Received Date : 22-Apr-2016
Revised Date : 23-Aug-2016
Accepted Date : 24-Aug-2016
Article type : Opinion

Title: Building strong relationships between conservation genetics and primary industry leads to mutually-beneficial genomic advances

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Keywords: conservation genomics, high-throughput sequencing, next-generation sequencing, interdisciplinary research, applied research

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Running Head: Strong relationships lead to genomic advances

ABSTRACT:
Several reviews in the past decade have heralded the benefits of embracing high-throughput sequencing technologies to inform conservation policy and the management of threatened species, but few have offered practical advice on how to expedite the transition from conservation genetics to conservation genomics. Here, we argue that an effective and efficient way to navigate this transition is to capitalize on emerging synergies between conservation genetics and primary industry (e.g., agriculture, fisheries, forestry and

horticulture). Here, we demonstrate how building strong relationships between conservation geneticists and primary industry scientists is leading to mutually-beneficial outcomes for both disciplines. Based on our collective experience as collaborative New Zealand-based scientists, we also provide insight for forging these cross-sector relationships.

One does not need to read beyond the pages of *Molecular Ecology* to see how emerging technologies are revolutionizing the way we conduct research in ecology and evolutionary biology (i.e., EEB) and conservation biology. This is exemplified by rapid advances in genomics, where in the span of two decades the field of molecular ecology has grown from using Sanger technologies to sequence single target loci to using high-throughput sequencing (HTS) technologies to affordably sequencing entire draft genomes (Narum *et al*. 2013; Payseur & Rieseberg 2016; Tigano & Friesen 2016). When new technologies become available, there is a tendency for reviews to be published heralding their potential to address new and exciting questions. Beyond the value of these reviews, an even more important conversation needs to take place in the peer-reviewed literature: how do we efficiently incorporate new technologies into our research repertoire to make accelerated gains in applied and fundamental science?

The field of conservation genetics is currently in transition given rapid advancements in HTS technologies. Many reviews have highlighted the promise of embracing HTS technologies in conservation (Luikart *et al.* 2003; Kohn *et al.* 2006; Primmer 2009; Allendorf *et al.* 2010; Avise 2010; Frankham 2010a; Ouburg *et al.* 2010; Angeloni 2011; Ekblom & Galindo 2011; Funk 2012; McCormack *et al.* 2013; Narum *et al.* 2013; Steiner *et al.* 2013; Ellegren 2014; McMahon *et al.* 2014; Shafer *et al.* 2015; Andrews *et al*. 2016; Benestan *et al*. 2016; Grueber 2016). However, as recently discussed by Shafer *et al*. (2015, 2016) and Gardner *et al.* (2016), there are a limited (albeit increasing) number of published empirical studies that apply HTS data to conservation. We are aware of empirical genomic studies in EEB that are applicable

to questions in conservation (e.g., Defaveri *et al*. 2013; Hoffman *et al*. 2014; Knief *et al*. 2015; Bérénos *et al*. 2016; Hess *et al*. 2016; Prince *et al*. 2016) and there are many EEB researchers applying their genomics expertise to improve conservation outcomes for threatened species, including two of our co-authors (MK, AWS). In addition to the EEB sphere, there are conservation geneticists (e.g., our co-authors SJG, TRB, MLH, TES) who are successfully venturing into conservation genomics through collaborations with colleagues in another applied discipline well-versed in genomics: primary industry (a collective term referring to scientists in agriculture, fisheries, forestry and horticulture; such as our co-authors RE, JM, RM, PW). Through building these cross-sector relationships, it has become clear that there is immense potential for conservation geneticists and primary industry scientists to collaborate on applied research that addresses aligned questions using similar genomic approaches. In this opinion piece, we use our experience as a collaborative group of New Zealand-based scientists to argue that building strong relationships between conservation genetics and primary industry can lead to improved genomic outcomes for both disciplines and offer advice on how to best build meaningful cross-sector relationships.

Conservation genetics and genomics

Before discussing mutually-beneficial genomic synergies between conservation genetics and primary industry, we feel it is important to first address what conservation genetics is, what can be gained by using a genomic approach and what obstacles may impede geneticists from adopting genomic technologies. Conservation genetics is a subdiscipline of conservation biology (Soulé 1985) which uses genetic data to inform the management of threatened species in collaboration with conservation practitioners (Frankham 1995; Avise 2008; Frankham 2010b; Haig *et al*. 2016). While there is overlap between the fields of conservation genetics and EEB, we distinguish conservation genetics as an applied subdiscipline with

direct implications for the management and of threatened species. Many threatened taxa have experienced significant population declines (i.e., demographic bottlenecks, see Keller *et al*. 1994), leading to small populations that are susceptible to genetic factors (i.e., loss of genetic diversity, inbreeding and inbreeding depression) associated with extinction risk (Frankham 1995). Conservation geneticists have traditionally used few targeted neutral genetic markers including mitochondrial sequences, microsatellites and amplified fragment length polymorphisms (AFLPs) to measure inbreeding, relatedness and genetic diversity within threatened populations, estimate population genetic structure and gene flow among threatened populations, delineate species boundaries in threatened taxa and detect hybridisation and introgression between threatened and non-threatened species (Allendorf *et al*. 2010; Ouborg *et al.* 2010).

