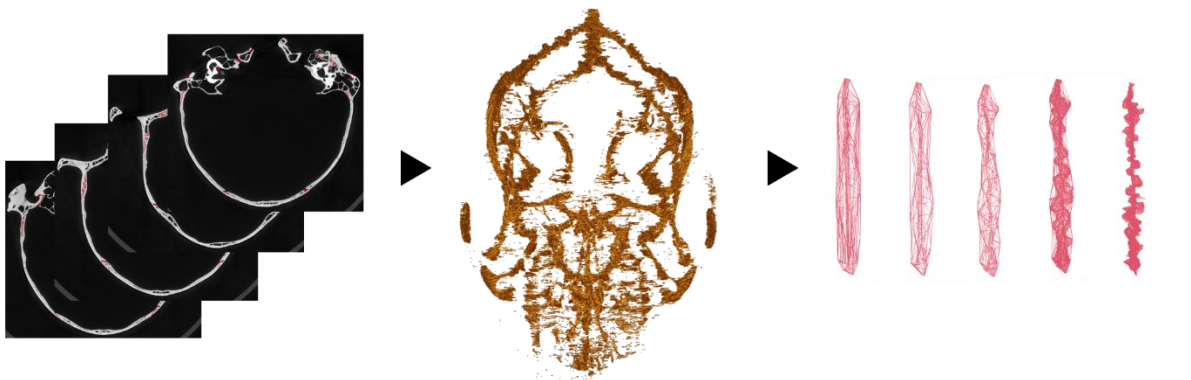


Figure 8. A workflow for extracting sutures on micro-CT scans. This workflow includes (a) segmenting sutures on micro-CT scans of mammal skulls. Segmented sutures are used to generate (b) 3D reconstructions, which can then be used to calculate (c) suture measurements.

In addition to segmentation, isolating regions in 3D meshes is a method of separating scans into biologically meaningful regions (Case Study 5). This approach, however, comes with some important challenges, such as the tradeoff between computational cost and the quality of 3D data. Current methods typically employ human-created 3D meshes as benchmarks (Chen et al., 2009), which tend to have low polygon counts and thus do not reflect most biological datasets. As a result, the isolation of regions in 3D meshes has proven challenging, with various methods

attempting to overcome quality issues in the CT data (Shu et al., 2022; Sun et al., 2023). For example, 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 important 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 feature extraction of known phenotypes from supervised learning is relatively straightforward, 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, applying AI to 3D data with species or features not included in the training set 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 5: Feature Extraction and Region Isolation on 3D Meshes

In another example from our own work, we sought to conduct a landmark-free 3D morphometric study of skull shape in mammals on 3D meshes, 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 (Blender Online Community, 2018). To

segregate regions, edges of a mesh are assigned to a specific class (e.g., horns/antlers, teeth, skull in Figure 9), resulting in meshes annotated with the regions of interest. A model is then trained on the annotated meshes which can then be applied to other specimens.

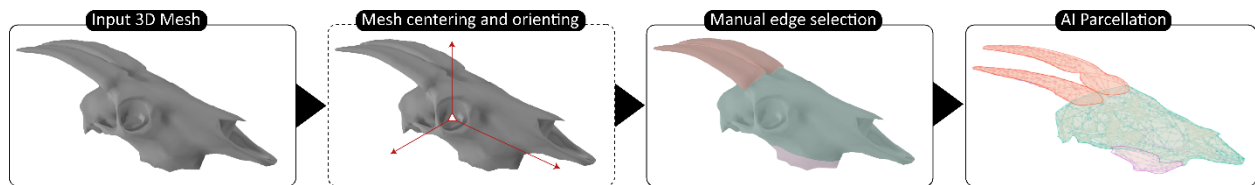


Figure 9. Workflow for segmenting horns/antlers and teeth from a skull using Blender.

Phenomics

Phenotypes encompass morphology, behaviour, development, and physiology, all of which mediate an organism's interactions with other species and its habitat. Phenomics is the organism-wide, high-dimensional extension of the study of phenotype (Houle et al., 2010).

Analysis of phenomes thus entails a variety of traits, all of which are essential in understanding 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, colour, and pose estimation.

Discrete and Meristic Traits

Morphological traits underpin the study of phenotypic evolution within phylogenetic systematics (Hennig, 1966). Discrete and meristic traits are those manually scored by researchers, with

discrete data including presence and absence and meristic data referring to counts. Discrete and meristic traits are 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). Discrete traits are also 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). However, morphological traits for phylogenetic applications have many limitations (Lee and Palci, 2015), as they can be time-consuming and difficult to collect due to personal interpretations and potential errors (Wiens, 2001).

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% accuracy (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, these algorithms have the potential to be used in morphological trait extraction and phylogenetic analysis.

Univariate Measures

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 enabled 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). Some of these methods have the ability to concurrently extract multiple length measurements or features from 3D images (Wu et al., 2021; Yu et al., 2021). Moreover, they can provide volumetric measures of multiple components through segmentation (Lösel et al., 2023; Mulqueeny et al., 2024a).

Shape

Univariate or linear morphometrics has been a tool in evolutionary morphological analysis for centuries (Zelditch et al., 2004), but recent years have seen an explosion of geometric (landmark-based) and surface morphometrics, greatly increasing the scope for capturing and quantifying organismal shape (Mitteroecker and Schaefer, 2022). While surface methods are relatively new, they are expanding rapidly and offer great potential to increase understanding of evolutionary dynamics (Bardua et al., 2019b). Currently, this step is overwhelmingly manual, representing a significant bottleneck for big data phenomic analyses from comparative datasets (Goswami and Clavel, 2024). Thus, having automated approaches that can provide high-resolution measures of shape would be hugely influential in allowing large-scale comparative analyses and allowing for more reproducible decisions in trait descriptions.

