Original Research & Review

Is the genomics cart before the restoration ecology horse?

Insights from qualitative interviews and trends from the literature

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ABSTRACT

Harnessing the power of new technologies is a vital component to achieving the global imperative to restore degraded ecosystems. We explored the potential of genomics as one such tool. We aimed to understand the barriers hindering the uptake of genomics, and how to overcome them, via exploratory interviews with leading scholars in both restoration and its sister discipline of conservation – a discipline that has successfully leveraged genomics. We also conducted a systematic mapping review to explore publication trends that have used genomics to address restoration and conservation questions. Our qualitative findings revealed multiple tensions in harnessing genomics. For example, scholars without genomics experience felt pushed to use genomics prematurely. In contrast, scholars with genomics experience emphatically emphasized the need to proceed cautiously. Both genomics-experienced and less-experienced scholars called for case studies to demonstrate the benefits of genomics in restoration. However, our qualitative data contrasted with our systematic mapping review findings, which revealed 70 restoration genomics studies in total, particularly studies using environmental DNA as a monitoring tool. We provide a roadmap to facilitate a more rapid uptake of genomics into restoration, which should help the restoration sector meet the monumental task of restoring huge areas to biodiverse and functional ecosystems.

BACKGROUND

> "*We're looking for any tools available that can help us find solutions [to understanding ecosystem processes and functions]. And, genomics provides, you know, a new set of glasses to look at and understand our systems, and therefore, to seek solutions from*" (Scholar 4 in our study).

Humans are now the dominant force in nature, having caused substantial degradation to ecosystems globally and significant biodiversity loss [1, 2]. Ecosystem restoration is tasked with reversing humanity's ecological footprint by returning and reinstating lost ecosystem services, ecological processes and biodiversity [3], the scale of which is enormous, as highlighted by the United Nations declaration of the *Decade on Ecosystem Restoration* (https://www.decadeonrestoration.org/). The global community have pledged to restore over 350 million hectares of degraded land by 2030 under The Bonn Challenge [4]. Thus, there is great urgency to the upscaling of ecological restoration interventions, from local levels to entire landscapes.

Restoration ecology is experiencing a monumental transformation as it wrestles with challenges posed by climate change, ambitious restoration mandates, and social and political considerations. Tackling such global challenges is no easy feat and requires innovation, science-informed practice, and drawing knowledge from sister disciplines for insight [5-7]. New techniques and methods, such as genomics, offer potential to address restoration challenges [8], but they also invite debate and controversy. Pioneering techniques, like genomics, may be viewed as unproven, and therefore risky by the majority of the field [9], resulting in a significant lag on the uptake of innovation.

Disciplines often experience controversy when new approaches challenge existing paradigms and existing practices [10]. Changes in methods can take years to unfold, as information gets disseminated, new practitioners trained, and the conventional wisdom retired. In addition to barriers from status-quo thinking, innovations may require significant financial investments that are often perceived as risky given that the viability of the innovation may not be immediately realised [11]. Indeed, in some situations, new models and paradigms may prove to be less beneficial than originally expected, have unintended consequences, be un-scalable, or be superseded by even better techniques [12]. Further, innovations often require collaborations across disciplinary and geographic boundaries, which can present barriers to progress and delayed uptake [13].

Despite facing many barriers to its application, genomics has made a considerable impact on the field of conservation [14-17]. Among the first applications in conservation was population genomics [18], which offered conservation scientists and practitioners detailed insight into species lineages and population demographics. Such data are central to precise delineation of conservation units and key to conservation management [19, 20]. Genomics also has been applied to detect and monitor species of conservation concern [21].

In contrast, restoration is yet to leverage genomics to a similar degree [8]. However, to achieve its ambitious targets, restoration must adopt new techniques and approaches [6, 22]; genomics may be one such technique. Genomics is a valuable and cost-effective technology that, if used appropriately, could greatly advance restoration [8]. To better understand the barriers hindering the uptake of genomics, and how to overcome them, we aimed, firstly, to understand how leading scholars view the potential role of genomics in restoration ecology. We also explored what insights scholars in restoration ecology's sister discipline of conservation could offer, a field that has leveraged genomics to address many important issues [19, 23]. Secondly, we explored the trends in publications that have used genomics to address restoration or conservation. Addressing these two objectives, we provide a roadmap to facilitate and leverage genomics to meet global restoration targets.

METHODS

Qualitative interviews

To better understand the nexus between genomics and restoration, we used qualitative research. Qualitative research methods are appropriate when the phenomenon of interest is complex or poorly understood [24, 25], and such methods are used in both restoration ecology and conservation [26, 27]. We used in-depth, semi-structured interviews to explore scholars' perceptions of (a) the current and potential role of genomics in restoration and conservation, and (b) the barriers to and enablers of using genomics in these disciplines.

We used purposeful sampling, a method that identifies study participants based on their ability to provide rich information on the phenomenon of interest. We identified both restoration ecology and conservation scholars based on their background and experience [28]. We sought scholars of different career stages (based on their publication records and scholarly reputations; Table 1), and scholars who relied extensively on genomics and those who do not. Unlike quantitative research, the sample size needed for qualitative research depends on the nature of the research question, with a focus on sample adequacy rather than statistical power. The adequacy of sampling is usually assessed in terms of ‘saturation’ [29], where researchers continue interviewing until no new information emerges [i.e. until saturation is reached; 30].

Our in-depth interviews included four senior scholars with ≥30 years’ experience, three mid-career scholars with 10-29 years’ experience, and two early-career scholars with <10 years’ experience (Table 1). Of the respondents, six were genomics experts, while three were familiar with genomics, but did not conduct genomics research themselves. Four respondents worked primarily in restoration ecology, two primarily in conservation, and three conducted research that spanned both conservation and restoration. Each respondent was assigned a number for anonymity. Interviews were conducted July-September 2019.