Advancements in HTS technologies are enabling the development of genomic resources for threatened species including the *de novo* assembly and annotation of high-quality reference genomes (e.g., Li *et al.* 2014, Zhang *et al.* 2014) and characterization of a large number genome-wide markers such as single-nucleotide polymorphisms (SNPs) (e.g., Benestan *et al*. 2015; Kraus *et al*. 2015; Lemay *et al*. 2015). For conservation geneticists who have traditionally used small panels of neutral genetic markers to estimate population genetic parameters above and below the species level, HTS technologies are appealing as they enable an affordable means to discover and genotype a large quantity of genome-wide SNPs (Avise 2010; McCormack *et al*. 2013; Shafer *et al*. 2015) and these large SNP datasets are more representative of genome-wide variation and can result in higher resolution estimates of population genetic parameters (Väli *et al*. 2008; Ljungqvist *et al*. 2010; Santure *et al*. 2010; Taylor *et al.* 2015). In the field of conservation genetics and EEB, a small but rapidly growing number of empirical studies have demonstrated the utility of genomic markers in

estimating population genetic structure and gene flow (Bowden *et al.* 2012; Dierickx *et al.* 2015; Lew *et al.* 2015; Oyler-McCance 2015), estimating relatedness (Bérénos *et al*. 2016), measuring genome-wide diversity (Robinson *et al*. 2016) and detecting hybridisation and introgression (Hohenlohe *et al*. 2013). We anticipate even more conservation geneticists will begin to embrace HTS technologies as empirical evidence demonstrating the superiority of using genomic markers to inform conservation decisions grows and the costs of doing so diminishes (Box 1).

The paradigm underlying many conservation genetic studies is that a genetically diverse population as measured by neutral genetic markers is also likely to be functionally diverse (Bataillon *et al*. 1996) and therefore better able to adapt to environmental change (Frankham 2005). While many have aspired to move past this paradigm, it remains entrenched in most conservation genetic studies that use neutral markers (Caballero & García-Dorado 2013; Vilas *et al*. 2015). As a result of the lack of empirical data on functional genetic diversity in species of conservation interest, beyond studies that include immunocompetence genes like those in the major histocompatibility complex and toll-like receptors (reviewed in Grueber 2016), it has been difficult to assess the validity of this conservation genetic paradigm. Further, even if supported by empirical data, neutral genetic data might not be a suitable proxy for functional genetic data for threatened species. For example, the translocation of individuals from a large genetically diverse population to supplement a small genetically depauperate population might introduce new genetic diversity (Weeks *et al*. 2011; IUCN 2013), but it might also inadvertently lead to outbreeding depression if source and recipient populations are each locally adapted (Edmands 2007; Frankham *et al*. 2011, but see Frankham 2015; Whiteley *et al.* 2015; He *et al*. 2016).

There is exceptional interest in using a conservation genomics approach to detect regions of the genome that underlie phenotypic variation linked to fitness in threatened populations (i.e., adaptive variation; Luikart *et al.* 2003; Kohn *et al.* 2006; Ouburg *et al.* 2010; Angeloni *et al.* 2011; Harrisson *et al.* 2014; Shafer *et al.* 2015). There are several methods available to study adaptive variation, including gene mapping approaches (i.e., genome-wide association studies or GWAS, and quantitative trait loci mapping or QTL; Slate *et al.* 2010; Stapley *et al.* 2010), outlier locus analysis (Luikart *et al*. 2003; Haasl & Payseur 2016), and selective sweep mapping (Pardo-Diaz *et al*. 2015). However, determining the genetic basis of phenotypic traits, especially those linked to fitness, is complex, owing to the fact that most fitness-related traits are likely to be controlled by multiple loci (Savolainen *et al*. 2013) and many are likely to be under at least some environmental influence (Falconer & Mackay 1996; Lynch & Walsh 1998). In addition, the success of these approaches is often contingent on large sample sizes (e.g., Ball 2005) which will be challenging to generate for most species of conservation concern.

While there are challenges associated with the detection of adaptive variation in threatened populations (reviewed in Shafer *et al.* 2015), there is potential to answer new questions previously not tractable by employing small sets of targeted genetic markers. In particular, an understanding of the genetic basis of fitness traits will allow more robust predictions of the evolutionary potential of threatened species (Ouberg *et al*. 2010; Harrisson *et al*. 2014), including a better understanding of genetic trade-offs between traits that might constrain adaptation (Slate *et al*. 2010). Further, identifying loci underlying local adaptation is likely to help identify candidate populations for conservation translocations (Seddon 2010; He *et al*. 2016). Finally, identification of genes responsible for detrimental traits associated with inbreeding depression will have immediate impact on the management of threatened species,

especially where matings between individuals are managed (e.g., captive populations; Angeloni *et al.* 2011; Harrisson *et al.* 2014; Shafer *et al.* 2015).

Despite having been available for over a decade (Margulies *et al.* 2005), a limited number of publications have applied HTS technologies to conservation (Shafer *et al.* 2015, 2016a; but see Garner *et al.* 2016), with the term 'conservation genomics gap' first being used in 2015 to describe the paucity of conservation geneticists using HTS technologies to inform conservation management (Shafer *et al.* 2015). While there are a growing number of examples that show how genomic data is being used to inform conservation decisions (Gardner *et al.* 2016; but see Shafer *et al.* 2016; see Fig. S1) and many conservation geneticists who are currently producing HTS datasets, there has been a substantial time lag between when these techniques have become available and uptake by the conservation research community, especially in comparison to other applied genetic disciplines like primary industry (e.g., agriculture, fisheries, forestry, and horticulture; see Fig. 1). In addition, much of the uptake in conservation biology has been restricted to threatened wild fish stocks (Garner *et al*. 2016; Shafer *et al*. 2016). Of the 51 articles in Fig. 1 classified as 'conservation genomics', 30% pertained to the management of declining, over-fished or threatened commercially fished species (e.g., Atlantic salmon, *Salmo salar*; orange-roughy, *Hoplostethus atlanticus*; delta smelt, *Hypomesus transpacificus*), which provides an excellent example of how conservation genomic research can also be relevant to other scientific disciplines including primary industry (e.g., these articles were classified as both 'conservation genomics' and 'primary industry' in Fig. 1).

