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Consistent divergence times and allele sharing measured from cross-species application of SNP chips developed for three domestic species

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Abstract

Recent advances in technology facilitated development of large sets of genetic markers for many taxa, though most often model or domestic organisms. Cross-species application of genomic technologies may allow for rapid marker discovery in wild relatives of taxa with well-developed resources. We investigated returns from cross-species application of three commercially available SNP chips (the OvineSNP50, BovineSNP50 and EquineSNP50 BeadChips) as a function of divergence time between the domestic source species and wild target species. Across all three chips, we observed a consistent linear decrease in call rate (~1.5% per million years), while retention of polymorphisms showed an exponential decay. These results will allow researchers to predict the expected amplification rate and polymorphism of cross-species application for their taxa of interest, as well as provide a resource for estimating divergence times.

Keywords: marker development, phylogenomics, population genomics, SNP chip, wild taxa

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Introduction

Marker development is the foundation from which all molecular ecology studies build. Techniques for marker discovery range from relatively low-throughput, targeted approaches (Palumbi 1996) to extremely high-throughput, multilocus methods (Baird *et al.* 2008; Morozova *et al.* 2009) which utilize next-generation sequencers. However, once a resource is developed for one species, it is often taken and applied to close relatives. For example, cross-species application of conserved primers has long been used to study mitochondrial DNA (Kocher *et al.* 1989), forming the basis for DNA barcoding (Hebert *et al.* 2003) and more recently metagenomic and environmental DNA analyses (Taberlet *et al.* 2012). Similarly, cross-species application has been widely used for microsatellite loci (e.g. Schlotterer *et al.* 1991; Primmer *et al.* 1996). Cross-species application of primers allows a researcher to skip development steps such as library construction and cloning, reducing costs and effort.

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Advancing sequencing technology has facilitated development of large panels of single nucleotide polymorphisms (SNPs) (Morin *et al.* 2004; Garvin *et al.* 2010). However, most of these marker sets are developed for model or domestic organisms and not for wildlife species. Development and application of large SNP sets is equally important in wild species where they would enable population genetic analyses writ large, examination of loci under selection, resolution of phylogenetic relationships and provide resources for conservation efforts (Stinchcombe & Hoekstra 2008; Decker *et al.* 2009; Allendorf *et al.* 2010; Seeb *et al.* 2011; Angeloni *et al.* 2012). Cross-species application provides a potential method for rapid marker development if there are genomic resources developed for a closely related relative (Kohn *et al.* 2006). Several recent publications have applied commercially available SNP chips created for domestic animals to wild relatives (Pertoldi *et al.* 2010; Miller *et al.* 2011; Haynes & Latch 2012; Ogden *et al.* 2012). However, all report a decrease in the number of loci that successfully amplify, and low retention of polymorphisms between species.

Here, we characterize the relationship between successful cross-species application of SNP chips and divergence time between the species for which the chip was

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made and the one to which it was applied. We compare results from three SNP chips developed for ungulates: the OvineSNP50 BeadChip (Kijas *et al.* 2012), the BovineSNP50 BeadChip (Matukumalli *et al.* 2009) and the EquineSNP50 BeadChip (McCue *et al.* 2012). Based on predictions from the neutral theory of molecular evolution (Kimura & Ohta 1969; Ohta 1992) and the binding dynamics associated with genotyping via oligonucleotide arrays (Sechi *et al.* 2010), we expected to observe slow declines in call rate as a function of divergence time, and a much more rapid decrease in retention of polymorphism.

Methods

Data sets

Development and genotyping using the OvineSNP50 BeadChip are described in the study by Kijas *et al.* (2012) and Miller *et al.* (2011). DNA from wild sheep and outgroup species (Table S1, Supporting information) was genotyped using the same methods as described for domestic sheep (Kijas *et al.* 2012). Raw intensity data were converted into genotype calls using GenomeStudio, before genotypes with GT score lower than 0.8 were removed. All subsequent analysis of the SNP file was conducted with PLINK (Purcell *et al.* 2007). We extracted loci which were successfully amplified in a given species (>50% of individuals typed), including those mapped to the X chromosome in domestic sheep. We then determined the number of polymorphic loci, that is, those with a minor allele frequency $\geq 1\%$. Data for the BovineSNP50 and EquineSNP50 arrays were collected from previous publications (Table S1, Supporting information). If multiple quality filtering metrics were presented for the same species, we retained only data corresponding to the most stringent criteria.

Analyses

We first considered the percent of markers on a chip that were called for each wild species. Note that in two cases (Pertoldi *et al.* 2010; Haynes & Latch 2012), call rates were presented as averages over all species examined in the respective studies ($N = 3$ for each), all other estimates were species-specific. We then conducted weighted regression of call rate against time to last common ancestor (LCA) for each chip type individually. Weights corresponded to the number of individuals of each taxon that were typed. Estimates of time to LCA came either from the text of the individual studies, or from the studies by Fernandez & Vrba (2005); Hiendleder *et al.* (2008); Steiner & Ryder (2011). Lastly, we assessed whether the relationships differed between chips using ANCOVA, fitting an interaction term among chip type and time to LCA.

To assess retention rate of polymorphic loci, we conducted a single weighted regression of percentage of polymorphic loci (as a function of those called for a species) against time to LCA for all chips pooled using a fitted curve. Samples were pooled given that there were no differences in the call rate among arrays (see Results). All regressions and curve fitting were carried out using R v2.13.0.