Prior to the interview, a brief script was read to the respondent, adhering to informed consent guidelines, per Institutional Review Board standards (lead author’s institution #144-19). An interview guide (see Appendix 1 in the Supplementary Information for details) ensured comparability across interviews. Respondents answered questions about their academic background, their understanding of genomics, how genomics was or might be used in their research field, as well as about their perceptions and experience regarding barriers and enablers. All interviews concluded with a set of reflective questions related to cross-pollination from conservation to restoration ecology, as well as advice to “restoration ecologists interested in increasing the uptake of genomics”. The interviews had a conversational quality; respondents guided the flow of the discussion. Three researchers participated in all interviews, with one of the team serving as the lead interviewer. The other two researchers were invited to interject questions to clarify and probe at selected spots in the interview. This semi-structured approach provided the benefits of organization and flexibility, while minimising the risk of interviewer-induced bias [31]. Each interview lasted about one hour, was recorded, and professionally transcribed verbatim.

Qualitative data are analysed using an iterative process to identify themes emerging from the data [32]. The three research team members involved in the interviews each analysed three-to-four transcripts in detail for insights and themes. Based on this iterative process, data were organized into key themes [i.e. 'thematic analysis'; 33]. We then triangulated these themes by sharing our individual interpretations, discussing discrepant views, and cross-checking themes against the transcripts. These findings were then reflected back to the research participants in a written form to ensure the themes resonated with their experience and perceptions. The themes that survived this validation process are discussed in the results below. Data excerpts illustrate specific findings and provide empirical evidence for the themes.

Systematic mapping review

To determine the characteristics of studies that use genomics in restoration ecology or conservation (see Box 1 for definitions), we undertook a systematic mapping review. Systematic mapping reviews are used to categorise and map the existing literature, utilising a replicable systematic search [34]. We conducted the systematic search on March 1, 2020 to identify all peer-reviewed articles published in English language that used genomics within conservation or restoration ecology. The search was performed in Web of Science Core Collection and Scopus (see Appendix 2 for search terms).

Results from the database searches were exported into Endnote X9 for management. Within Endnote, duplicates were manually removed, then the titles and abstracts were screened by two authors for inclusion/exclusion, based on predetermined criteria (Box 1). The full texts of all remaining articles were obtained and screened against the same criteria. Where there were uncertainties regarding inclusion of a study, another author independently assessed the study.

The following data were manually extracted from all included articles into a Microsoft Excel spreadsheet: country of the study, year(s) of data collection, publication year, whether the study related to conservation and/ or restoration ecology (based on the definitions in Box 1), and the genomic methods used (e.g., eDNA, population genomics). A second author independently coded the data from any study where the other author was uncertain.

RESULTS AND DISCUSSION

Our qualitative research findings revealed that scholars with high levels of experience in using genomics expressed different perspectives on harnessing genomics in restoration compared to scholars with less genomics experience. These differences were organized into three inter-related areas of tension – academic training and background, methodological, and philosophical – which we discuss in turn below. The insights gained from these qualitative data prompted us to explore the trends in the literature via a systematic search to better understand where and how genomics tools were being applied in conservation and restoration, which are discussed following the qualitative findings.

Qualitative Findings

<u>Differences in academic training and background</u>: Scholars experienced in genomics had background training in genetics and/or evolutionary biology. As Scholar 2 expressed, the understanding of genetics "*and all that stuff about small populations and genetic bottlenecks is well-embedded in conservation thinking and much less so in restoration.*" In contrast, "*the restoration field is more ecologist-driven than geneticist driven*" (Scholar 8). Scholars less experienced in genomics acknowledged this field-based training difference and expressed concerns about the stereotype of restoration "*as a gardening exercise*" (Scholar 3). To harness genomics, restoration ecologists require at least some training in genetics and/or evolutionary biology, and it was noted that, without this training, experts expressed concern about how "*anyone who manages an ecosystem could do so effectively*" (Scholar 6). Paradoxically, the more classically-trained restoration ecologists expressed concern about genomics scholars 'overpromising' what genomics can do for the field, that genomics scientists "*have the hammer and are looking for the nails*" (Scholar 3).

Another key difference in training voiced by genomics experts is their proficiency in handling the 'big data' aspects of high-throughput sequencing and requisite bioinformatics. Genomics scholars describe themselves as "*total data nerds* [who] *dive into two terabytes of data with great enthusiasm (Scholar 8).*" Scholar 9 noted that traditional restoration ecologists may be "*unprepared for the fact that they can't open this data in Excel and you can't eyeball it…It requires specialist expertise to be able to handle this sort of data.*"

Methodological differences: Three clear differences emerged between more and less experienced scholars regarding the interpretation of results from genomics data and the experimental design underlying the data. First was the importance of a rigorous research design. Scholars who were not as experienced using genomics expressed concern that genomics researchers might be putting the "*cart before the horse*" (Scholar 3), that *genomics is important but it's not everything*" (Scholar 7: "*People who embrace new technologies can forget the old school methods of just growing plants in a glasshouse*"). However, the experienced genomics scholars themselves noted the need to ensure defendable research designs. Scholar 5 noted that "*we're still analysing and trying to figure out the best analyses to take for these big … genomics studies. The challenge is, even with the expertise, getting the analysis right, making decisions around which comparisons and what analysis do you run*".

The second methodological difference concerned the confidence in drawing conclusions based on methods developed using model organisms. The field of conservation benefited from publicly-available genomic resources, such as assembled and annotated genomes stemming from human medicine or agriculture [35]. "*Most of the first examples of using genomics in conservation benefitted from agriculture, where they had already collected and analysed the genomic information*" (Scholar 1). Experienced genomics scholars were comfortable using these model organisms. Scholar 5 stated, *"As an evolutionary biologist, I can say fundamentally, how genetic diversity drives population dynamics and persistence is universally the same, regardless of taxa."* However, Scholar 5 expressed concern that less experienced genomics scholars *"are reticent to accept arguments about the importance of considering genetic diversity when that data comes from model organisms. [They wonder how] does that translate to my particular species or my ecological context?"*

A final methodological difference was the ability to use genomics data to understand genetic variation between populations that is relevant to restoration. On the one hand, experienced genomics scholars were comfortable using genomics to understand the genetic basis of adaptation. For example, Scholar 9 said, "*As much as anything, I've been following my nose; genomics can help us take more apart and start to understand adaptive differences*". In contrast, restoration ecologists with less experience in genomics expressed worry and concern about the inability to draw precise conclusions from genomics data. For example, one suggested that genomics allows researchers to describe important genetic differences between plant populations faster, but "*we still need to ascribe functional significance to those differences*", stressing the need for classic experiments with control groups in order to "*close the loop on the functional impacts of genomics findings*" (Scholar 3).