Shafer *et al.* (2015) predominantly attribute the conservation genomics gap to a persistent disconnect between academia and real-world conservation issues. We agree strong relationships between academics and conservation practitioners are crucial, but argue the conservation genomics gap as defined by Shafer *et al.* (2015) is more akin to a 'research-implementation gap' (Knight *et al.* 2008; Hogg *et al*. 2016). Indeed, if strong relationships between academics and conservation practitioners are absent, the likelihood that *any* research will be translated into conservation action is exceptionally low (Haig *et al.* 2016). Here, we predominantly attribute the apparent shortage of conservation geneticists using HTS technologies (i.e., the conservation genomics gap *sensu stricto*) to several interconnected challenges associated with the generation, analysis and interpretation of genomic data.

Prior to identifying these interconnected challenges, we recognise some questions in conservation are still being readily addressed with genetic data (e.g., Dowling *et al*. 2015; Li *et al.* 2015a; Pacioni *et al.* 2015; Trask *et al*. 2015; Cubrinovska *et al.* 2016; Hammerly *et al*. 2016; Overbeek *et al.* 2016). We anticipate studies such as these to persist, at least in the short-term, because existing panels of genetic markers remain a sufficient low-cost option in some situations (Angeloni *et al.* 2011; McCormack *et al.* 2011; McMahon *et al.* 2014). Although we acknowledge that direct cost can be a factor contributing to the conservation genomics gap, we do not think it underpins it, especially when reduced-representation approaches (e.g., restriction-site associated DNA sequencing, genotyping-by-sequencing, exome capture, and RAD Capture; Baird *et al*. 2008; Elshire *et al*. 2011; Jones & Good 2015; Ali *et al*. 2016) make it possible to characterize tens-of thousands of SNPs in hundreds of individuals for non-model species at a lower cost than developing and screening relatively few novel microsatellite markers (Narum *et al*. 2013; Andrews *et al*. 2016; Box 1). Beyond direct cost, the shortage of high-quality reference genomes is an often cited impediment to

SNP discovery and genotyping for non-model species (e.g., Allendorf *et al*. 2010; Ouberg *et al.* 2010; Shafer *et al*. 2015), particularly when approximate SNP location is of interest (e.g., Kardos *et al*. 2015). However, an ever increasing number of high-quality and high-coverage genomes are becoming available (Ellegren 2014). It has also become apparent that low-coverage draft genomes (sometimes referred to as 'landing-pad' or 'skim' genomes), or even highly-quality and high-coverage genomes of closely related taxa, can enable reference-guided mapping assembly and SNP characterization in some taxa (Card *et al*. 2014; Wang *et al*. 2014). The lack of bioinformatic expertise and pipelines required to analyze large population genomic datasets has also been frequently cited as a challenge that precludes the use of HTS technologies in conservation (e.g., McCormack *et al.* 2013; Shafer *et al*. 2015). Steep analytical learning curves are generally associated with new technologies, particularly for rapidly advancing fields like genomics where bioinformatic expertise is needed to analyse large genomic datasets. However, the analysis of large population genomic datasets is no longer exceptional. For example, in regards to SNP discovery and genotyping alone, several comprehensive bioinformatic pipelines are readily available (e.g., Puritz *et al*. 2014; Glaubitz *et al*. 2014; Herten *et al.* 2015; Sovic *et al*. 2015; Melo *et al*. 2016).

Depending on the conservation genetics project at hand, one or a combination of the challenges listed above might impede conservation geneticists from transitioning to HTS technologies. Given the recent developments in HTS technologies and the potential it has for benefitting conservation outcomes, we suggest it is time for researchers to start sharing practical advice on how to expedite the transition from conservation genetics to conservation genomics. Here, we argue that an effective and efficient way to navigate the conservation genomics gap is to capitalise on emerging synergies between conservation genetics and

primary industry, and demonstrate how building strong relationships between these two disciplines is leading to mutually-beneficial genomic outcomes.

Strong Relationships Lead to Mutually Beneficial Genomic Advances

Conservation geneticists are skilled at building strong relationships in an interdisciplinary landscape to improve conservation outcomes (Haig *et al.* 2016; Hogg *et al*. 2016). However, by pushing the boundaries of the conservation 'silo', conservation geneticists will be better able to navigate the conservation genomics gap if they forge novel relationships with scientists that have shared genomic goals, albeit in a different discipline such as primary industry (Fig. 2). As a discipline, primary industry represents a diverse group of scientists from universities, private institutions and government organisations that apply scientific data to the benefit of primary production output (e.g., meat, fish, eggs, dairy, fruits, vegetables, fibers and timber). Some of the early draft genomes were published to improve commercial outcomes, including rice (*Oryza sativa*; Goff *et al*. 2002), red jungle fowl (*Gallus* gallus; Hillier *et al*. 2004), silkworm (*Bombyx mori*; Xia 2004) and cattle (*Bos taurus*; Schibler *et al.* 2004). With these early reference genomes and the accumulation of massive SNP datasets coupled with phenotypic data, many primary industry scientists have years of expertise with the application of genomic data. Approximately 1,981 HTS studies using genomic data have been published in primary industry from 2005-2015, which outnumbers those produced in conservation biology by more than an order of magnitude (Fig. 1).

