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THE CONCEPTUAL LANDSCAPE OF ANCIENT DNA RESEARCH: CURRENT STATE AND FUTURE PROSPECTS

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Abstract

Recent developments in next generation sequencing technologies have triggered a rapid growth in both the volume of ancient DNA (aDNA) sequence data and the number of publications concerning this interdisciplinary field. As the size of scientific literature regarding aDNA and complexity of the field have increased tremendously, it has become difficult to decipher research trends and identify central issues within it based on personal knowledge alone. In this article we've used a bibliometric approach to outline the scope and structure of aDNA research. Publication records concerning aDNA, paleogenetics and paleogenomics from the Web of Science were used to generate a dataset for the creation of bibliographic maps based on text co-occurrence, bibliographic coupling and author co-citation patterns. Three major research areas, five narrower research fields and 13 smaller highly interconnected sub-fields of aDNA studies were identified at different levels of clustering resolution in text co-occurrence analysis. Although the majority of the studies are centered around human population history, the highest average number of citations is associated with the articles, regarding the application of aDNA to evolutionary research. At the same time the most rapidly developing avenue of aDNA research is connected with reconstruction of environmental history (particularly with the use of environmental DNA approach) and conservation genetics.

***Keywords**: Paleogenetics, Ancient DNA, Environmental DNA, Bibliometrics, Molecular paleontology, Conservation paleontology, Conservation biology, Archeology*

Introduction

The earliest publications in the area of paleogenetics outlined the possibility of molecular "restoration" studies of extinct taxa based on comparison between homologous amino acid and nucleotide sequences in contemporary organisms and contributed to the establishment of the molecular clock concept [1]. This area of research can be attributed to quantitative paleogenetics, which continues to develop. However, the works dating back to the early 1980s, reported the possibility of retrieval of ancient nucleic acid sequences from various biological substrates and their direct investigation [2, 3]. It opened up a completely new branch of paleogenetics, the study of aDNA as degraded genetic material, recovered from various substrates, such as biological remains, sediments and soils. Since the time this relatively young discipline has already crucially transformed many scientific fields [4].

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Advancements in techniques of extraction and sequencing of aDNA, application of second-generation sequencing technology in this area of research have pushed the time limit of aDNA recovery to as deep as early Middle Pleistocene [5]. However, breaching even this age boundary, as a number of authors have concluded [6], is entirely possible. The scale of aDNA studies has already expanded to whole populations. Thus, due to recent technological advances, this interdisciplinary field of research has grown rapidly and its complexity has increased tremendously, making it hard to decipher research trends and identify central issues within the field based on personal knowledge alone. However, deciphering of a conceptual framework is vital, especially in young disciplines [7-9]. In this article we want to outline the scope and structure of current aDNA research, highlight new frontiers in development of this field, and visualize the discipline using bibliometric approach.

Survey methodology

Bibliometrics is a quantitative analysis of publications and their citations, which is used to evaluate research performance and assess shifts in research focus using citations data [10]. It can also be used to map a discipline for characterization of its structure and dynamics [9]. Visualization of the intellectual landscape of a field can be done by means of network modeling. It can show the set of questions, the scientific community is currently addressing [9].

In order to create bibliometric networks to represent the structure of aDNA research, the data were downloaded from Web of Science™ (WoS) Core Collection, which contains over 1.4 billion cited references going back to 1900s from over 20000 journals. To make sure, that the searched phrases are significant for the publication, WoS was searched by “Topic”, which implies searching in the title, abstract, author keywords and Keywords Plus® fields within a record. The articles were captured, if they contained any of the following search terms: “paleo*genom*”, “paleogenetic*”, “ancient DNA”, “aDNA”. Insertion of the wildcards into the first two search terms was used to expand the topic search to include records with variations of the prefix “paleo” with the root “gene” to represent the full breadth of the field. At the same time the variations of the term “Paleogene” were omitted by using such inquiry structure.

Construction of bibliometric maps and their visualization was carried out with VOSViewer software [11, 12]. It uses a VOS (which stands for “visualization of similarities”) mapping technique for constructing distance-based maps [13]. It is an alternative to multidimensional scaling, which generally produces better structured maps [14]. The data from WoS can be directly imported into the VOSViewer to visualize relationships between authors, keywords and sources of information, represented as nodes in a network. They can be grouped according to strength of their connection so that nodes within the same group are more densely connected, than those between different groups.