<u>Philosophical differences</u>: The last difference that emerged surrounded the scholars' attitudes and beliefs about embracing both the upside potential and downside risks that come with using genomics in restoration, including concerns about using genomics to surface new knowledge. On the one hand, scholars experienced in

genomics evinced scepticism and caution on the use and interpretation of genomics data in order to avoid "*putting the cart before the horse*" (Scholar 4), with explicit recognition of the work yet to be done to validate genomics' potential and the need to explore the potential of genomics even if it does not pan out as expected. On the other hand, scholars with less genomics experience were more hesitant to experiment with unknown protocols and were concerned about the ambiguity surrounding unknown aspects of genomics. Less experienced scholars expressed the perspective that genomics was 'over-hyped' and perhaps over-promised what it could deliver. These scholars with less experience in genomics characterized other restoration ecologists as being risk averse: "[some] *restoration people don't like anything new at all…"* (Scholar 2), as well as possible concerns about how "*scary and troublesome*" genome editing is: "*if you unleash this technology into nature, you're unleashing the 'dogs of hell' and it's all going to be bad*" (Scholar 2).

Despite the need for "*creative thinkers, people willing to take the chance, to jump upon those new methods, and think outside the box*" (Scholar 8), experienced genomics scholars simultaneously acknowledge the need to temper the hype. Scholar 7 said, "*There's a lot of scepticism on the method [genomics] but there's also a lot of excitement—which we're trying to temper by saying we need to do a lot of research to actually show how well this is going to work*." Scholar 7 continued, "*People are running to it because it's new and shiny…we need to set realistic expectations about how well genomics is going to work, how much work we need to put in to prove how well it's going to work."* Scholar 8 agreed with the need for tempering: "*I understood how difficult genomics was, how uncertain it was, and I was like, 'Hold on. Pump the brakes. I've worked really hard to get through to the more* *senior people the difficulty and the uncertainty surrounding these data…It's not a silver bullet. There's so much we need to do to make it a usable and reliable, trustworthy tool for restoration assessment*."

Shared views: A final set of qualitative findings regards similar views. Firstly, both genomics experts and those less experienced with genomics stressed the need to "*build up enough case studies to demonstrate positive outcomes in terms of the success of particular restoration programs"* (Scholar 5). This scholar emphasized the importance of identifying and validating "*current use cases where genomics could offer tangible value in research today and addressing pressing questions now.*" Similarly, Scholar 3 noted that *"the greatest challenge for genomics is to demonstrate 'runs on the board'*", to show that it is a cost-effective tool that provides relevant answers to restoration questions that, without which, practitioners may make less optimal management decisions. We note that this stated desire for case studies contrasts with the findings from our systematic mapping review (see below), which counted 70 studies that leverage genomics to address restoration issues—evidence of the clear interest in using genomics in restoration ecology. In addition, the interviewed scholars emphasized the need for greater education and training regarding what genomics is, the types of research questions it can usefully address today, and generally, building capacity, skills and knowledge.

Moreover, scholars emphasized the importance of collaboration: between conservation biologists and restoration ecologists, between classically-trained restoration ecologists and genomics experts, and between practitioners and scientists. Scholars 3, 4, and 6 each emphasised the benefits of interdisciplinary approaches and collaborative teams comprising people with very distinct skill sets. Scholars 5 and 7 noted that collaborations between practitioner and scientists are as important as collaborations between genomics experts and classically-trained restoration ecologists. Scholar 5 believed that having joint discussions with practitioners regarding the design of field-based studies could advance uptake and demonstrate the benefits genomics might offer in certain areas of practice (e.g., assessing soil function; for ecological monitoring) to close the gap between science and practice. However, Scholar 3 worried that scientists see the value in the tool, but practitioners will not. Indeed, a less experienced genomics scholar described "*the genomics people*" as "*the guys in the other room*", who "*have to demonstrate that they understand what the restoration community does*" to bring the conversation about genomics in restoration "*into the fold.*" This us-them distinction could stymie collaborative efforts.

We advocate for thinking proactively about how to ensure that genomics does not widen the gap in adoption by practitioners, as collaboration alone is likely to be insufficient, an issue raised previously in discussions of the value and uptake of genomics in conservation [19]. Without improved training in evolutionary biology and genetics, restoration ecologists may find it difficult to harness genomics to address critical questions in climate change adaptation, ecosystem resilience and soil health, for example. Scholar 7, a genomics expert, stated, "*Genomics complements traditional approaches. We've got to work together with people who use traditional approaches, work side-by-side with them. Our work will feed into theirs and their work will feed into ours. Together, we will make it better and, you know, have better restoration outcomes for the world.*"

Systematic Mapping Review

Our systematic search identified 1845 unique articles, 176 of which met our inclusion criteria and were included in our review (see Appendix 3 for the flow chart of study inclusion/exclusion; full details of all included papers are in Appendix 4). Based on the field definitions we used in our review (Box 1), 106 articles were classified as conservation only, 35 were restoration only, and another 35 had results applicable to both conservation and restoration. The studies that span both conservation and restoration highlight the potential for bridging the discourses between the two disciplines as identified above (see “Differences in academic training and background”). Indeed, collaborations between the two disciplines can help diffuse the use of genomics and knowledge more broadly.