Landmark-based Geometric Morphometrics

Landmark-based geometric morphometrics is a multivariate methodology which 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 translation to register objects to a common reference frame so that only biological variation remains (Bookstein, 1997). The main advantages of geometric morphometrics include the capacity 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 (e.g., Goswami et al., 2022) to biomechanical analysis (e.g., Pollock et al., 2022). However, the manual placement of

landmarks is time-consuming and lacks repeatability (Shearer et al., 2017), especially for big comparative datasets, even when using semi-automated methods (Bardua et al., 2019a).

Automated landmarking techniques have been developed to minimise the user's workload by automating the placement of homologous landmarks. A variety of approaches for automated landmarking via statistical image analysis have been developed in recent decades, frequently relying on image registration to propagate landmarks from one set of scans, or a generic template, to another (Maga et al., 2017; Young and Maga, 2015). While these methods have improved in accuracy, they still often lack precision in identifying anatomical loci, even in closely related taxa, particularly around highly variable regions (Devine et al., 2020). Therefore, to improve the obtained results, others have attempted to use DL and computer vision to address the problem of landmark annotation.

One promising approach, currently applied only to 2D images, uses deep learning for the full process of automatically placing landmarks on specimens (Porto and Voje, 2020; Case Study 6). Approaches currently available for 3D images combine image registration and AI, such as Devine et al., (2020), wherein deformable image registration is used to detect the landmarks and then DL is used to optimise their placement, thereby improving accuracy after mapping of landmarks from a template to specimens. Both of these approaches 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, all present applications behave poorly with even a moderate amount of variation, effectively limiting applications to analysis of conspecifics or congeneric species at present.

Case Study 6: Geometric Morphometrics - Automated Landmarking

AI has been successfully applied to automate placement of landmarks and semilandmarks in samples of fruit flies (Porto and Voje, 2020; Salifu et al., 2022), bryozoan colonies (Porto and Voje, 2020), and mice (Devine et al., 2020; Porto et al., 2021). 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 gradient 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 potential of AI applications to geometric morphometrics and the need to develop implementations for 3D data.

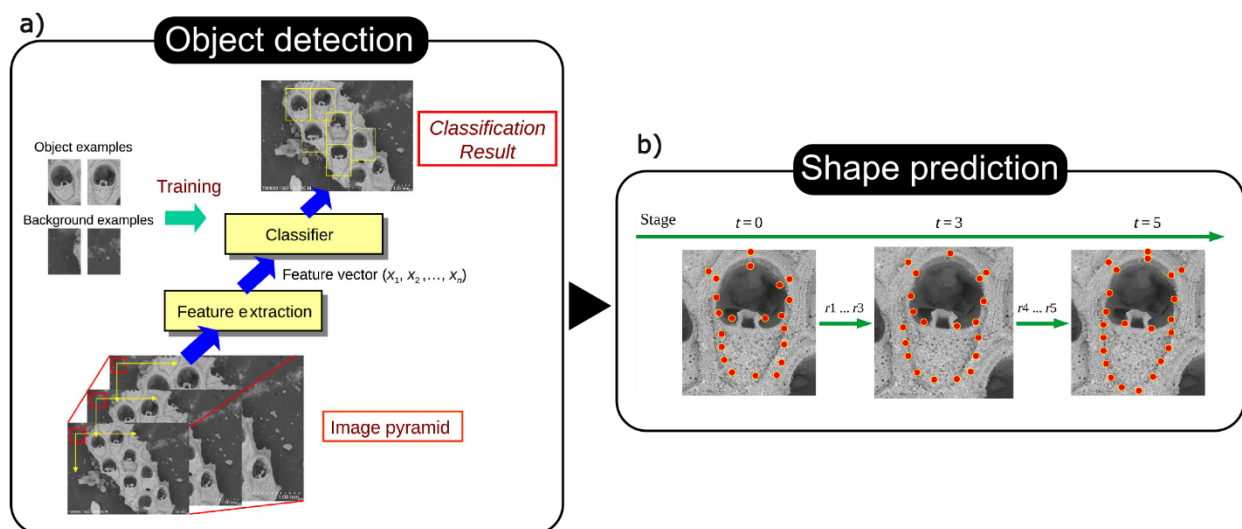


Figure 10. Workflow for automated landmarking in Porto and Voje (2020), showing (a) the object detection framework where a training set is used to first extract features and then perform classification, and (b) perform shape prediction using a cascade shape regression model to refine the landmark predictions. Reproduced under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

Landmark-free Geometric Morphometrics

Despite these advancements in landmark-based methods they remain limited as 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 (Goswami et al., 2019). The introduction of new landmark-free 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.

Landmark-free or homology-free methods aim to describe the entire shape of specimens without using landmarks. There are several methods within this family and currently most do not directly use AI, but we note a few that 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). These approaches allow shapes that do not share homology to be compared and limit the loss of geometric information, but they may be sensitive to factors outside of shape, including alignment, scaling

and modality (Mulqueeney et al., 2024b). 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 their elastic nature, can be used to quantify dissimilarities between shapes, register shapes together, and analyse morphometry, all without requiring landmarking. As described in Hartman et al., (2023), these methods can be categorised into two sections, those that apply to parameterised surfaces and those on non-parameterised surfaces (i.e., containing no known point landmarks). Techniques that incorporate these methods include large deformation diffeomorphic metric mapping (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 (Salili-James et al., 2022a). 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 reparameterisation (i.e., where on the boundary the curve starts/ends).

Diffeomorphic methods can also 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. Here, elastic shape analysis, allows for dimensionality reduction with a tool analogous to the classic ML tool, PCA, within the true space of the shapes of the objects in a dataset (Srivastava et al., 2011).

Given these advances, there has been widespread recent research on elastic methods focused on surfaces (Hartman et al., 2023; Jermyn et al., 2017; Pierson et al., 2021).

Methods using integral geometry belong to another family of approaches used to compare the surfaces of the selected objects (L. Wang et al., 2021; Lin et al., 2024). These methods can avoid issues of invariance and alignment to the same extent as the landmark-free approaches noted above, however, their efficacy at comparing disparate datasets currently remains untested, resulting in limited applications. Additionally, these approaches have drawn some concerns over ignoring homology (Mitteroecker and Schaefer, 2022), though there is great potential for reintroducing homology by combining them with AI tools for feature or trait extraction, as described above and demonstrated in Case Study 5.