Conservation has already benefitted from genomic resources provided by primary industry. For example, genomic resources developed for cattle including the draft genome (Schibler *et al.* 2004) and the Bovine SNP chip (Gunderson *et al*. 2005; Steemers *et al*. 2006;

Matukumalli *et al*. 2009) have been used to estimate the extent of introgression from cattle to American bison (*Bison bison;* Halbert *et al.* 2005), measure genomic variation in American and European bison (*B. bonasus*; Pertoldi *et al*. 2009) and develop genomic resources for scimitar-horned and Arabian oryx (*Oryx dammah* and *O. leucoryx*, respectively; Ogden *et al.* 2012). Similarly, genomic resources developed for domestic sheep have been used to describe genome-wide diversity and assess genetic rescue for bighorn sheep (*Ovis caanadensis*; Poissant *et al*. 2009; Miller *et al*. 2012). Of course, there are species of mutual interest to both conservation and primary industry, including species in the fishery and forestry sectors (e.g., Monterey pine, *Pinus radiata* D.Don; New Zealand tōtara, *Podocarpus spp.*; chinook salmon, *Oncorhynchus tshawytscha*; orange roughy, *Hoplostethus atlanticus*) and therefore genomic resources produced by one discipline can be easily used by the other (Dillon *et al*. 2013; Larson *et al*. 2014; da Silva *et al*. 2015; Marshall *et al*. 2015). We anticipate conservation geneticists may opt to use closely-related commercial or model species to inform adaptive variation studies in threatened species, given that gene-mapping approaches are contingent on large sample size (Ball 2005; see discussion above) and the small census size of threatened populations may be inadequate.

Collaborations between conservation geneticists and primary industry scientists are logical because researchers in these two disciplines are beginning to address similar questions in an applied genetic discipline (see Table 1). For example, primary industry scientists have been using neutral genome-wide SNPs to calculate inbreeding coefficients in sheep (*Ovis aries*; Li *et al*. 2011), reconstruct parentage assignments in cattle (Hayes *et al*. 2011) and calculate diversity measures for genetic improvement in poultry (red jungle fowl, Muir *et al.* 2008; domestic turkey, *Meleagris gallopavo*, Aslam *et al*. 2012). Pipelines that have been used or developed to address these questions in commercial species are likely to be of interest to

conservation geneticists, but are sometimes published in discipline-specific peer-reviewed journals such as the *Journal of Dairy Science* or *Plant Biotechnology Journal* (e.g., Allen *et al*. 2012; Li *et al*. 2015b). Similarly, there are some conservation genomic articles from non-academic sources that are not represented in peer-reviewed literature (Garner 2016). These examples highlight how relationships between conservation genetics and primary industry scientists can enable the dissemination of discipline-specific publications and will allow scientists from both disciplines to learn about recently developed pipelines.

Understanding the genetic basis of desired commercial traits is also a main focus in primary industry (Womack 2005; Tuberosa & Salvi 2006; Sellner *et al.* 2007; Collard & Mackill 2008; Neale & Kremer 2011; Sonah *et al.* 2011; Hu *et al*. 2013). Primary industry has benefitted from collaboration with researchers in human health to determine the genetic basis of phenotypic traits in complex pedigrees and structured populations using QTL mapping and GWAS (George *et al.* 2000; Aulchenko *et al.* 2007; Price *et al.* 2010). In turn, these gene mapping approaches have been successfully applied to understanding the genetic basis of ecologically relevant traits in many wild populations (Schielzeth & Husby 2014). While there are numerous research groups outside of primary industry exploring adaptive variation (e.g., Rietveld *et al*. 2013; Brachi *et al*. 2015; Chaves *et al*. 2016), we anticipate that conservation geneticists in particular will benefit from forging relationships with primary industry scientists given that both groups work in an applied discipline with species characterised by small effective population sizes. Additionally, there is potential for conservation geneticists to adopt a genomic selection approach (e.g., Heffner *et al*. 2009; Hayes *et al*. 2009) to generate breeding values to inform the selection of individuals for captive breeding. Lastly, we recognise that both conservation geneticists and primary industry researchers routinely work with species with complex genomes (Clevenger *et al*. 2015) and therefore researchers

from these two disciplines have an opportunity to work together and think of creative bioinformatic solutions for species that present bioinformatic challenges (Box 3). Given these commonalities, synergies between both conservation genetics and primary industry can lead to the development of improved HTS techniques and pipelines to address mutual problems in species of both conservation and commercial interest (Box 2; Box 3; Table 1).

Relationships between conservation geneticists and primary industry scientists can result in improved commercial outcome for primary species as well. Conservation geneticists strive to preserve genetic diversity and the ecological and evolutionary processes that generate it (Groom *et al*. 2006; Haig *et al.* 2016). There is growing discussion among primary industry scientists regarding the need for commercial breeding programmes to maximise genetic diversity and minimise inbreeding (Medugorac *et al*. 2009; Windig & Engelsma 2010; Joost *et al.* 2011; Lenstra *et al.* 2012; Pryce *et al.* 2012; Kristensen *et al.* 2015). Livestock and crops are often of a small effective population size (i.e., $N_e < 100$) due to many generations of artificial selection for desired traits and are thus susceptible to loss of genome-wide variation via inbreeding and genetic drift (Windig & Engelsma 2010; Leroy *et al.* 2013; Kristensen *et al.* 2015; Jiménez-Mena *et al.* 2016; Shepherd *et al*. 2016). There is evidence for inbreeding depression in rare breeds, such as cashmere goats (*Capra aegagrus*; Dai *et al.* 2015), Iranian Guilan sheep (Eteqadi *et al.* 2015) and Iberian pigs (*Sus scrofa*; Saura *et al.* 2015). There is also an increasing awareness of the risks associated with deploying very few genotypes, particularly in the presence of novel crop pathogens (Kim *et al*. 2015) and an increasing concern among rare breeds regarding the loss of genetic variation associated with traits that might be useful in future markets (e.g., Catalonian donkey *Equus africanus*, Gutierréz *et al.* 2005; Famennoise poultry, Moula *et al.* 2009; black Slavonian pigs, Luković *et al.* 2012). Conservation geneticists have many years of expertise regarding the conservation genetic

management strategies for threatened species (Frankham 2010a). As a consequence, conservation geneticists can provide this biodiversity expertise to commercial species for improved primary production (Fig. 2).