The finding of 35 studies that use genomics in restoration (in addition to the 35 that span both disciplines) contrasts with the qualitative data that emphasized the need for “*runs on the board*” and “*case studies of restoration using genomics*”. Distilling the reasons for this discord is complex; perhaps the studies employing genomics may not yet represent a viable approach for the restoration discipline. Alternatively, it is possible that ecology scholars focus their literature reading within their own area of expertise and are not exposed to genomics research [36]. Or perhaps the lexicon and presumed knowledge that complicate new technologies may hinder the recognition of value that genomics may offer. Regardless of the reasons, the need for relevant and understandable case studies was voiced by both less and more experienced genomics scholars. Box 2 provides broadly-applicable examples that illustrate the use of genomics in a restoration context. The cross-pollination of specialist journals in these disciplines offer a further potential to increase the visibility of genomics in restoration.

The earliest application of genomics in conservation or restoration that we detected in our dataset was 2008 [37], followed by a period of very few studies between 2009 to 2012, after which there was an exponential increase in studies applying genomics in both restoration and conservation (Figure 1). Most studies were published between 2018-2020 (59 conservation, 26 restoration, 21 conservation and restoration). This temporal trend appears consistent with other review studies on conservation genomics [38]. While we counted more studies that used genomics to address conservation issues than restoration, the temporal trend showed a rapid increase in restoration studies that used genomics over the past two years. The temporal trend in growth of publications suggests genomics studies applied in a restoration context may surpass the prevalence of genomics in conservation studies. While the use of genomics in restoration is increasing, this trend might also reflect increased cross-over between the two disciplines.

With respect to geography, most conservation genomics studies were undertaken in North America (n = 36) and Europe (n = 17; Figure 2). These same two continents were among the least common locations reporting restoration genomics studies (Europe: n = 4; North America: n = 8; Figure 2). The number of conservation papers from North America and Europe has generally increased annually, which has not occurred in restoration genomics papers (Appendix 5). However, the number of restoration genomics papers from Russia, China, South Asia shows a clear increase, with the number of restoration studies overtaking the number of conservation studies in 2020 (Appendix 5).

Across the studies assigned to conservation, restoration, and conservation and restoration, the majority of articles reported the use of eDNA approaches (conservation: n = 47; restoration: n = 33, conservation and restoration: n = 27), and a steady increase over time (Figure 3). This genomics approach was most used in conservation and restoration studies from Russia, China, South Asia (n = 27), North America (n = 21), and Europe (n = 20; Figure 2). These findings indicate that there may be broader opportunities in restoration genomics through the appropriate utilisation of eDNA over population genomics, as suggested in previous studies [39], but there remains a clear use of population genomics in restoration to inform seed sourcing practices [8].

Population genomics was utilised in 53 conservation studies, 1 restoration study, and 8 studies that crossed over between conservation and restoration (Figure 3). Between 2018-2020, there was a marked increase in the uptake of population genomics, which was most pronounced in the conservation studies (n = 31) and conservation and restoration studies (n = 6; Figure 3). The use of population genomics in conservation was most evident in studies from North America (n = 25); however, we detected no restoration studies from North America that utilised population genomics (Figure 2). Rather, Latin America (n = 4; pooled across restoration and conservation and restoration) and Oceania (n = 3) were the most common locations to use population genomics in a restoration context.

Helping genomics cross the chasm into restoration

A prominent model used to develop a strategy to hasten the market uptake of novel innovations such as genomics is ‘crossing the chasm’ [40]. The chasm refers to the gap between early adopters of a new technology and more pragmatic adopters; a key differentiator between these two groups is their appetite for risk, comfort with uncertainty, and willingness to try novel solutions [9, 40].

The strategy first requires identifying what is referred to as a beachhead: a single application area and/or industry use case where the novel innovation offers a compelling solution to problems faced in that area. Breed *et al.* [8] proposed that a compelling application for genomics is using population genomics to inform seed sourcing practices. Genomics offers critical information that is not easily attainable using other methods. For example, it can rapidly identify signals of genetic based adaptations that have the potential to increase resilience of seed stocks to future environmental change. Breed *et al.* [8] also proposed that eDNA approaches offer crucial benefits to track important ecological components and interactions during restoration (e.g., soil microbial communities; plant-pollinator communities). In addition to these application areas of genomics, beachheads can focus on a particular industry that faces a critical need to solve a problem or issue for which the novel technology is uniquely suited. For example, with respect to restoration ecology, the mining sector has increasingly regulated rehabilitation requirements that place tremendous pressure on the availability of cost-effective restoration practices [41]. The desire of scholars in our qualitative study to identify use cases where genomics offers compelling value illustrates the face validity of the ‘crossing the chasm’ model.

Matching the value proposition of genomics to a critical application area allows pragmatists a compelling reason to overcome their uncertainty and move forward.

The notion of targeting a specific application area in a particular industry to gain broader market acceptance is somewhat paradoxical: why would a new technology narrow its focus rather than pursue multiple application areas and industry applications all at once? The answer lies in both the nature of word-of-mouth communications--a critical consideration for pragmatic adopters' decision making--as well as important subtleties in how a new technology is deployed across industries and applications. Hence, a second consideration in developing a strategy for genomics to cross the chasm in restoration ecology is to explicitly consider how word-of-mouth communication might flow between areas within restoration ecology (e.g., do those who focus on seed sourcing and provenance issues interact regularly with those who focus on soil microbial communities and ecological monitoring?) as well as between different industries that face restoration pressures (e.g., do those in the mining industry share knowledge and insights with those in agriculture and/or reforestation sectors?). Another consideration is how word-of-mouth networks operate geographically, both different countries as well as types of ecosystems (rainforests vs. temperate forests vs. deserts; aquatic vs. terrestrial ecosystems).