Overall, these approaches could be used not only to study the shape of specific homologous elements, but also could accelerate studies of modularity and integration (Zelditch and Goswami, 2021), 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. As with landmark-based geometric morphometrics, 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 (Caro, 2017). Colour patterning can help researchers to recognise and discriminate between species and is commonly used in taxonomic, behavioural, and ecological studies (e.g., Sinpoo et al., 2019). 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 (Hoyall Cuthill et al., 2024). 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 (Hoyall Cuthill et al., 2024; Van Der Bijl et al., 2020). Automated and semi-automated methods have been developed to segment colour from images (He et al., 2022; Weller et al., 2024) and to quantify and analyse colour patterns (Maia et al., 2019).

ML offers a potential solution by processing vast amounts of data and using large image datasets of museum specimens for training and analysis (Case Study 7). ML uses feature extraction and classification to process images in species identification (Wäldchen and Mäder, 2018), enabling the comparison of 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. This reduces the workload by removing the need to manually process images (Maia et al., 2019). One successful implementation is the analysis of field-based camera trap images, with one study that focussed 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.

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 for processing colour information (Cooney, et al., 2022; He et al., 2022). This approach has also applied pose estimation methods to identify specific points of bird anatomy regions for extracting colour information per body part (He et al., 2023). 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, covering only 2% of the estimated 18,500 extant species of butterflies.

Case Study 7: Colour

The wings of butterflies (Lepidoptera) are often brightly coloured and conspicuous, and have evolved a high diversity of colour and pattern complexity across ~18,500 extant species. In many species colour patterns are often highly variable between sexes and are thought to have evolved through sexual selection, a hypothesis supported by behavioural studies (Panchen, 1980). Qualitative observations have suggested that male birdwing butterflies (Lepidoptera: Papilionidae) can be more brightly coloured than females (Vigneron et al., 2008), and that males from different regions may be visually more divergent than equivalent females. Hoyall Cuthill et al., (2024) tested these observations by using ML to quantify and characterise sexual and interspecific variation in wing patterning within this group. Euclidean spatial embeddings of

16,734 dorsal and ventral photographs of birdwing butterfly specimens (3 genera, 35 species, and 131 recognised subspecies) were generated by using deep learning with a triplet-trained CNN. In this method, CNN was optimally trained to place all images so that the Euclidean distances between images from the same species are comparatively close relative to distance to images of different species (Figure 11). CNNs are able to capture and compare features across multidimensional image embeddings and can access any variation within the image that is informative for their designated task, opening up new avenues of analysis which were not previously possible. The approach was able to reconstruct phenotypic evolution of wing patterns and quantify sexual disparity difference for the first time, revealing high male image disparity in some species and supporting divergent selection of wing patterns in males, consistent with sexual selection. The dataset represents the entire collection of the Natural History Museum, London (NHMUK), the largest and most comprehensive collection of birdwing butterflies on Earth, highlighting the high-throughput ability of ML methods.

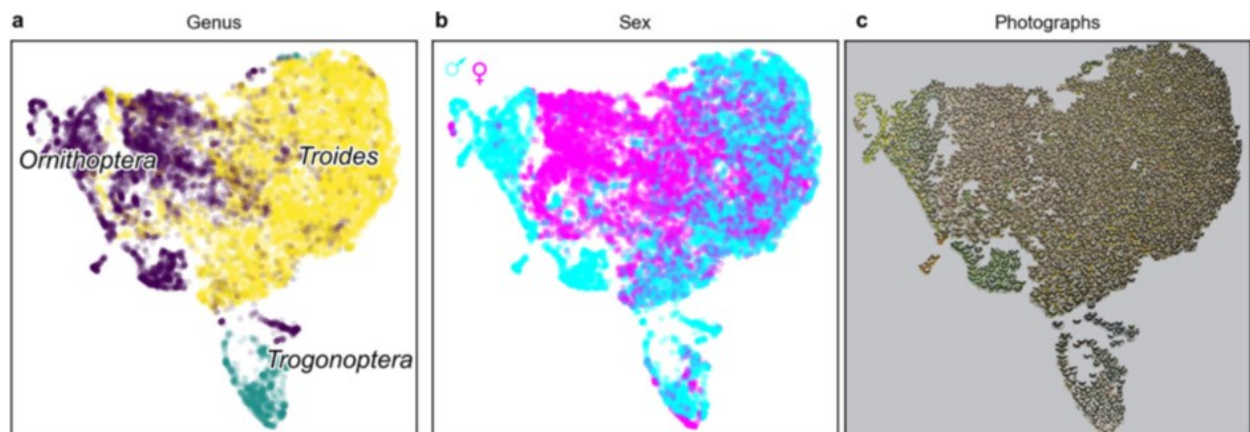


Figure 11. Patterns of phenotypic similarity in birdwing butterfly genera and sexes, from Hoyall Cuthill et al., 2024 and reproduced under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>). Points represent individual photographs,

and proximity represents image similarity. Shown are (a) genera, (b) sex, and (c) embedded images.

Pose Estimation

Pose estimation predicts the relative position of body parts to each other and is used to recognise different animal poses and their changes during locomotion (Pereira et al., 2019). While estimation is usually conducted on static images (Wei et al., 2016), these capabilities have also been adapted to recognise and quantify movement (Mathis et al., 2018). Indeed, parsing kinematic patterns from videos has become the hallmark of locomotion, biomechanics, and behavioural studies, contributing to the rapid transformation of these fields (e.g., Karashchuk et al., 2021). Pose estimation is a relatively simple computer vision problem, based on the annotation of training sets from images. 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 because motion blur also constitutes 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 important in the games and animation industries where there is a need to model animal behaviours and can be applied to evolutionary morphology. Manually editing each keyframe can be a painstaking task, and so physics-based models have been employed for years, e.g., 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).