Conservation biologists and primary industry scientists also share similar goals regarding how best to mitigate the impact of climate change (Kristensen *et al*. 2015). For example, plant and animal breeders are prioritizing the selection of heat-tolerant plants (Ye *et al*. 2015) and low-emission animals (Hayes *et al*. 2013) and conservation scientists are debating a role for intentional introgression of desired phenotypic traits (e.g., heat tolerance) among locally adapted species or populations (Hamilton & Miller 2015; Kovach *et al.* 2016; Miller & Hamilton 2016). Given these shared goals, there is merit for scientists in primary industry and conservation to work together to maintain the evolutionary potential of commercial and threatened species in a changing climate.

A compelling rationale for building strong relationships between primary industry and conservation biology is that scientists in both disciplines conduct applied genetic research. Whereas primary industry scientists respond to the needs of primary industry practitioners (i.e., plant and animal breeders, farmers, fishermen and loggers), conservation scientists respond to the needs of conservation practitioners (i.e., wildlife managers and policy makers; Gordon *et al*. 2014; Haig *et al*. 2016). Considering the research-implementation gap that has been discussed in conservation genetic and genomic literature (Knight *et al*. 2008; Laikre *et al*. 2010; Shafer *et al*. 2015; Taylor & Soanes 2016), researchers from conservation genetics and primary industry can collaborate on how to best communicate research needs and results between scientists and practitioners. In the policy arena, both conservation geneticists and primary industry scientists work to develop improved policy regarding the utilisation and

dissemination of genetic and genomic information (e.g., the *Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization*, https://www.cbd.int/abs; the *International Treaty on Plant Genetic Resources for Plants for Food and Agriculture*, http://www.planttreaty.org) and we anticipate that relationships between the two disciplines will allow for discussion on how to best form policy regarding the application of genomic information to threatened and commercial species.

Cross-sector collaborations will provide exciting opportunities to strategize how best to engage with stakeholders (e.g., private landowners, local governments, and research-funding bodies; Jacobson & Duff 1998; Dubbeling & Merzthal 2006); but where we see an even greater opportunity for considerable gains is for conservation geneticists and primary industry scientists to learn from one another about the importance of building meaningful partnerships with local and indigenous communities. Partnering with these communities enriches conservation and primary industry science because it creates research projects that are informed by the traditional knowledge and needs of these communities from the initial research proposal to the final report. In New Zealand, scientists and practitioners have clear directives to engage with Māori (indigenous peoples of Aotearoa/New Zealand) regarding the management of taonga (treasured) species (i.e., *Ko Aotearoa Tēnei/This is New Zealand*, conventionally known as WAI 262, http://www.waitangitribunal.govt.nz/) and various approaches have been developed to facilitate such engagement (Tipene-Matua & Henaghan 2007; Wilcox *et al*. 2008; Hudson *et al*. 2010). In addition, researchers are required to consult with relevant Māori tribes (iwi or hapu) when applying to receive permits for scientific research on taonga species from the Department of Conservation. New Zealand endemic species of cultural importance include threatened species (e.g., tuturuatu/shore plover and

kakī/black silt; Box 1) and commercial species (e.g., pōrohe/green-lipped mussel, *Perna canaliculus*) and therefore we urge conservation genetic and primary industry scientists to collaborate on how to build productive partnerships with relevant Māori communities to develop research that is responsive to the needs and expectations of those communities. Beyond New Zealand, researchers based in any of the 92 countries around the world that are signatories to the *Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization* (https://www.cbd.int/abs/) have an opportunity to do the same. However, we argue that as global citizens, all scientists should be acting as if their country was a signatory, because as we get closer to generating population genomic datasets that include whole genomes for species of cultural importance we need to be more aware of how these genomic resources can affect and benefit local and indigenous communities.

Moving Forward

While multi-tasking empirical research, relationships with practitioners, stakeholders and interdisciplinary partnerships can be cumbersome, we are confident that the biggest gains in both conservation genetics and primary industry will be made under this approach. Given the mutual problems that can be solved when conservation geneticists and primary industry scientists work together, we encourage scientists in both disciplines to be leaders in interdisciplinary research and we offer the following advice on how to best forge these relationships:

1. *Get out of your silo.*

The first step to building successful interdisciplinary relationships is for researchers to get out of their silos and meet people with aligned research goals across disciplines. To accomplish this task for conservation genetics and primary industry, we advocate for small (<100 people) and diverse cross-sector meetings that allow participants from academia, government agencies and private institutions to actively engage with every presentation, especially those outside of their silos. In a New Zealand context, annual meetings such as MapNet (see Box 3), the Canterbury 'Omics Symposium, and the Queenstown Research Week exemplify small, diverse, cross-sector meetings that allow scientists from both conservation and primary industry to meet and expand their research networks. For larger countries, these diverse and small meetings might be more effective on a regional versus a national level. In addition to meetings, we encourage conservation geneticists and primary industry scientists to attend genomic and networking workshops to meet people with aligned vision for genomic research, albeit in another discipline.

2) Practice leadership in interdisciplinary research.