Putting these two considerations together (selecting a beachhead and considering word-of-mouth communication) results in a strategy that, if implemented correctly, can build momentum for a new technology. A useful analogy for this strategy is to view the beachhead like a lead pin in a bowling alley: if hit properly, this lead pin will knock down adjacent pins behind it (e.g., through the word-of-mouth networks). For example, one possible “bowling alley” could start with using genomics to assess seed sourcing and transfer zones in the reclamation for degraded mining sites; then momentum could build on the one hand, to applying genomics to monitor ecological communities in those reclaimed mining sites, and on the other hand, to using genomics to inform seed sourcing and transfer zones in a related industry, such as repairing degraded agricultural ecosystems.

Finally, all new technologies require additional elements in catalysing market uptake. First, a communications strategy is required to build awareness about the value proposition that this new technology has to the identified beachhead, as well as to educate potential adopters about how to leverage this new technology [42]. Our qualitative findings highlighted the need for greater education and training with regard to what genomics is, the types of research questions it can usefully address today, and generally, building capacity, skills and knowledge. Hence, efforts to build awareness and capability could include workshops, education, training, and outreach, again, strategically delivered to a specific industry for a specific application to build momentum for communication via word-of-mouth networks to related applications and industries.

Second, funding for genomics research is equally critical. There is anecdotal evidence that some areas of restoration practice have the funding, knowledge, and motivation to use genomics, for example, to understand the impact of mining rehabilitation practices on soil microbial communities [43, 44]. Other areas of restoration suffer from insufficient funding, such as large scale restoration efforts and adequate restoration project monitoring [45], and in these cases genomics may not be easily available or a priority investment.

Third, most novel technologies require related products and services to function properly, a concept referred to as the "innovation ecosystem" [46, 47]. For example, bioinformatics and technological infrastructure are critical components for leveraging genomics. Even while attention is given to the various genomics tools and applications, equal attention must be given to properly preparing samples in the field and laboratory, managing the bioinformatics challenges, and appropriately analysing and interpreting the data.

Fourth, as our depth interviews noted, collaboration allows the benefits of bringing the power of genomics to solving restoration problems while not requiring that all members of a team be genomics experts. Rather than each person needing to bring all skills required, interdisciplinary teams are a logical solution can bring together the unique and disparate skills to a project.

CONCLUSIONS

> "*This tool [genomics] allows us to be much more sophisticated in our understanding of ecosystem recovery following restoration*" (Scholar 7).

Genomics offers opportunities to better understand many fundamental issues facing declining ecosystems, yet it is often a missing tool in the restoration ecologist toolbox. The goal of our study was to identify and understand the barriers slowing the uptake of genomics in restoration ecology by collecting qualitative data from semi-structured interviews and conducting a systematic mapping review.

We identified multiple tensions between experienced genomics scholars and traditional ecological scholars regarding the field-based training differences, designing studies and interpreting genomics data, and the need to weigh up the benefits versus the risks of using genomics compared to traditional approaches. Our interviews revealed that scholars without genomics experience feel pushed to use the tool “prematurely” in their view. In contrast, scholars with genomics experience emphatically emphasized the need to “pump the brakes”, to proceed cautiously in ascertaining where and how genomics can be usefully applied. These differences across categories of adopters with respect to perceptions and willingness to leverage novel technologies such as genomics are well-established in the innovation literature [9, 40].

We also identified that scholars were unified on the need for case studies to demonstrate the benefits and applications of genomics in tackling restoration problems and for collaboration to overcome barriers to the uptake of genomics. However, evidence from our systematic mapping review revealed that genomics is indeed being leveraged to address restoration issues, and in fact, its use has increased rapidly in the past few years. This increase was mostly facilitated by eDNA applications, which is by far the most widely used genomics tool, with population genomics rarely applied to restoration problems. We urge a synthesis of the 70 studies that show use of genomics to address restoration challenges.

We have proposed a roadmap that explicitly considers the various aspects necessary for genomics to cross the adoption chasm. For restoration ecologists, this roadmap requires demonstrating the value of genomics in areas with a well-established ecological framework rather than applying genomics where the ecology is less well-understood, providing education, training, and outreach, ensuring funding for the research, and developing a robust set of ancillary elements (e.g., bioinformatics and computing infrastructure) to round out the necessary component of the innovation ecosystem. With these elements in place, the likelihood of genomics to address the critical issues facing restoration will be increased.

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Declaration of interests

The authors declare no competing interests.

Ethics

This project was done under ethics approval by University of Montana's Ethics Review Board (approval number #144-19, for “Barriers to and Facilitators of Genomics in Ecological Restoration”) in accordance with the Code of Federal Regulations, Part 46, section 104(d).

Supplementary information

Appendix 1. Interview guide

Appendix 2. Search strategies

Appendix 3. Inclusion/exclusion flow chart

Appendix 4. Details of the included studies

Appendix 5. Frequency of published studies from the systematic mapping review by geographic region, across time

Box 1. Definitions and inclusion/exclusion criteria

Conservation: “The protection, care, management and maintenance of ecosystems, habitats, wildlife species and populations, within or outside of their natural environments, in order to safeguard the natural conditions for their long-term permanence” [48].

Restoration ecology: “the science that supports the practice of ecological restoration, and from other forms of environmental repair in seeking to assist recovery of native ecosystems and ecosystem integrity” [3].