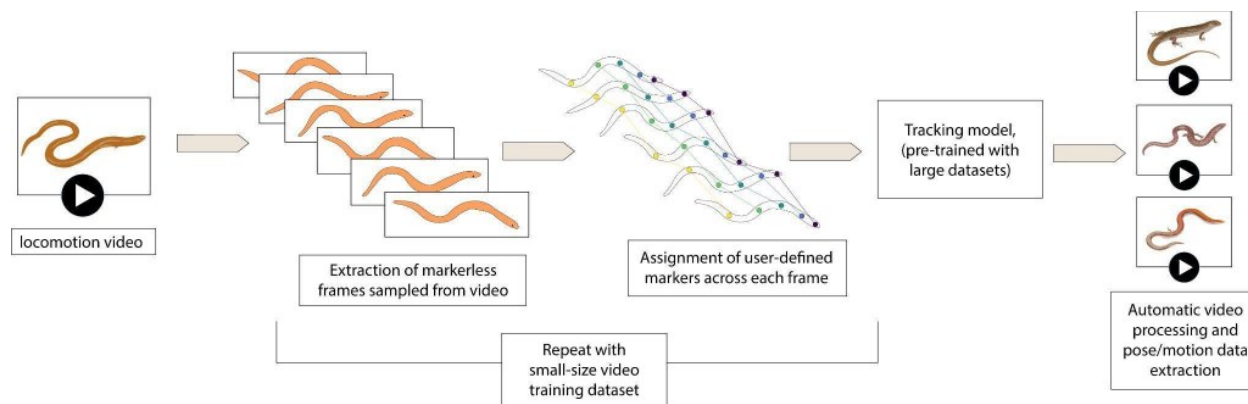


Figure 12. Simplified pipeline for markerless motion tracking and pose estimation from videos using DeepLabCut (Mathis et al., 2018). Limb-reduced skinks (Camaiti et al., 2023) are here used as an example of locomotion tracking.

Evolutionary Analysis

AI has the capacity to transform our ability to capture morphology for evolutionary analysis, as detailed above. Thus far, it has perhaps had the greatest impact on data acquisition, which has long been a primary bottleneck for studies of evolutionary morphology. Nonetheless, we are already seeing the implementation of AI approaches for the analysis of diverse questions in evolutionary biology but these have not reached the full potential applications of AI across the field yet. 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 promising 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. In recent years, more efficient methods using ML image clustering have become widespread in the classification of individuals into distinct species (Barré et al., 2017; Hsiang et al., 2019; Punyasena et al., 2012; 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. 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 each family, and the results demonstrate that this approach was accurate for family-level classification and, to a lesser extent, for topology estimation.

Morphometric data is also available for use in species classification, and in recent years ML methods have been employed to accurately classify species using morphometric data (e.g., Devine et al., 2023; Lin et al., 2024; Salifu et al., 2022; Case Study 8). For instance, Elsayed (2023) developed an automated approach using CNNs for identifying and classifying 2D images of tooth fossils from various animals, including sharks, elephants, hyrax, and primates.

Additionally, elastic shape analysis can be used as a pre-processing technique for machine learning by quantifying differences between object shapes, before feeding into classic ML tools such as K-Nearest Neighbour (KNN), as in Salili-James et al., (2022a). Here, diffeomorphic methods were used to quantify differences between the shapes of objects in various 2D image datasets, from gastropod shells to leaves. A KNN classifier was then trained to classify the genus and species, based purely on the morphology of the objects in the image. Moreover, there have recently been studies that have incorporated DL techniques with elastic shape analysis, such as Hartman et al., (2021), where a Siamese neural network was trained to predict geodesic distances between curves with diffeomorphic methods to analyse and classify objects such as the boundary curves of leaves from the notable Swedish Leaf Dataset (Söderkvist, 2016, 2001).

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.

Case Study 8: Specimen Classification from Images

In a recent study, 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 CNN (Su et al., 2015), PointNet (Charles et al., 2017), and VoxNet (Maturana and Scherer, 2015). The ADMorph dataset is valuable for developing and evaluating DL algorithms to precisely analyse and classify microfossil structures. Building on this foundational work, a subsequent project by Hou et al., (2021) further expands the application of DL by automating the segmentation process. This study delineated and classified approximately 500 fish microfossils within CT images, showcasing the potential of DL models to significantly streamline and enhance the accuracy of morphological analysis in paleontological research.

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 assignment of individuals as new taxonomic entities (Case Study 9). Genomic species delimitation methods have been extensively used in the last decade, including Bayesian species delimitation (Yang, 2015) and unsupervised ML algorithms predicting clusters of individuals from genomic data (Derkarabetian et al., 2019). More recently, CNNs have been employed to build a morphology-molecule network that integrates morphological and molecular data for species delimitation (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.

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 employing a maximum likelihood approach have commonly been used (Baylac et al., 2003; 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. Combined with the increasing ability to acquire image or trait data rapidly, they may allow for a more nuanced and comprehensive understanding of taxonomy.

On balance, 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, 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.

Case Study 9: Delimiting Species

Species delimitation methods have the possibility to discover new species in natural history collections. Hansen et al., (2020) created an image database of 65,841 museum specimens comprising 361 carabid beetles from Britain and Ireland (Figure 13). A pre-trained CNN model was fine-tuned on 31,533 images, validated on 25,334 images, and tested on 19,164, assigning 51.9% of test images to correct species and 74.9% to correct genus. The authors acknowledge that specimen size was a key factor in correctly identifying specimens, but model improvements may correct for this and the applications can be extended beyond high-throughput museum collections analysis to identifying species in the field using camera traps. Combined with further classification and clustering tools, such as with heatmap analysis (Hollister et al., 2023), these models can one day be used to identify potential new species.