The second step to forging mutually beneficial partnerships between conservation and primary industry is to actively communicate with and collaborate with researchers outside of one's silo. Doing so invariably requires leadership, respect and motivation to tackle shared problems (see Table 1), generally by expanding your own research programme to incorporate collaborative interdisciplinary projects between conservation and primary industry (e.g., Banks 2004; Knowler & Bradshaw 2007; Hobbs *et al.* 2008; Blank 2013; Sardinas & Kremen 2015; Box 3). Upon launching these collaborations, it is essential that leaders from both parties open an honest dialog concerning expectations, limitations, and potential hindrances to interdisciplinary work such as intellectual property issues. If collaborative groups choose to develop new methods or bioinformatic pipelines, we encourage these groups to test these

tools on different species representing a wide-range of genomic complexities (i.e., ploidy levels, genome size and number of repetitive elements, see Table 1) so these tools are robust and widely applicable to any research study (see also Box 2; Box 3). We also advocate for these collaborative groups to develop methods and pipelines that are open-source (see Box 2), which inspires others to use and improve upon cross-disciplinary tools. Pursuing co-funding opportunities between conservation and primary industry can be an excellent means of building mutually beneficial research collaborations, especially given that some grant providers favor collaborative proposals that tackle complex problems with broad research impact (Ledford 2015; but see also Bromham *et al*. 2016). Worldwide, there are groups that are forming to tackle complex problems through an interdisciplinary approach, including the Virtual Institute of Statistical Genetics (see Box 3) and Te Pūnaha Matatini (translated to "the meeting place of many faces", http://www.tepunahamatatini.ac.nz/). As leaders from conservation and primary industry initialise interdisciplinary research, we encourage the formation and utilisation of these groups to facilitate the scientific process and encourage the involvement of new partners.

3) Promote a community of interdisciplinary research.

Leaders in both the conservation and primary industry sphere can go beyond collaborating with interdisciplinary scientists to promote a culture of interdisciplinary research. To accomplish this, we encourage editorial teams at conservation and ecology and evolution journals with a broad readership like *Molecular Ecology* to periodically invite perspective articles from colleagues in primary industry. We equate this approach to the recent decision made by the editorial team at *Animal Conservation* to invite submissions from conservation practitioners so conservation academics can better understand the needs and challenges of real-world conservation (Gordon *et al.* 2014). Leaders who are organising meetings and

conferences in primary industry, conservation and genomics can strive to incorporate cross-sector talks and break down organisational silos by minimising field-specific sessions, as proposed by Taylor & Soanes (2016) and practiced by cross-sector meetings like MapNet (see Box 3). We also challenge scientists in both primary industry and conservation to become good interdisciplinary mentors to promote a culture of interdisciplinary research. This can involve mentors in conservation and primary industry promoting genomic seasonal internships or research positions to students in different silos. Not only will this encourage an interdisciplinary field, but it will also produce well-rounded and informed students with excellent inter-personal skills and a network of colleagues to help solve shared problems.

After relationships between conservation genetics and primary industry are forged, we do not anticipate relationships will end once genomic gains are made in both disciplines. Instead, we envision these relationships will continue to grow and enable both disciplines to problem solve and incorporate new technologies for the improvement of threatened and commercial species. With other emerging techniques being discussed and used in both conservation and primary industry, including other -*omic* techniques (e.g., transcriptomics, proteomics, metabolomics; Diz & Calvete 2016; Todd *et al*. 2016), epigenetic studies (Verhoeven *et al*. 2016) and genome editing (Johnson *et al*. 2016), we expect conservation genetics and primary industry to continue to collaborate and solve mutual problems while incorporating new technologies in an applied discipline.

We are confident that building strong interdisciplinary relationships will enable genomic advances in both conservation genetics and primary industry. However, we appreciate our colleagues in the global conservation community may be pursuing different strategies to successfully navigate the transition from genetics to genomics and we look forward to

hearing about them in due course. In the meantime, our hope is that new technologies including genomics will be effectively incorporated into applied genetic disciplines like conservation and primary industry, because there is much to gain by using HTS technologies to improve outcomes for the world's threatened and commercial species.

Acknowledgements

We appreciate the constructive insights from all anonymous reviewers of this article, particularly in regards to comments that helped us shape the action plan for interdisciplinary research between conservation genetics and primary industry. We thank Margaret Paterson, Mauricio Gonzales Chang and Ilina Cubrinovska for their assistance with the literature search. We are grateful to Paul Gardner for inadvertently inspiring this manuscript. We acknowledge Marty Faville for his valuable discussion. Finally, we thank Leonie Heyder for the tuturuatu image.

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Data Accessibility

Text files including all literature search results presented in Fig. 1 and Supplemental Fig. 1 are available on Dryad: DOI:10.5061/dryad.32j55

Author Contributions

SJG and TES were the lead investigators on this research. SJG and TES designed the research in collaboration with all authors, SJG compiled the literature search, TES, RE, and PW contributed perspective boxes, and all authors wrote the manuscript and provided feedback on the Reviewer's comments.

Table 1. Common genomic issues facing conservation genetics and parallel examples addressed by scientists in primary industry.