Genomics: Generated de novo genomic data using modern (i.e., non-Sanger) sequencing approaches (i.e., high throughput sequencing), or that used genomic datasets that had already been generated and ran comparative genomic analyses

Studies were *eligible* for inclusion where they were:
- published in English language
- published in full text (e.g., not abstracts only)
- published in a peer-reviewed journal [as per UlrichsWebTM Global Serials Directory; 49]
- used genomics for either conservation or restoration ecology, or that propose methods that could be applied to conservation or restoration ecology (i.e., methods with potential implications specific to conservation or restoration ecology, or provided genomic data on a target species)

Studies were *excluded* where they were:
- reviews, perspectives, or essays
- studies of plastid genomes (e.g., chloroplast or mitochondria), or
- studies that used genomics to develop microsatellite markers

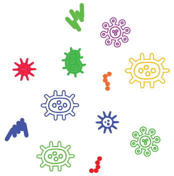
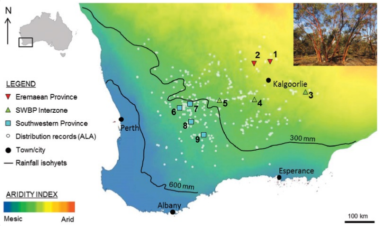
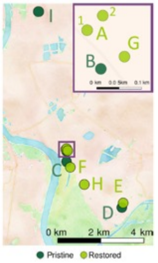
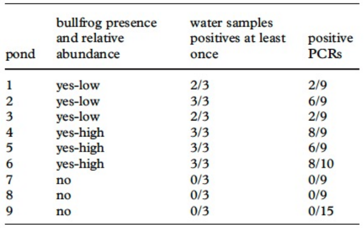
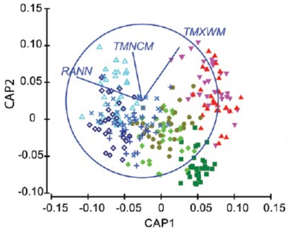
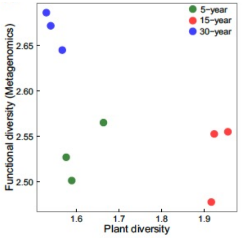
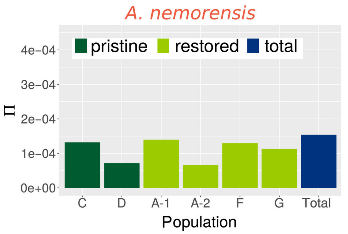
Box 2. Examples of studies that used genomics to answer restoration questions. We identified 70 studies from our literature search that used genomic methods in a restoration context. Here we provide details of four examples of these studies, where these studies include: (A) the earliest eDNA study (and restoration genomics study in general); (B) the equal earliest population genomics study; (C) a more recent eDNA study that used more advanced molecular methods than typically employed; (D) the only study that combined both eDNA and population genomics.

Ficetola *et al.* (A) [37] used eDNA methods in a laboratory environment to demonstrate how this approach could be used to detect the presence of an invasive frog species in freshwater environments. These findings are important for restoration as detecting aquatic vertebrate species – whether invasive, rare or common natives – is often an expensive exercise that is challenging in certain hard to access environments and especially when the organisms are in low abundance.

Steane *et al.* (B) [50] used population genomics to identify adaptations across the range of a tree species that is commonly used in restoration plantings. The use of population genomics here helps to inform seed sourcing decisions that take into account the adaptive variation among populations, which for long-lived plants such as most trees would otherwise require many years of common-garden field trials.

Guo *et al.* (C) [51] used eDNA methods in a field environment to determine how the taxonomic and functional gene diversity and composition of soil microbes had changed after restoration plantings. The monitoring of soil microbial communities in restoration is important as they provide key ecosystem services (e.g. nutrient cycling) and are a rich source of biodiversity in their own right. However, microbial communities are impossible to monitor accurately without the assistance of molecular methods since most taxa are not culturable or easily identifiable. The authors combined a more advanced molecular technique – shotgun metagenomics – with the commonly-used amplicon sequencing.

Dittberner *et al.* (D) [52] used a combination of eDNA and population genomics to monitor species hybridisation and population admixture between populations of two Arabis plant species. eDNA was used to identify the two species, and population genomics was used to determine population admixture. Sometimes plant species are challenging to identify using traditional morphological approaches and eDNA approach used here can assist in this process. Measuring gene flow and admixture between populations is nearly extremely challenging without the use of molecular methods, and population genomic methods provide great insight into these aspects of habitat connectivity and adaptive potential of populations.

Topic	**(A) Frog species detection using eDNA from water samples** – *Ficetola et al. 2008*	**(B) Genetic adaptations in a eucalypt species used in restoration plantings** – *Steane et al. 2017*	**(C) Soil bacterial taxonomic and functional differences with natural revegetation** – *Guo et al. 2018*	**(D) Monitoring effect of restoration on intraspecific genetic diversity** – *Dittberner et al. 2019*
Genomic method	eDNA	Population genomics	eDNA	eDNA & Population genomics
Taxonomic group		 *Eucalyptus loxophleba* ssp. *lissophloia*		*Arabis nemorensis* & *A. sagittata* 
Study location	Laboratory (France)	 	 Active "Grain for Green" restoration site, Loess Plateau, China	River Rhine floodplain, Germany 
Study type	Laboratory experiment	Field observational study	Field observational study	Field experiment
Molecular analysis	Sequencing of fragment of *cyt-b* gene on Roche 454 GS20 	4,851 SNPs via DArTseq (unknown platform)  	Shotgun metagenomic sequencing & sequencing of fragment of *16S rRNA* gene on Illumina HiSeq 2500  	32,880 SNPs via RADseq on Illumina HiSeq & sequencing of fragment of *ITS* gene (unknown platform) 
Statistics	Generalized mixed models	Genetic diversity & genetic-environment associations	Diversity, linear models, PERMANOVAs	Genetic diversity & admixture

pond	bullfrog presence and relative abundance	water samples positives at least once	positive PCRs
1	yes-low	2/3	2/9
2	yes-low	3/3	6/9
3	yes-low	2/3	2/9
4	yes-high	3/3	8/9
5	yes-high	3/3	6/9
6	yes-high	3/3	8/10
7	no	0/3	0/9
8	no	0/3	0/9
9	no	0/3	0/15