The structure and dynamics of aDNA research was explored in this study using a combination of bibliometric analyses. Two different types of mapping approaches were utilized: based on text (co-occurence) data and based on bibliographic data (co-authorship, bibliographic coupling). Bibliographic coupling network construction was carried out with sources (journals) as units.

Results of the survey

Web of Science query results

Topic search in the WoS Core Collection for the aforementioned phrases yielded 4245 records. The number of records produced per year grows rapidly from 1990-s (Fig. 1). Average number of citations per publication, according to WoS assessment, is 25.97. Distribution of them among WoS categories shows that the field is highly multidisciplinary, involving various biological, anthropological, medical, geological and geographical subjects. This is also reflected in a range of journals, in which the articles concerning aDNA have been published. They are dedicated to anthropology, archaeology, ecology, evolutionary biology and molecular biology as well as multidisciplinary studies.

The captured records were downloaded in a tab-delimited format using "Full Record and Cited References" option. It resulted in 9 separate files (due to a limit of such type of export to 500 records in the WoS), which were subsequently imported into VOSViewer for further analysis.

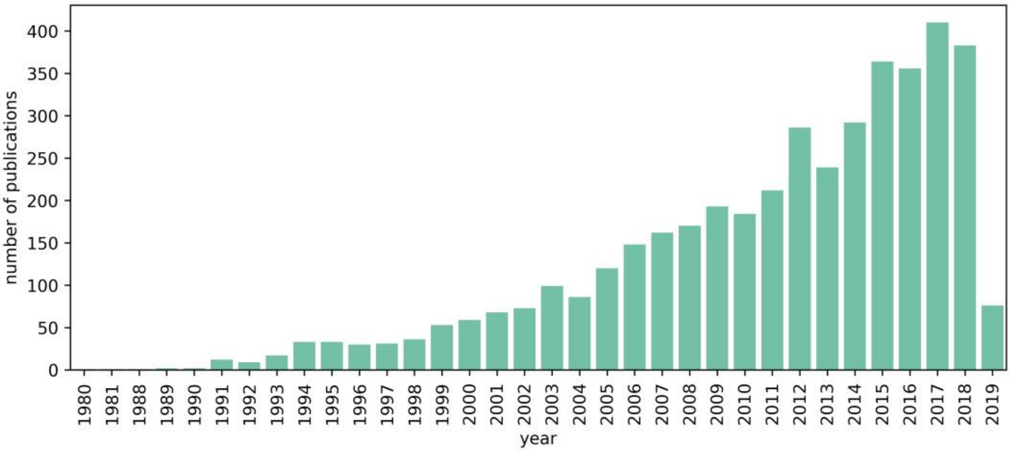

Fig. 1. Number of publications from 1980 to the spring of 2019. The histogram is based on the records, resulting from searching the following terms in the WoS Core Collection: "paleo*genom*", "paleogenetic*", "ancient DNA" and "aDNA" (the database was accessed in April 2019)

Text co-occurrence networks

In order to decipher sub-fields of aDNA research, text co-occurrence visualizations were created in VOSViewer [15]. In this type of visualizations, keywords from documents are mapped so that the more frequently words co-occur, the closer they reside on the map. Clusters of keywords in this type of map represent various sub-fields of a discipline. To detect fast-growing emerging topics of research and identify research frontiers, temporal overlays can be applied in VOSViewer to networks, constructed using this approach. To identify the most actively cited terms (and sub-fields), overlays, representing citation scores, such as average number of citations received by the documents in which a term occurs, can be applied. The sizes of the nodes, which represent terms, can be adjusted to reflect the number of occurrences of each term in the selection of publications to identify the most frequently used terms.

After the importation of bibliographic database files from WoS into VOSViewer, terms were extracted from titles and abstracts and counted using "Binary Counting" option (which implies taking into account only the presence or absence of a term, not the number of occurrences of it in a document). Minimum number of occurrences of a term was set to 10 and 60% most relevant terms were selected. Data cleaning was performed using a thesaurus file, containing information on possible synonyms for merging them and a list of general words and words, not reflecting research topics, such as names of taxa, geographical locations, and time intervals to be omitted (for example, such words as "*Mammuthus primigenius*", "month", "length", "base", "17th century", "Italy", "new opportunity", "limited amount" were in this file). Additional manual inspection and cleaning was done apart from application of the thesaurus file. The final selection consisted of 759 terms. The analysis was performed with 4 levels of clustering resolution (0.5, 0.8, 1.1, 1.8) to examine the structure of aDNA research with different levels of detail.