Figure 13. Images of carabid beetles used by Hansen et al., (2020) to train and test a CNN model for identifying beetle species. Image has been cropped from the original, and is reproduced under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

Phylogenies - Building Trees

Evolutionary studies frequently require data structured on the relatedness between taxa in the form of phylogenetic trees. ML is increasingly applied to address some of the limitations of traditional methods (Mo et al., 2024; Sapoval et al., 2022). This includes often extremely high computational expense common to Bayesian and maximum likelihood approaches (Azouri et al., 2021; Azouri et al., 2023), model misspecification (Abadi et al., 2020; Burgstaller-

Muehlbacher et al., 2023), as well as issues with missing data for distance-based approaches (Bhattacharjee and Bayzid, 2020). However, the accuracy and scalability of these methods remains uncertain (Sapoval et al., 2022). Additionally, a significant obstacle for ML methods is the scarcity of training data for tree inference (Sapoval et al., 2022). Due to the uncertainty associated with phylogenetic inference, a ground truth of phylogenies is fundamentally unknowable, leading to a reliance on simulated data that may not accurately reflect evolutionary relationships (Sapoval et al., 2022).

In recent decades, genetic data has dominated phylogenetic studies, due to well-studied models of nucleotide evolution and the sheer quantity of genomic data available (Misof et al., 2014; Álvarez-Carretero et al., 2022). Consequently, recent reviews of ML approaches for tree building (Mo et al., 2024; Sapoval et al., 2022) have focused on molecular-based phylogenetics instead of morphology-based phylogenetics. However, for many extinct species, molecular data is often not available, meaning morphological data must be used (Lee and Palci, 2015).

Approaches that have been applied to sequence data have the potential to be adapted for use on 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). Simulated quartet experiments outperform traditional methods like maximum likelihood, especially in scenarios of high substitution heterogeneities, which is challenging for many standard models (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 (Goodfellow et al., 2014).

While ML methods to estimate evolutionary relationships using genetic data have begun to be explored, either by approximating distances between taxa or by directly inferring topologies, application to morphological data remains challenging (Case Study 10). For molecular phylogenetics, there are many complex substitution models available to describe the evolution of sequence data (Hasegawa et al., 1985; Tavaré, 1986). However, the same cannot be said for morphological evolution where the underlying processes are more difficult to model (Lee and Palci, 2015) and where there is a lack of clearly defined smallest units of change across the tree of life. Methods such as Phyloformer (Nesterenko et al., 2022; Case Study 10a) still rely on models of sequence evolution to compute topologies. 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 (Case Study 10b). 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.

Estimating nucleotide substitution models for large sequence datasets through traditional maximum likelihood methods are computationally intensive. More recently, DNNs were used to create ModelTeller (Abadi et al., 2020) and ModelRevelator (Burgstaller-Muehlbacher et al., 2023), two approaches to phylogenetic model selection that focus specifically on identifying the most appropriate substitution models for large datasets which are otherwise not achievable due to computational constraints. With continuous increases in the size of datasets used for generating phylogenetic hypotheses, methods such as these will be key to assess most suitable models before phylogenies are built. While these DNNs both focus on molecular substitution

models, their existence opens the possibility of developing new systems for selecting morphological evolutionary models.

One common issue for several phylogenetic methods (including maximum likelihood, Bayesian, and maximum parsimony) regardless of data type is the use of heuristic searches. In the case of Bayesian approaches, model parameters (e.g., tree topology, branch length) are adjusted and the likelihood 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 applied to improve the 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., 2021, 2023).

Another major challenge in both molecular and morphological phylogenetic studies is the impact of missing data, especially for distance-based methods where many of the most commonly used methods (e.g., Neighbour Joining) require data with no missing entries (Bhattacharjee and Bayzid, 2020). 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 and 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.

Case Study 10: Creating Phylogenetic Frameworks

A) Molecular and ML Tree Building: phyloGAN and Phyloformer

Machine learning based phylogenetic inferences have been limited to inferring unrooted tree topologies for quartets of taxa as the number of plausible trees increase exponentially with increase in the number of taxa (Felsenstein, 1978; Suvorov et al., 2020). The phyloGAN model is an ML approach that utilises heuristic search strategies through GAN to build trees with molecular data (Smith and Hahn, 2023). It 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 (Figure 14). 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 as demonstrated using seven species of fungi, 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.