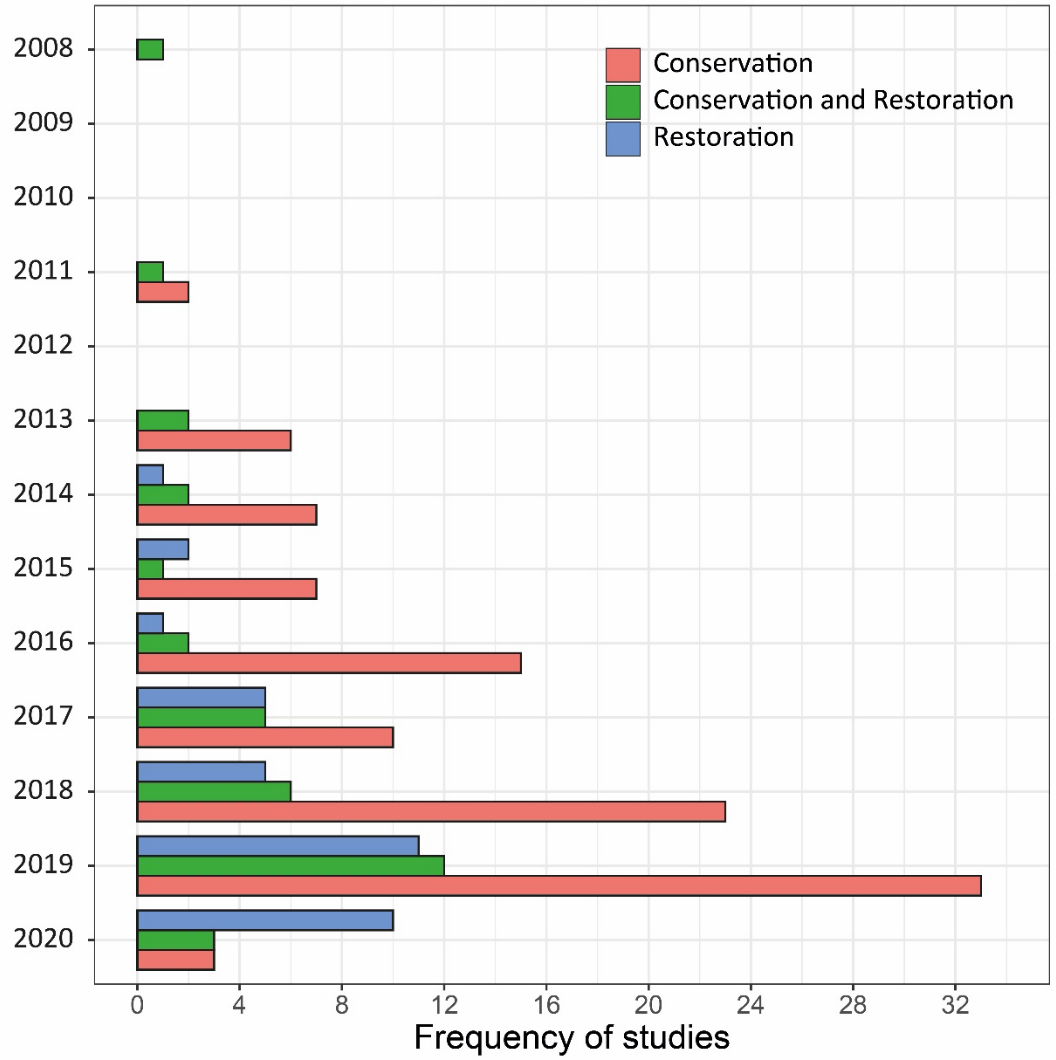


Figure 1. Frequency of published studies from the systematic mapping review over time, from Jan 2008 to March 1, 2020. Studies were divided into conservation (orange), conservation/restoration (green), and restoration (blue).