Structure of aDNA research field according to the results of the text co-occurrence analysis

Clustering with resolution set to 0.5 revealed two major modules in aDNA research (Fig. 2A). The most frequently occurring terms among the 407, forming the first module, include: “PCR”, “protocol”, “contamination”, “DNA extraction”, “tissue”, “teeth”, “skeletal material”, “skeleton”, “recovery”, “disease”. Most of them are connected with technical implementation of aDNA research. The second module consists of 352 terms and is related to theoretical interpretation of the data, obtained from aDNA analysis. Among the most frequent terms in this cluster are: “genetic diversity”, “haplotype”, “haplogroup”, “migration”, “extinction”, “domestication”, “clade”, “decline”, “ancestor”, “society”, “demographic history”. The majority of them is connected with population genetics and phylogenetics, as well as problems, which are resolved by means of these approaches.

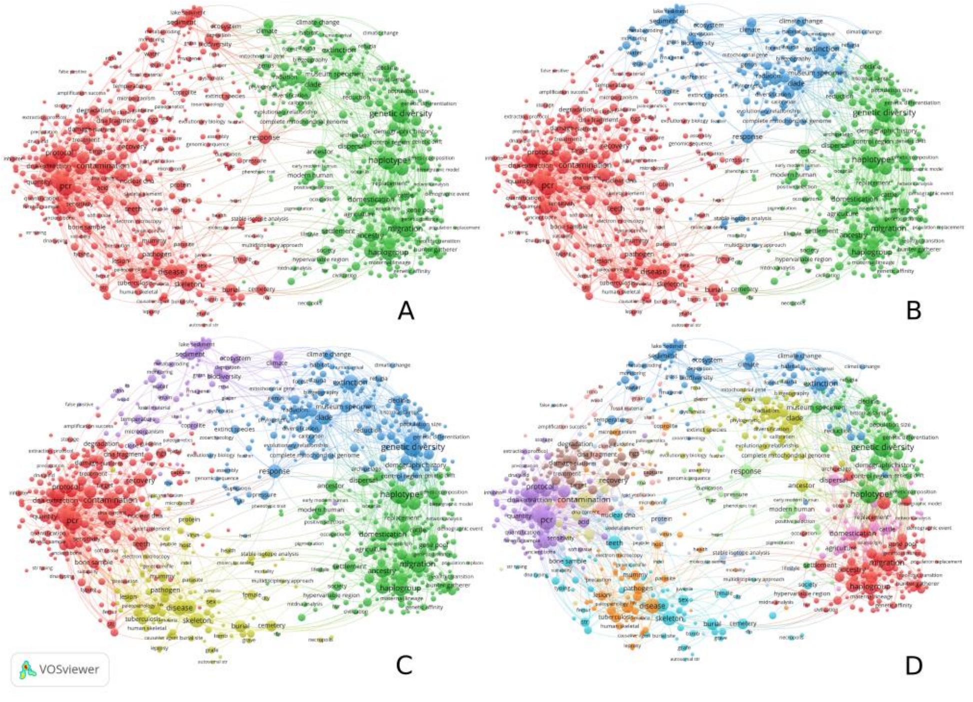

Fig. 2. Intellectual landscape of aDNA research field. Visualization of text co-occurrence networks of the 60% most relevant terms, occurring at least 10 times in the publications, regarding aDNA. Nodes are weighted by the number of occurrences of each term. Colors signify the revealed modules of terms with clustering resolution set to 0.5 (A), 0.8 (B), 1.1 (C) and 1.8 (D)

At the clustering resolution 0.8, the third major module appears at the intersection of the two modules, described above (Fig. 2B). This module consists of 174 terms, the most frequent of which are: “extinction”, “response”, “clade”, “climate change”, “extinct species”, “sediment”, “biodiversity”, “ecosystem”, “water”, “systematic”. This module is largerly related to conservation biology. The first module, which is left with 333 items, remains dominated by terms, connected with technological side of aDNA research. The terms, related to pathology also reside in this module. The second module, along with the terms, related to population genetics and phylogenetics, becomes relatively enriched with those connected with human history and culture (such as “society”, “civilization”, “domestication”, “modern human”, “agriculture”). This module consists of 252 terms. Thus, 3 major modules of aDNA research can be distinguished. The first is centered around technological aspect of aDNA research, the second – around population genetics and human history, the third – around application of aDNA to various problems related to conservation biology. Here and below numbers are assigned to the modules according to their volume (from the larger ones to the smaller ones).