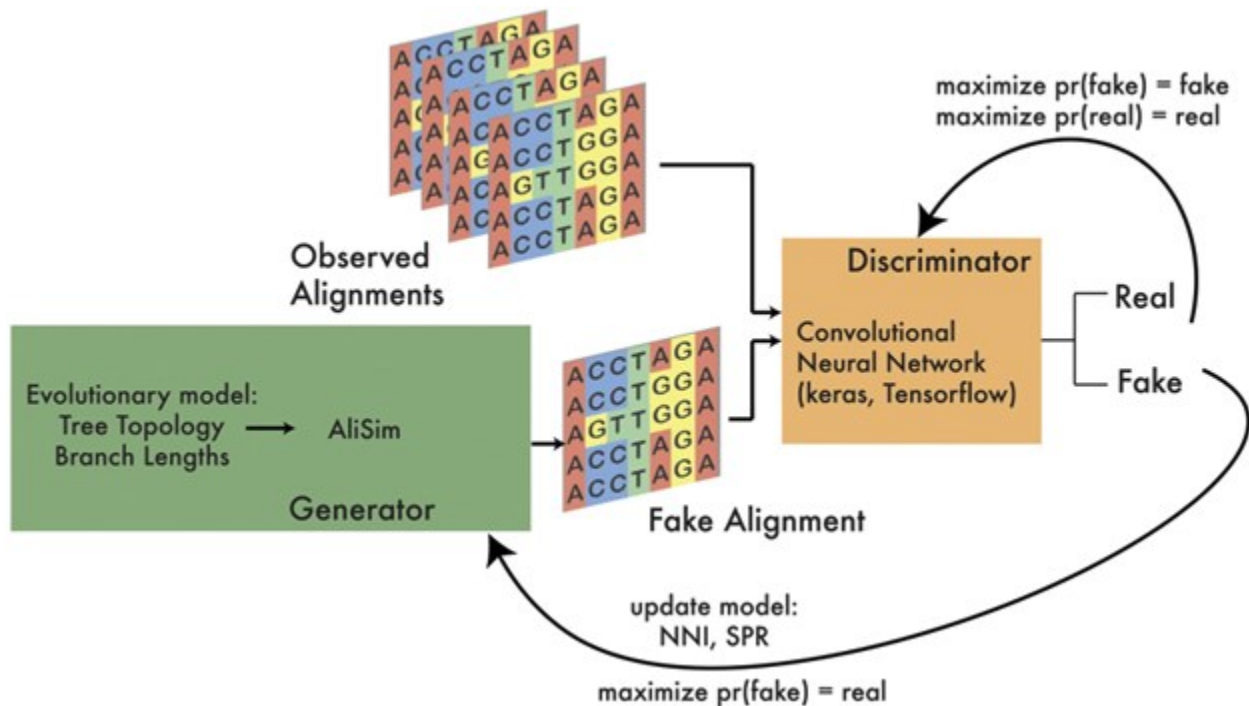


Figure 14. Overview of phyloGAN (Smith and Hahn, 2023) wherein a generator generates tree topologies with branch lengths utilising nearest neighbour interchange (NNI) and subtree pruning and regrafting (SPR) methods. These trees are then evaluated within the discriminator to identify real versus generated data. Reproduced under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

B) Convergence in Morphological ML Tree Building

One of the key challenges in utilising morphological data to build phylogenetic trees has been morphological convergence. Kiel (2021) used feature extraction to estimate family-level classifications of bivalves and by grouping them into orders and subclasses, has attempted to

overcome the limitation posed by convergence of traits. 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.

C) Supplementing Morphological Data with “Known” Phylogenetic Data

Adaimé et al., (2024) present a novel method incorporating pre-existing phylogenetic information into ML training. Pollen grains were classified into “known” or novel taxa by multiple CNNs trained on morphological characters (shape, internal structure, and texture). 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 uses “known” phylogenetic positions of taxa as a template to guide how the morphological characters are used to estimate phylogeny, and 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 (Figure 15). They tested the accuracy of the method by taking taxa that had “known” phylogenetic placements and treating them as if they were novel. The model placed these pseudonovel taxa 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. However, there are potential concerns over the assumption of a ground truth in phylogenetics.

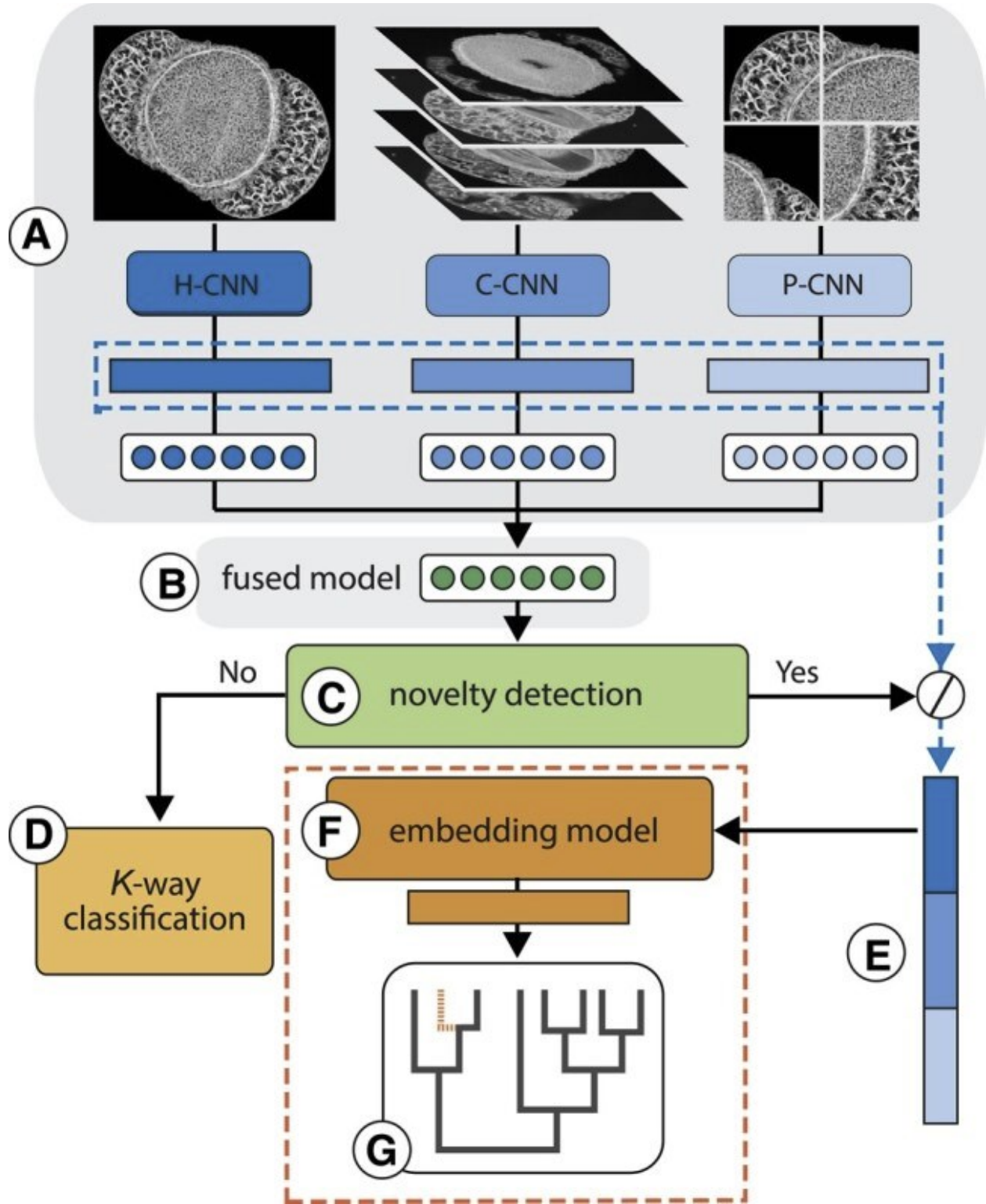


Figure 15. Three neural networks trained in Adaïmé et al., (2024) to score the shape, internal structures, and texture. The scores are combined and images are classified into known versus new taxa. Reproduced under a Creative Commons CC-BY-NC-ND license.