Topic	Challenge for conservation genomics	Examples of corresponding research from primary industries
Polyploid genomes	Developing effective tools for genome-wide SNP discovery and genotyping for plants, invertebrates and some vertebrates with polyploid genomes	Genome-wide SNP studies on polyploids[1] including wheat[2], cotton[3], potato[4], peanut[5]
Genetic basis of adaptive variants	Discovery of variants underpinning traits of relevance to conservation including adaptative variation	Trait mapping for economically important traits using GWAS and QTL mapping[6,7] in rice[8], dairy cattle[9], pig[10], soybean[11].
Gene copy number variation	Quantifying genome-wide copy number variation and estimating its contribution to phenotypic variation	Quantifying genome-wide copy number variation and estimating its contribution to economically important traits in apple[12], pig[13], wheat[14].
Inbreeding and Relatedness	Measuring inbreeding (*f*), detecting inbreeding depression, and estimating relatedness (*r*) for small populations to maintain evolutionary potential	Measuring inbreeding (*f*), detecting inbreeding depression, and estimating relatedness (*r*) in sheep,[15] pigs[16,17] and salmon[18] to enhance traits for commercial selection

Clevenger et al. 2015[1]; Allen *et al* . 2012[2]; Byers *et al* . 2012[3]; Uitdewilligen *et al* . 2013[4]; Bertioli *et al* . 2014[5]; Collard & Mackill 2008[6]; Hu *et al* . 2012[7]; Begum *et al* . 2015[8]; Li *et al.* 2015b[9]; Zhang *et al* . 2015[10]; Zhou *et al* . 2015[11]; Boocock *et al* . 2015[12]; Wang *et al* . 2015[13]; Wuerschum *et al* . 2015[14]; Li *et al* . 2011[15]; Herrero-Medrano *et al* . 2012[16]; Silió *et al* . 2016[17]; Dodds *et al* . 2015 [18]

List of Figures

Box 1. The costs of using a conservation genomic approach. *Perspectives are those of Tammy Steeves*.

Since I arrived in New Zealand from Canada in 2004, I have had the privilege of developing conservation genetic management recommendations in collaboration with several Department of Conservation recovery or specialist groups to assist the recovery of endemic taonga (treasured) bird species. To date, these recommendations have been predominantly based on genetic markers, namely mitochondrial sequences or microsatellite genotypes (e.g., Steeves *et al.* 2010; Hagen *et al.* 2011; Overbeek *et al. In press*). In collaboration with primary industry colleagues in the MapNet community (see Box 2 & 3), I recently assessed the direct and indirect costs associated with shifting from a conservation genetic to a conservation genomic approach and decided to develop genomic markers (SNPs) for the endangered tuturuatu/shore plover (*Thinornis novaeseelandiae*; Fig. A) and the critically endangered kakī/black stilt (*Himantopus novaezelandiae*; Fig. B).

Tuturuatu/Shore plover - I was recently invited to be an expert advisor to the Shore Plover Specialist Group. The Specialist Group was interested in sampling captive and wild birds to estimate the extent of population genetic structure, and compare levels of genetic diversity, between captive and wild shore plover. To achieve this, I knew the cost to develop, screen and genotype ~20 polymorphic species-specific microsatellites for 94 individuals (~10K NZD) would be more than using a reduced-representation approach to simultaneously discover and genotype >20,000 SNPs for the same number of individuals (Elshire *et al.* 2011; ~8.5K NZD). I also knew it would be possible to expedite the characterisation of SNPs if I was able to use a reference-guided approach. As a member of the Avian Genome Consortium, I was aware bird genomes are small, compact and highly conserved (Zhang *et al.* 2014), and that one of the newly available high quality bird genomes (killdeer, *Charadrius vociferus*) would likely be an appropriate proxy-reference genome for SNP discovery and genotyping in shore plover because both species are members of the Family Charadriidae (Card *et al.* 2014). Thus, the main driver of my decision to embrace a conservation genomic approach for tuturuatu/shore plover was to ensure that I could develop a comprehensive postgraduate research project that could deliver pertinent results to the Shore Plover Specialist Group in a timely fashion.

Fig. A. Tuturuatu/Shore plover

Kakī/black stilt - As a member of the Kakī Recovery Group, I have used species-specific genetic markers to inform the conservation genetic management of captive and wild kakī populations for many years. For example, I routinely use genetic-based measures of relatedness based on microsatellites to inform captive pairing decisions (as per Hagen *et al.* 2011). However, emerging evidence indicates genetic-based measures are relatively poor indicators of genome-wide diversity, particularly in genetically impoverished species like kakī, and a better indication of genome-wide diversity should be obtained from genomic-based measures of relatedness based on genome-wide SNPs (Taylor *et al.* 2015; Willoughby *et al.* 2015). Thus, the main driver of my decision to generate SNPs for kakī was to establish the Kakī Recovery Programme as an exemplar of 'best practice' conservation genomic management.

Fig. B. Kakī/Black stilt

Box 2. Retrospective and prospective of Genotyping-by-Sequencing (GBS). *Perspectives are those of Rob Elshire*.

In 2007, I joined the Buckler Lab at Cornell University and the next-generation sequencing revolution simultaneously. My first task was to develop a new library preparation method for the nascent Illumina sequencing platform. The technology was not nearly as robust as it is today and the reads were very short (i.e., 32bp in length). Our challenge was to sequence the non-repetitive fraction of the maize genome. To do that we used a combination of digestion by restriction enzymes and gel based size selection to exclude the repetitive fraction. The data generated formed the basis for the first Maize Hapmap paper (Gore *et al*. 2009). When that project neared completion, I was tasked with building a low-cost, high-throughput genotyping method as an extension of my previous work. The overall goal was to develop a genotyping system that would allow simultaneous marker discovery and genotyping and also address the issue of marker discovery bias. Other researcher groups at the time were developing similar methods, as there was a high demand for an affordable and reproducible method of genotyping and it was the next logical thing to try. One aim was to provide enough genetic markers at the right price point to enable plant breeding by genomic selection. To maximise the benefit of our work and encourage others to take what we did and create new methods appropriate for new questions, we made our work openly available. The resultant genotyping-by-sequencing (GBS) method was published in *PLoS One* in 2011 (Elshire *et al*. 2011).