When the clustering resolution is set to 1.10 and the minimum cluster size – to 20, the structure of aDNA research is represented by 5 modules (Fig. 2C). At this resolution the module, related to paleopathology, historical forensics and genetics of human individuals (at sub-population level) emerges primarily from the module, connected with technological sphere of aDNA research. The major module, considered to be connected with conservation science becomes split into two. Most of the terms, forming one of them are related to environmental DNA research. This module is largely associated with application of paleometagenomics to reconstruction of changes in plant and animal communities over time. The second module, besides the rest of the terms from the “conservation” module, includes significant number of the terms from the second major module. As a result, many of the terms, forming this module, are centered around extinction, phylogenetics, genetic diversity and its dynamics. The rest of the second major module is connected with the history of human populations and their interactions with environment, including domestication.

More detailed picture of aDNA research field structure was examined using clustering resolution 1.80 with minimum cluster size set to 10. 13 modules were detected (Fig. 1D). Labels were assigned to each of them based on the term composition.

Relationships between the modules of the last two levels of resolution and their abbreviations used in the text below are represented in the Table 1. Assignment of the subordinate modules is based on the distribution of the majority of the terms from them among the larger modules.

Table 1. Association between the modules revealed in the text co-occurrence analysis of aDNA research field at the clustering resolution 1.80 with those at the clustering resolution 1.10. The assignment of the subordinate modules is based on the distribution of the majority of the terms from the smaller modules among the larger ones. Names are given to the modules based on their term composition

Modules at clustering resolution 1.10	Modules at clustering resolution 1.80
1. Techniques and technologies involved in aDNA research	Extraction and amplification of aDNA (EX) Next generation sequencing of aDNA (NGS) Quality control in aDNA research (QC)
2. History of human populations and their interaction with environment (including domestication)	Historical genomics of human populations (HP) Paleogenomics of plant and animal domestication (D)
3. Genetic diversity and its changes through time	Genetic diversity studies (GD) Phylogenetic studies (PH) aDNA research in evolutionary biology (EV)
4. Paleopathology and historical forensics, paleoproteomics	Historical forensics (F) Paleopathological studies (PP) Paleoproteomics (PRT)
5 . Environmental history, paleometagenomics	Environmental paleogenetics (EP) Taphonomy of aDNA and its potential sources (T)

Dynamics of aDNA research field according to the results of text co-occurrence analysis

To understand dynamics of aDNA research field, network visualization was created, showing average publication year of the articles, in which each term figures as well as numbers of citations for each term (Figs. 3 and 4). Average year of publications per module (defined at clustering resolution 1.80) was assessed. It varies between 2009 and 2013 (Fig. 3B). This score is the highest in two modules: in the module EP, connected with application of aDNA research to the reconstruction of environmental history and biodiversity changes through time and in the module D, related to domestication studies. They are also generally the youngest sub-disciplines within aDNA research (Fig. 3C).