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 (Álvarez-Carretero et al., 2022). 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 of AI to reconstruct trait evolution within a phylogenetic framework has been theoretically documented. For instance, Ruder (2017) described a multi-task learning approach that involves an ML framework consolidating data from various tasks. It is achieved through an algorithm that minimises the variance of estimators by employing a penalty term to align models more closely, facilitating the simultaneous estimation of ancestral states for multiple characters. Similarly, Ho et al., (2019) illustrated the theoretical application of ML to the ancestral estimation of phenotypic traits through a multi-task learning approach applied to Brownian Motion models of continuous biological traits. The study showed that this approach enhanced ancestral

estimations compared to maximum likelihood models, albeit with a minor bias introduced in the phylogenetic estimates.

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). This would allow the assessment of trait covariations, studies of modularity and integration, changes through time using existing phylogenies, and probabilities of key innovations versus gradual variations.

ML approaches could also facilitate the comparison of simulations across trees. Furthermore, ML 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 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 (Niemi, 2020).

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 (McGhee, 1980, 1999; Simpson, 1984). They provide a visual representation of natural selection-driven trait space across the landscape of an adaptive landscape, where peaks of specific traits reflect higher fitness compared to putative trait space across the landscape (Arnold, 2003). Over evolutionary time, genetic variation, mutation, recombination, and natural selection drive the population towards regions of higher fitness (Arnold et al., 2001). 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 (e.g., Martin and Wainwright, 2013). 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. Neural networks have been suggested to provide more accurate FEA results than boosting regression trees or random forest algorithms (Vurtur Badarinath et al., 2021). Additionally, AI has been increasingly applied to FEA-based biomechanical modelling (Galbusera et al., 2020; Liu, 2019; Mooloodi 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). 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 (the sum of phenotypic traits) and the environmental context in which they evolved (e.g., Benevento et al., 2019; DeGusta and Vrba, 2005; Panciroli et al., 2017; Stubbs and Benton, 2016). The end goal of many studies using this approach is to assign an ecomorphological characterisation to phenotypic traits and to parse their ecological signal (e.g., Barr, 2018; Fortuny et al., 2011). 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 methods such as random forest (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 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 econometric 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, using 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 introduction (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 further 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 is 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. There are also numerous challenges with making AI tools accessible to non-specialists and finding affordable and sustainable solutions for the storage, annotation, and processing of datasets that are larger in both number and size. These areas should be the focus of efforts over the coming years. While we have detailed applications of AI to several research areas in 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 using AI in research.

Emerging fields

Retrodeformation - Several studies have demonstrated that fossil data are critical for accurately estimating phenotypic evolution through deep time (e.g., Slater et al., 2012; Goswami and Clavel, 2024, and references therein). A common challenge in palaeontology is encountering fossils that have undergone taphonomic distortion via brittle or plastic deformation (Kammerer et al., 2020; Schlager et al., 2018). This distortion can severely hinder attempts to assess and quantify intra- and interspecific shape by introducing non-biological variation. Consequently, in addition to the lack of integration in phylogenetic analyses, fossil data are often excluded from geometric morphometrics and phylogenetic comparative methods. Retrodeformation is the process of restoring the original shape of an object by reversing taphonomic distortion (Herbst et al., 2022; Lautenschlager, 2016). While landmark- and symmetry-based procedures to manually perform these operations are available (Schlager et al., 2018), they are time-consuming and can only be applied to relatively small datasets, limiting 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 recognise 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, thereby 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 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. Similarly, Zeng et al., (2021) used a support vector machine algorithm to detect small geological faults. Such methods could be adapted to estimate the extent of brittle and ductile deformation a fossil has undergone, thereby enabling evolutionary morphologists to apply the opposite forces to correct the distortion.

Histology - Histology examines the microscopic structure and morphology of tissues, encompassing both contemporary and fossil tissues in the field of palaeohistology. Historically, palaeohistology has provided insights into growth, physiology, and development, while its application has expanded to investigate tissue form and function. For instance, Bailleul et al., (2019, 2012) explored the function of duck-billed dinosaur dental batteries through palaeohistological techniques. The advent of AI tools has significantly advanced histology, particularly in histopathology, enhancing cancer recognition and clinical oncology (Shmatko et al., 2022). AI holds promise for increasing throughput in pattern recognition tasks. Current applications of AI in biological research include the quality assessment of histological images (Haghighat et al., 2022) and the characterisation of herbivore diets through micro-histological analysis (Filella et al., 2023). Moreover, neural networks have been employed to identify primary and secondary osteon regions, producing segmented maps of various osteon regions. This segmentation, in conjunction with phylogenetic analysis, has elucidated developmental pathways leading to miniaturisation in theropod dinosaurs (Z. Qin et al., 2022). The potential for AI in histological studies is substantial, particularly within the context of investigating evolutionary morphology using landmark-free morphometrics, marking it as a promising avenue for future research.

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. Different AI algorithms have been applied in a variety of genome-wide association studies related to human health, helping to link genetic variants to different pathologies in complex ways (Long et al., 2023). Neural-network approaches have also been developed to both understand the association between small genomic mutations and clinical phenotypes (Mieth et al., 2021) and also the complex correlation between microbial communities and diseases (Y. Liu et al., 2021). In an agricultural setting, similar neural network approaches have been used to predict potential phenotypes in genetically modified rice crops (Islam et al., 2023). More complex approaches have recently been tested on both human and agricultural datasets and have been found to predict not just the genomic or phenomic component, but also potential new associations between the two through the use of weighted deep matrix GPA (Tan et al., 2022). GPA approaches have clear implications for the future of evolutionary biology and phenomics studies, for example by allowing to connect morphological changes with specific mutations. Though these methods are still in their infancy and have yet to find wider applications outside of the medical and agricultural fields.