We achieved our goal of developing a new genotyping method that was inexpensive, both in terms of cost per sample and cost per data point (i.e., fractions of a cent per marker). The low-cost and high-throughput nature of GBS allows plant breeders to genotype thousands of plants per cycle in genomic selection driven breeding programs (He *et al*. 2014). Primary industry programmes in animal breeding have also taken up GBS. Unlike microsatellites or SNP chips, no previously generated genomic resources are necessary to deploy GBS. This allows researchers working in non-model species, such as orphan crops (i.e., crops of regional commercial importance, but not global), to take advantage of powerful genomic tools (Varshney *et al*. 2012). The situation for researchers in ecology and conservation biology is not dissimilar to that of those working with orphan crops. The budgets are small, resources meager and the questions are of local importance with small (if any) obvious economic returns. It is no wonder that ecologists were amongst the earliest adopters of GBS.

During the development of the GBS, we tested it on species other than maize. Confident that it worked in a variety of kingdoms, we welcomed interested early adopters to the lab for assistance. Two of those early adopters worked in the ecology space. Dr. Thomas White worked with the invasive bank vole (White *et al*. 2013) in Ireland which had small sample sizes and no reference genome. Dr. Nancy Chen studied the Florida scrub jay and developed a method using GBS data and Mendelian inheritance to improve SNP discovery (Chen *et al*. 2014). It became clear that we had developed a generally useful genomics research tool and it could be used by researchers across disciplines. We had already published the method in an open access journal and provided analysis software under a free software license. To allow researchers to more easily use this technology, we set up a GBS service at Cornell. By early 2016 the Cornell service had performed GBS analysis on over 1,500 species.

After our initial GBS publication, a plethora of method modifications and additional software tools have emerged. The recently published epiGBS method (VanGurp 2016) allows the interrogation of the methylome and does not require a reference genome, thereby extending the utility of the base method greatly. The GBSX toolkit (Herten *et al*. 2015) is a set of software designed to assist in the design of GBS based experiments. Many software packages have been developed to analyse GBS data (e.g., TASSEL-UNEAK, Stacks, GBS-SNP-CROPS, GlbPSs; Lu *et al*. 2013; Catchen *et al*. 2013; Hapke & Thiele 2016; Melo *et al*. 2016) that are appropriate for species without reference genomes. Extensions to the molecular method and new software tools make these types of genomics approaches more broadly accessible; however, barriers to using this technology still exist in many disciplines, including the cost of laboratory and informatics setup and reservations in transitioning to new analytical tools.

Marker technology adoption has a long tail distribution. In 2013, I gave a talk on GBS at the *Molecular Markers in Horticulture Symposium*. Perusing the poster session, I found that researchers were using every type of marker technology that I knew about: from isozymes to GBS. Why were some researchers using cutting edge technologies? Why were others using antiquated, expensive and low information content technologies? Researchers in conservation genomics are in a similar situation. Across disciplines, the biological sciences are encountering rapidly changing technologies and increasingly larger data sets. Industry service providers with expert knowledge and experience, like my small New Zealand-based company (Elshire Group,

Ltd.) and many others, can help bridge the gap. By developing relationships spanning human health, primary industry and conservation, as well as actively participating in research communities like MapNet (Box 3), we can work together to expedite the adoption of genomic technologies applicable to the questions at hand, effectively, efficiently and with confidence.

Box 3. Building strong interdisciplinary relationships: MapNet and VISG. *Perspectives are those of Phil Wilcox*.

MapNet is a genomics collaboration that was formed in 2005 by a collective of New Zealand-based researchers from agriculture, horticulture, forestry and human medical genetics that quickly identified analytical gaps in international statistical genetics research. In response, MapNet members formed the Virtual Institute of Statistical Genetics (i.e., VISG) in 2007 and successfully obtained research funding to address these gaps. Through these synergies, methods developed for large human data sets (e.g., *CNVrd*, *CNVrd2*, *selectionTools*; Nguyen *et al.* 2013, 2014; Cadzow *et al.* 2014) have been successfully applied to apple data to identify genes of interest in commercial species (e.g., Boocock *et al.* 2015). Other workflows, such as the *selectionTools* pipeline developed and applied to human datasets such as the *1000Genomes* human data (Cadzow *et al.* 2014) are applicable to other outcrossed species where genetic maps are available. Recently, these relationships have also expanded to include cross-sector projects with scientists from the EEB and conservation genetics sector, who are able to provide insight into how these pipelines can be more broadly applicable to other applied genetic disciplines.

Critical for these cross-sectoral collaborations is effective and ethical behaviours among researchers, distributed leadership, commitment to an explicitly articulated vision, and effective resourcing for method development and testing. Ongoing cost reductions in both high-throughput sequencing and genotyping will constantly challenge data analyses. Thus collaborations among researchers in primary industry, human medical genetics, EEB and conservation genetics are an effective option to develop and apply genomic methods in a financially limited environment.

The benefits of the above- mentioned collaborations would ensure (a) relevant data analysis tools could be produced by adding relevance and utility to primary sector researchers proposing to develop such tools, and (b) providing a platform for more efficient utilisation of resources such as laboratory spaces and analytical capabilities, further reducing costs and therefore increasing data generation capacity. Collaborating with primary sector researchers working on closely related species would also benefit conservation genetics by improving efficiency. In some cases, the same species may be endangered within its natural range, but be of commercial value in other regions – such as *Pinus radiata*, which is widely planted as an exotic in the southern hemisphere but endangered in its natural range in Baja and northern California. An additional benefit of such collaborations is valuable experience and learnings from primary sector colleagues regarding experiment design, data analyses and interpretation of results. The MapNet collective was formed and run at essentially no cost, by utilising the resources of collaborating institutions and labour of those who were committed to this initiative, thus such cross-sector networks are easy to establish and operate – and often professionally rewarding for all involved.