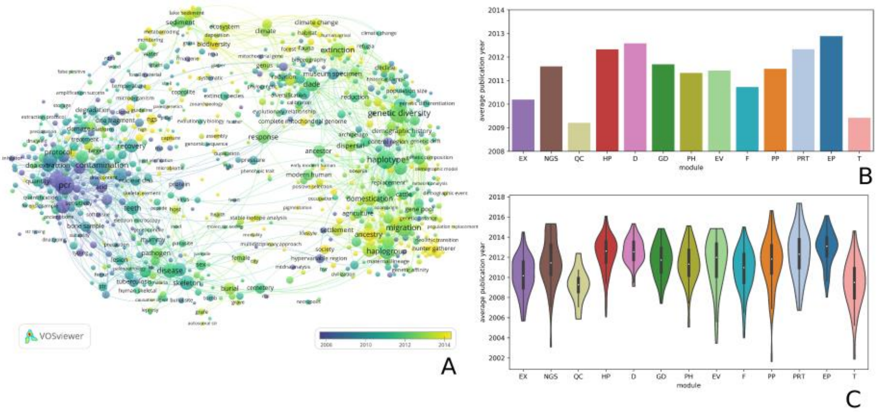

Fig. 3. Dynamics of aDNA research field. (A) Visualization of text co-occurrence network of the 60% most relevant terms, occurring at least 10 times in the publications, regarding aDNA with a temporal overlay. Colors signify the average publication year of the articles, in which a term figures with warmer colors representing more recent terms. (B) Average publication year for each module, defined with clustering resolution set to 1.8. The colors of the bars correspond to the colors of the modules in the Fig. 2D. (C) Violinplot, showing distribution of the number of terms among publication years for each module (the "violins" are scaled to equal width). The colors of the "violins" correspond to the colors of the modules in the Fig. 2D. Abbreviations used for the names of the modules: EX – extraction and amplification of aDNA, NGS – next generation sequencing in aDNA research, QC – quality control in aDNA research, HP – historical genomics of human populations, D – paleogenomics of plant and animal domestication, GD – aDNA application in genetic diversity studies, PH – phylogenetic studies, EV – aDNA research in evolutionary biology, F – historical forensics, PP – paleopathological studies, PRT - paleoproteomics, EP – environmental paleogenetics, T – taphonomy of aDNA and its potential sources

However, the modules with the highest average citation scores are different (Fig. 4). One of them (EV) is connected with the studies of evolutionary processes and genotype-phenotype interactions with the aid of aDNA and the other module is related to application of NGS methods in aDNA research (Fig. 4B).

However, the results, presented above, give only rough general overview, because the scores are averaged for each module. In order to decipher emergent topics of aDNA research, 40 most recent terms, according to the average publication year of the articles, in which they occur, were captured from the aforementioned dataset. Only the terms with average number of citations of the articles, in which they occur, above 3 were taken into account. The modules, to which the terms belong at three clustering resolution levels, were determined.

Most of the terms from the selection belong to two modules: the module EP and the module NGS (Fig. 5). The EP module, as has been mentioned above, is connected with application of aDNA to the study of environmental and biodiversity changes. This module is one of the most closely related to conservation biology (the term "conservation biology" is present in this module). It's worth noting, that its average publication year is one of the highest among all the modules.

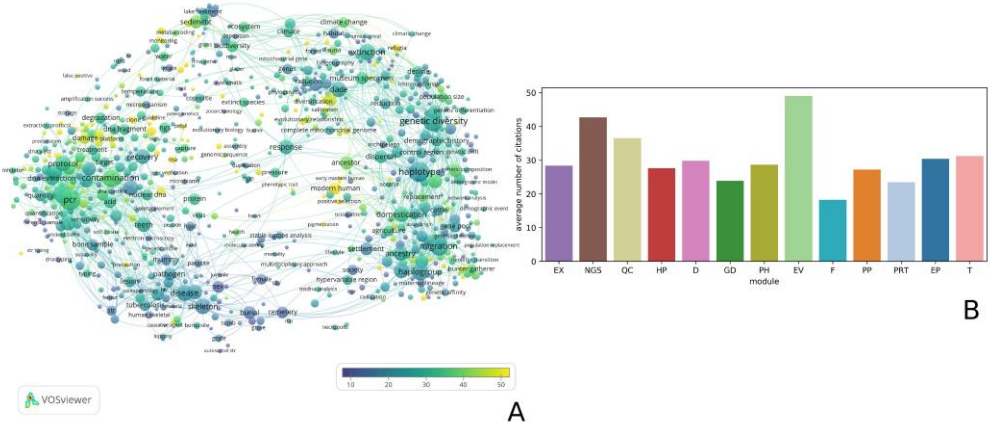

Fig. 4. Citation rates of different areas in aDNA research field. (A) Visualization of text co-occurrence network of the 60% most relevant terms, occurring at least 10 times in the publications, regarding aDNA. Colors signify average number of citations of the articles, containing the terms. (B) A barplot, showing average number of citations of the articles, containing the terms from each module, defined with clustering resolution set to 1.8. For the module labels' abbreviations see figure 3