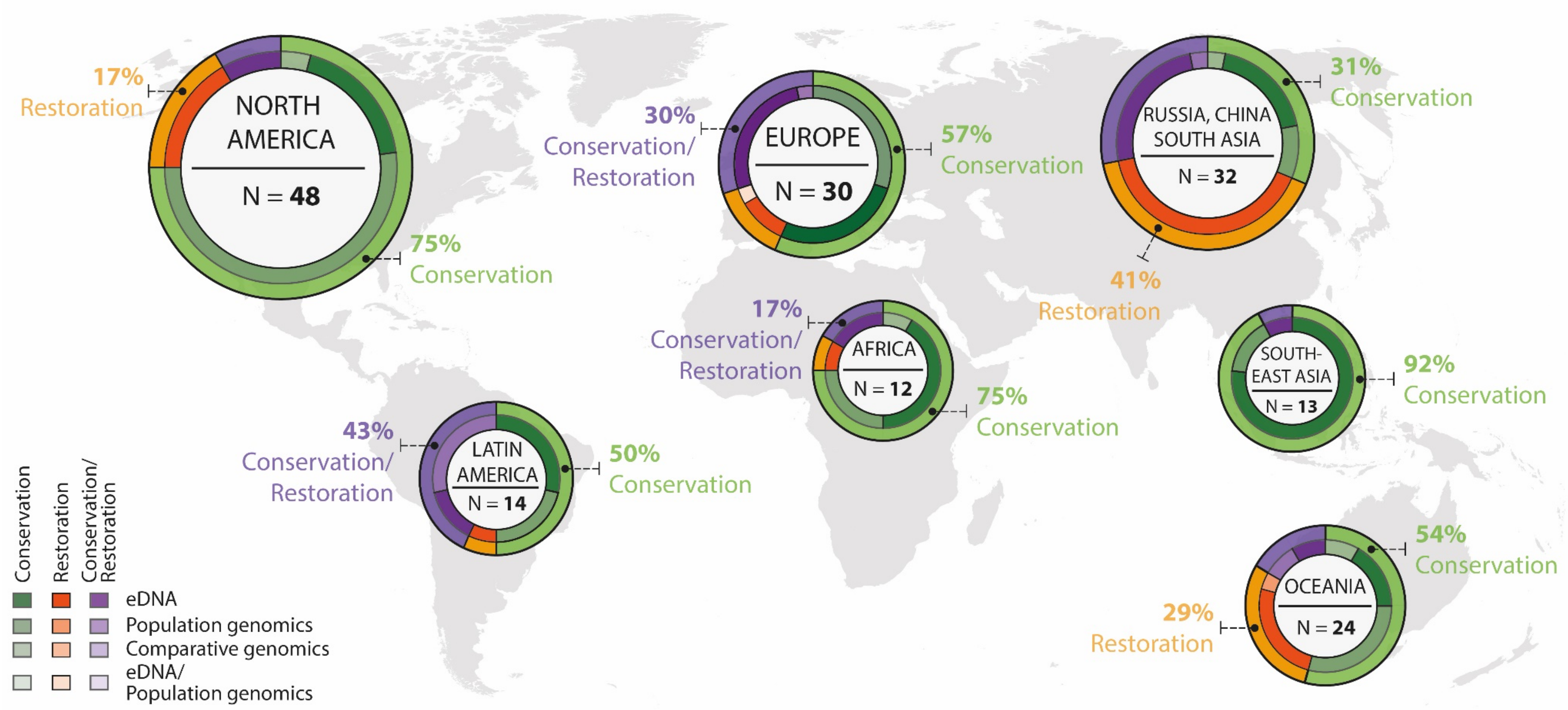


Figure 2. Proportion of studies from the systematic mapping review for seven geographic regions. The outer circle of the donut plot corresponds to the total proportion of studies belong to conservation (green), restoration (orange), and conservation/restoration (purple). The inner circle of the donut plot shows the break-down of each study into the applied genomics method.

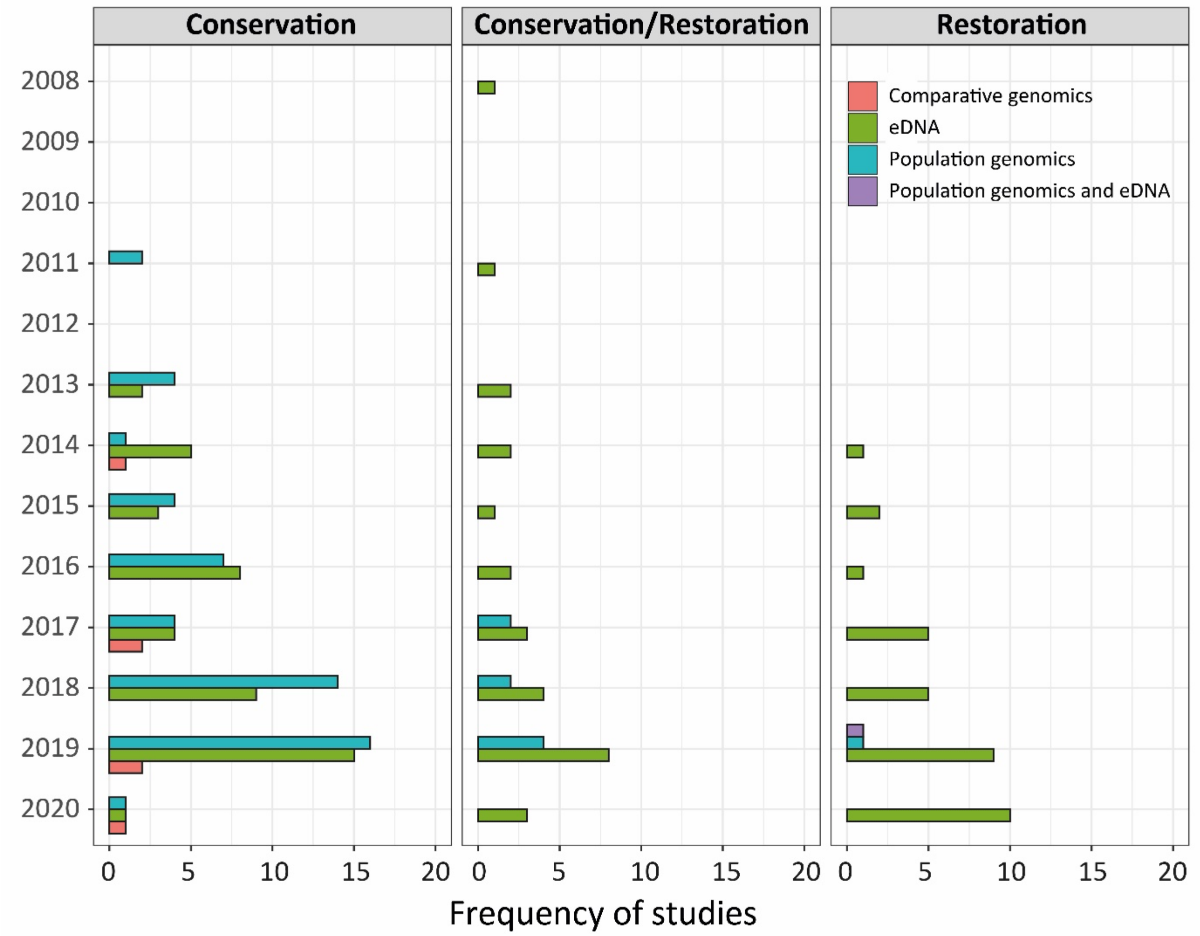


Figure 3. Frequency of published studies from the systematic mapping review across time for conservation, conservation/restoration, and restoration. Studies within each of these divisions were broken-down to the applied genomics method, including comparative genomics (orange), eDNA (green), population genomics (blue), and population genomics combined with eDNA (purple).

Table 1. Years since PhD, discipline expertise and citation and publication data of respondents (citation and publication data from Google Scholar [accessed 1 July 2020]).

Scholar	Years since PhD	Conservation or restoration	Genomics used in Research	Citations	Publications
1	>30	C	Y	>10,001	>100
2	>30	R	N	>10,001	>100
3	>30	R	N	>10,001	>100
4	>30	Both	Y	5,001-10,000	>100
5	10-29 years	Both	Y	5,001-10,000	50-100
6	10-29 years	R	N	1,500-5,000	50-100
7	10-29 years	R	Y	501-1,499	50-100
8	<10 years	C	Y	1,500-5,000	50-100
9	<10 years	Both	Y	<500	<49

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