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 recognise diseases and malformations (e.g., Al-Saaidah et al., 2017; Jeanray et al., 2015). In evolutionary developmental biology (evo-devo), these methods have only recently been applied to phenotype identification. A few pilot studies have been conducted using both image and morphometric 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). Through further development of these methods and their applications to non-model organisms, it will be possible to conduct more thorough studies comparing developmental phenotypes across multiple lineages.

Data Engineering - Focus should be not only on potential fields and AI methods but also on the morphological data itself. Data engineering involves the preparation of data before any analysis or methods 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 (., MorphoSource: Boyer et al., 2016; Phenome10K: Goswami, 2015; DigiMorph: Rowe, 2002), the volume of usable data is increasing. In order to take full advantage of the potential of AI and “Big Data” in evolutionary morphology studies, firstly the previously collected data should be transformed into AI-ready formats. This data is then suitable to be used to explore 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 methods to better suit the specific data. Preparing these large phenomics datasets for algorithm training is the first step to integrate AI methods into large scale phenomics studies.

Accessibility and Considerations

Until very recently, most AI models were built and applied using Python libraries such as Caffe, TensorFlow, and PyTorch (Abadi et al., 2015; Jia et al., 2014; 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 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 models without investing in local GPUs. Furthermore, with the expansion of large language models in the public domain, via services such as ChatGPT (Brown et al., 2020), many researchers can now use AI to learn how to code, enabling them to program and train their own models (Cooper et al., 2024).

Despite these advancements, there are many challenges and certain aspects that require a degree of caution. AI relies on the data it has been trained on, and the people who have developed it. Biases in data as well as cognitive bias, can cause or emphasise biases in the algorithm, and can lead to incorrect results (Mehrabi et al., 2021; Zhang et al., 2022). Attention must also be given to data cleaning and pre-processing to mitigate unrefined training data. Additionally, when it comes to data within the natural sciences, especially within the public domain, particular attention must be given to maintain consistency during the data processing stages, for example, to ensure morphological or taxonomic annotations are following standard framework.

Moreover, even with cloud-based AI services, storage and processing power are expensive and will be limiting factors for many researchers. 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 [see associated cover page file].

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

	extracting scientific words/taxonomic names from journal articles.			
TaxoNERD <i>(python library)</i>	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)

<p>pytesseract</p> <p>(python library)</p>	<p>Optical character recognition (OCR) to turn images to text. Python wrapper for Google's tesseract engine.</p>	<p>Images</p>	<p>Python</p>	<p>(Dome and Sathe, 2021; "Tesseract documentation," 2021; Hoffstaetter, 2022)</p>
<p>Google Vision</p>	<p>Deep Learning Application Programming Interface to perform OCR.</p>	<p>Images</p>	<p>N/A</p>	<p>(Walton et al., 2020; "Vision AI," n.d.)</p>
<p>Deep Learning</p>				

<p>PyTorch, TensorFlow,</p> <p><i>(python libraries)</i></p>	<p>DL frameworks.</p>	<p>Tabular data (arrays, matrices etc.)</p> <p>Image based data</p> <p>Text</p> <p>Audio</p>	<p>Python</p>	<p>(Abadi et al., 2015; Paszke et al., 2019)</p>
<p>Scikit-learn</p> <p><i>(python library)</i></p>	<p>Tools for ML. Classification methods (e.g., Support Vector Machine), clustering methods (e.g., K-means clustering), dimension reduction (e.g., PCA) and neural networks.</p>	<p>A variety of datatypes, from tabular data to image and sound data etc.</p>	<p>Python</p>	<p>(Pedregosa et al., 2011)</p>

<p>PIL, scikit-image, open-cv-python</p> <p><i>(python libraries)</i></p>	<p>Image processing and computer vision tools. For example, thresholding, contour extraction with Snakes (Active Contour).</p>	<p>Images</p>	<p>Python</p>	<p>(van der Walt et al., 2014)</p>
<p>Monai, Biomedisa</p> <p><i>(python libraries)</i></p>	<p>DL tools that are designed for processing medical images.</p>	<p>Images, especially medical images</p>	<p>Python</p>	<p>(Cardoso et al., 2022; Lösel et al., 2020)</p>
<p>LeafMachine</p>	<p>DL and CV tools for trait extraction and measurement,</p>	<p>Botanical images, particularly</p>	<p>Python or GUI</p>	<p>(Weaver and Smith, 2023)</p>

	from botanical images.	herbarium sheets		
Image processing software				
ORS Dragonfly, Avizo-Amira, VGSTUDIO MAX	Softwares for processing and segmenting medical and cross-sectional images. AI-based segmentation methods are also supported.	Medical images	The software is not open-source; but it supports Python scripting	(Dragonfly: Comet Technologies Canada Inc., 2022; Avizo: Thermo Fisher Scientific, 2021)

<p>3D Slicer, ImageJ, ilastik</p>	<p>Open-source softwares for processing medical and cross-sectional images. Users can add extensions such as SlicerMorph, and Weka Segmentation, or build new extensions.</p>	<p>Medical images</p>	<p>C++, Python, Qt</p>	<p>(Arganda-Carreras et al., 2017; Berg et al., 2019; Kikinis et al., 2013; Rolfe et al., 2021; Schneider et al., 2012)</p>
<p>Tools can be used in evolutionary morphology</p>				
<p>MeshCNN</p>	<p>Mesh classification and segmentation. Can be used for segmenting 3D</p>	<p>3D mesh models</p>	<p>Python</p>	<p>(Hanocka et al., 2019)</p>

	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)
FloralIncognita	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 ecological niches of taxa.	Species occurrence data, environmental rasters	Java	(Phillips et al., 2024)

Hierarchy-guided neural network (HGNN)	Combining hierarchical classification information with phenotypic data.	Images	Python	(Elhamod et al., 2022)
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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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