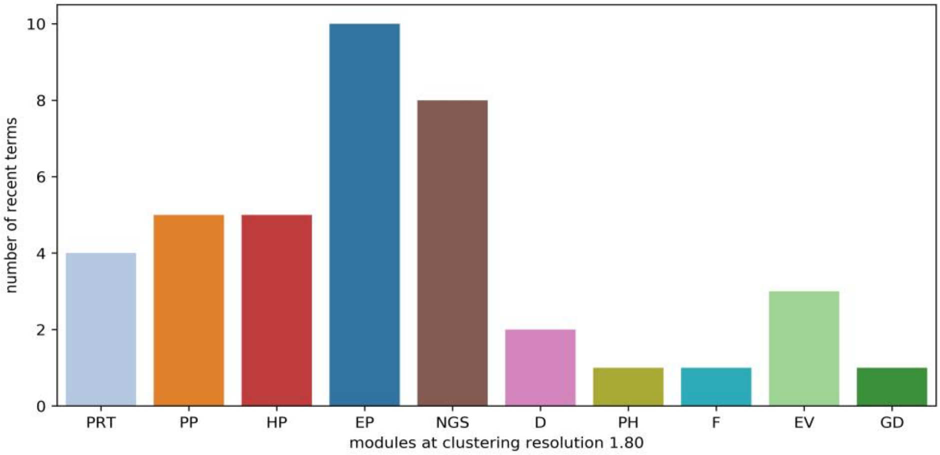

Fig. 5. Distribution of the 40 most recent terms in aDNA research field among the modules defined in text co-occurrence analysis with clustering resolution set to 1.8. For module labels' abbreviations see figure 3

Bibligraphic Coupling Networks

Bibliographic coupling is another type of bibliometric analysis, which can be used to represent a scientific field's knowledge base [16]. In this type of analysis similarity between papers is assessed based on the number of references they have in common [17]. Journal names (sources) from the references were used as units of analysis in this study and full-counting method was selected. A temporal overlay as well as citation score estimation was applied to determine the journals, publishing high impact and cutting edge papers, related to aDNA.

Out of 925 source names, 154 met the threshold of minimum 5 papers related to aDNA research. 5 modules of journals can be distinguished (Fig. 6A). The disciplines, which define these modules can be defined very vaguely. Probably, it is due to the influence of interdisciplinary journals with high impact, such as Science. The largest numbers of journals belong to the module, which comprises journals, publishing research related to human genetics and human history, forensic sciences and biochemistry (Fig. 6B). The highest average numbers of citations have the journals, publishing interdisciplinary research as well as papers in evolutionary biology and those covering general biological questions. These journals are followed by those, publishing research related to ecology and conservation (Fig. 7).

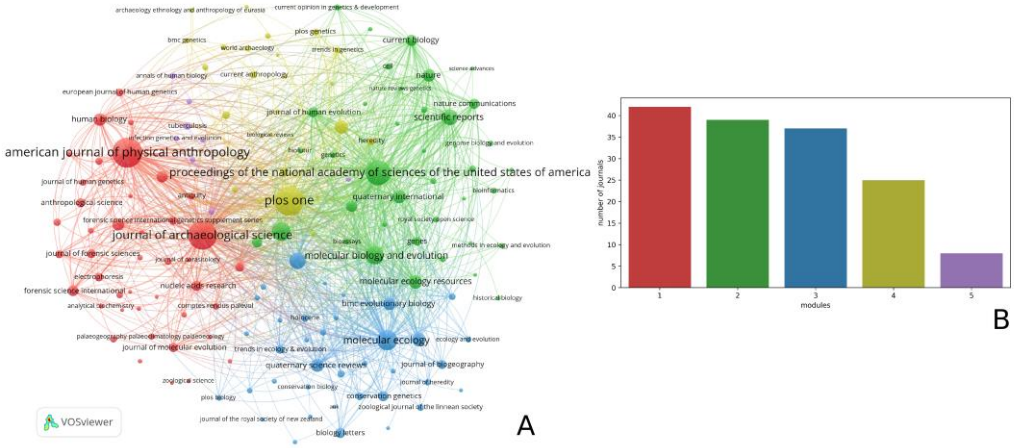

Fig. 6. Structure of the journal landscape of aDNA research. (A) Visualization of bibliographic coupling network using journals as sources with a threshold of minimum 5 papers related to aDNA research. Colors denote the 5 modules of journals, revealed in the analysis. Nodes are weighted by the number of documents. (B) A barplot, showing number of journals in each module, defined in the bibliographic coupling analysis. Colors of the bars correspond to the colors of the modules of journals in the network visualization

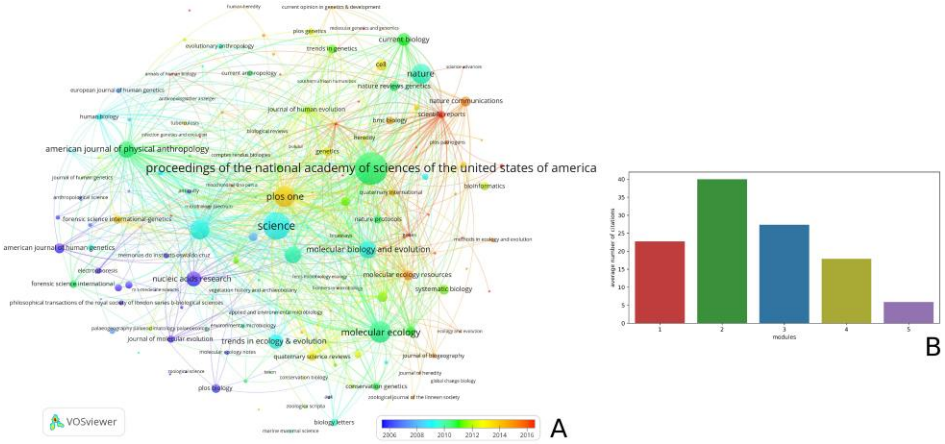

Fig. 7. Dynamics of the journal landscape of aDNA research. (A) Visualization of bibliographic coupling network using journals as sources with a threshold of minimum 5 papers related to aDNA research. Colors denote average publication year of the articles related to aDNA research, published in each journal (warmer colours signify more recent average publication year). Nodes are weighted by the total number of citations of the articles related to aDNA, published in each journal. (B) Barplot, showing average number of citations for each of the modules, defined in bibliographic coupling analysis. Colors of the bars correspond to the colors of the modules of journals in the network visualization shown in the figure 6A

The journals with highest numbers of citations in general include: Proceedings of the National Academy of Sciences of the United States of America (11692), Science (8105), Molecular ecology (5211), PLOS One (4887) and Nature (4303). Journals with the most recent average publication year are the following: Nature Ecology & Evolution (2018), Diversity-Basel (2018), Mitochondrial DNA parts A (2017), Evolutionary Applications (2017), Journal of Archaeological Science: Reports (2017).

Bibliographic Co-Authorship Nerworks

To understand the structure of aDNA research field, the most significant collaborations of scientists were determined based on co-authorship analysis [18-21], as the number of collaborations, which do not result in joint publications can be considered insignificantly small [22]. The larger is the number of co-authored publications, the stronger is considered to be the relationship between the authors in this type of analyses. To decipher the research groups, leading in the field now and understand shifts in publication activity, temporal overlays were used.

Full counting method was used. Of 13014 authors, 582 met the thresholds of minimum five documents and three citations. Isolated nodes, not connected with the others in the network were excluded from visualization.

The authors with the highest number of citations are: Svante Pääbo (11606), Michael Hofreiter (7625), Eske Willerslev (7521), Alan Cooper (5806), Thomas M. Gilbert (5445), of them E. Willerslev has the most recent average publication year (2011). The following authors have the highest average number of citations: David Serre (271), Matthias Krings (268), François Pompanon (222), Philip L. F. Johnson (182), Udo Stenzel (179). The most recent average publication year among them have F. Pompanon and P. L. F. Johnson (2011).

Most of the authors have the following general areas of specialization: biochemistry (genetics, proteomics), evolutionary biology, ecology, archeology (including archeozoology), anthrolpology, conservation genetics, paleopathology, paleomicrobiology, forensic medicine, biogeography, paleontology, geology. It indicates that aDNA research is highly interdisciplinary and contributes to a great many of other research areas.

21 clusters of authors were identified. The research groups, which are presumably contributing most to the field currently were determined using number of citations as an estimate and average publication year. The largest research group consisted of 57 authors, and the smallest one - of 3 authors. Groups lead by S. Pääbo, E. Willerslev P. Taberlet have the highest average citation scores. Of them the group of P. Taberlet has the highest average publication year (2014) and is the most cited among relatively recently emerged collaborations. Interestingly, the research interests of the latter group involve conservation genetics, DNA metabarcoding for biodiversity assessment, molecular ecology, environmental DNA.

Discussion of the results

The field of aDNA research is highly interdisciplinary, which is reflected in the diversity of journals, which publish the articles, concerning aDNA, as well as the wide range of specialists, involved in such research, among which are molecular biologists, computer scientists, evolutionary biologists, ecologists, anthropologists, archeologists, medical and forensic scientists, historians, paleontologists and geologists, geographers and others.

Text co-occurrence analysis revealed 13 sub-fields of aDNA research. The largest number of publications regarding aDNA is concerned with deciphering human population history, historical human migrations and origins of contemporary human genetic diversity. Many of the leading scientists, working with aDNA data, specialize in archaeology and anthropology. However, the publications including the terms, connected with application of aDNA to understand mechanisms of evolution have currently the highest average number of citations. As it has been mentioned by L. Orlando and A. Cooper [23], genome-wide surveys of ancient populations are playing increasingly important role in revealing, calibrating and testing evolutionary processes, including those, happening in human populations (as is indicated by the most frequently occurring terms in the corresponding cluster). The other area with one of the highest citation scores is connected with technological implementation of aDNA research, in particular with NGS and quality control issues, especially vital to aDNA research. The latter includes the problem of authentication and contamination control of aDNA. The sub-field of aDNA studies regarding the use of NGS is the second one among 13 in relation to the number of most recently occurred terms in the field.

Interestingly, that the most rapidly developing avenue of aDNA application seems to be connected with reconstruction of environmental history and conservation genetics. It is indicated by the results of both text co-occurrence and author co-citation analysis. In particular, the module characterized by the terms “extinction”, “biodiversity”, “climate change”, “ecosystem” etc. has the highest average publication year and contains the highest number of the most recently appeared terms (such as metabarcoding, sedimentary ancient DNA, relative abundance, baseline, extirpation). Moreover, of the most cited groups according to co-citation analysis, the one with the highest average publication year (2014) specializes in conservation genetics, biodiversity studies (involving environmental DNA) and ecology. This sub-field is closely related to the one, concerning the study of genetic diversity in general as well as to the field of phylogenetic analysis and the area dedicated to understanding of evolutionary mechanisms. All these avenues of research, according to text co-occurrence analysis, emerge largely from one major field related to the study of biodiversity and its changes through time, as well as problems, connected with its conservation (as indicated by the most frequent terms in the corresponding major module in text co-occurrence analysis). The group of journals, related to ecology, evolution and biodiversity has the second highest number of citations following the group, including major interdisciplinary journals publishing aDNA research in biobliographic coupling analysis.

The next module according to the average year of publications in text co-occurrence analysis is connected with animal and plant domestication. As it has been central in the formation of modern societies, this module is closely connected with the one regarding human population history. The study of aDNA has been revealing many aspects of origination of domesticated organisms, including temporal and geographic ones. Very promising new area of research, according to a number of authors [24] understands the role of epigenomics in domestication process and in regulating domestic phenotypes.

Another vital area of aDNA application is paleopathology. The goal of this discipline is to understand how pathogens emerge and evolve. Paleovirology, for example, provides information on virus evolution and biology, which can be impossible to obtain from examining current viral diversity, in part because of high evolution and extinction rates of their strains [25]. Such studies are crucial for prevention and elimination of emerging diseases. According to text co-occurrence analysis, paleopathological aDNA studies are most closely related to the area of aDNA research, connected with forensic genetics as well as to the area of paleoproteomics. All these three sub-fields together form a module, which, in turn, emerges from the one, related to the technological side of aDNA research. Indeed, technological breakthroughs are especially needed for the development of these areas. Thus, the recovery of proteome-wide information stays even more methodologically challenging than for genomic information; the increase in the variety of pathogens, which can be examined using aDNA methods, is highly dependant on the advances in the recovery of minute molecular fractions, and it is still exceptionally difficult to characterize viruses from ancient DNA and RNA extracts, largerly due to contamination problems [25-27].

Conclusions

The study of aDNA provides a unique means to obtain a time perspective with unprecedented levels of resolution in diverse research avenues. This is a highly interdisciplinary rapidly evolving field of research. Of the thirteen sub-fields of this scientific area, defined by means of text co-occurrence analysis, the largest in terms of the number of publications is connected with the study of the history of human populations and origination of the modern human genetic diversity. However the most rapidly developing area happens to be related to conservation biology. The use of aDNA seems to be a very promising proxy to the reconstruction of environmental history and changes of biodiversity as well as to deciphering the drivers and mechanisms of extinctions. Such studies are critically needed now, considering the fact that the Earth is suffering a severe mass extinction event with the rate of species loss as high as 100 times the "normal rate" throughout geological time [28-30]. The future of life on our planet and the future of humanity depends on our actions to fight biodiversity loss [30], and aDNA studies are helping us in this race.

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