Results

The OvineSNP50 Beadchip was applied to 16 wild taxa, and genotyping wild sheep revealed very high call rates (>98%) for species such as bighorn, argali and urial sheep that have LCA *c.* 2.4 MYA or less. The most distantly related species tested using the OvineSNP50 Beadchip (pronghorn antelope; LCA 33.2 MYA) revealed a call rate of 40.8%. These data were combined with six published studies that applied the BovineSNP50 to 74 taxa and EquineSNP50 to 17 taxa (see Table S1, Supporting information). All three chips showed linear declines in observed call rate with increasing time to last common ancestor (Fig. 1, Table 1). There were no significant differences in slope between the three chips (ANCOVA interaction between time and chip type: $F_{2,99} = 0.6173$, $P = 0.5415$). Polymorphism data were not available for eight taxa on the equine array. The relationship between polymorphism and time to LCA for the remaining 94

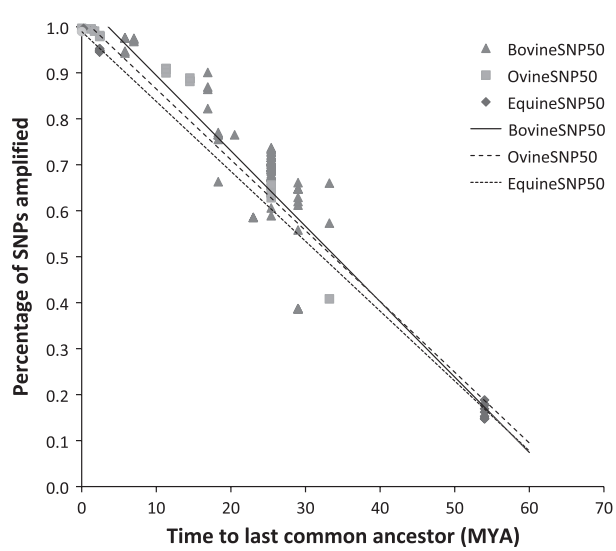

Fig. 1 Scatter plot of call rate (per cent) as a function of time to last common ancestor for each SNP chip examined in this study. Weighted regression lines are shown. MYA is millions of years ago.

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Table 1 Coefficients describing the relationship between call rate and time to last common ancestor for the three SNP arrays. All values are highly significant ($P << 0.0001$)

Chip	Slope	SE	Intercept	SE
BovineSNP50	−0.0164	0.0008	1.0582	0.0154
OvineSNP50	−0.0154	0.0011	1.0188	0.0128
EquineSNP50	−0.0152	0.0001	0.9896	0.0034

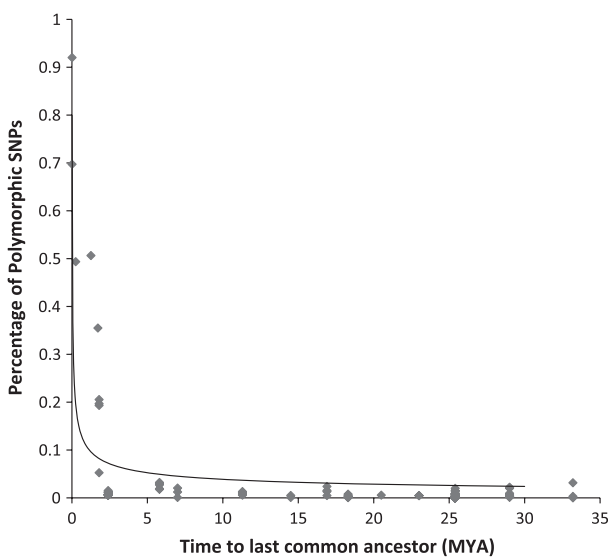

Fig. 2 Scatter plot of percentage of amplified loci which retained polymorphism as a function of time to last common ancestor for all SNP chips examined in this study. A nonlinear weighted regression line is shown. MYA is millions of years ago.

taxa was best described by an exponential decay function of $y = 0.1063x^{-0.4382} - 0.02$ (Fig. 2).

Discussion

Cross-species call rate decreases by about 1.5% with each million-year divergence between the species for which a chip was developed and the species it was applied to. This consistent pattern suggests it would be possible to gauge expected success of application of these chips in taxa of interest before investing in the costs of genotyping and accurately estimate divergence times between taxa. Linear decreases in call rate are consistent with expectations of neutral sequence evolution and heteroduplex formation between an oligonucleotide probe and genomic DNA. Specifically, hybridization is prevented if there are mutations in the flanking sequence of the SNP (Sechi *et al.* 2010). The accumulation of polymorphisms in flanking sequence should fit basic neutral substitution models (Kimura 1968; Ohta 1992) that are dependent on mutation rate, but linear with respect to time.

There was a much more drastic decline in percentage of loci that retained polymorphisms as a function of time to LCA. Low levels of shared polymorphisms are consistent with theoretical expectations as well. The retention or fixation of a SNP is expected to have a logarithmic decline at a rate that is dependent on population size as well as mutation rate (Kimura & Ohta 1969; Ohta 1992). These steep rates of decline may be exacerbated by the use of novel or rare alleles that arose as a result of the domestication process. Our regression indicates that 50% of loci will remain polymorphic only when species are less than *c.* 30 000 years divergent, and application of a chip to species which diverged 3 MYA from the species it was intended for will have only ~5% of amplified loci remain polymorphic. It is interesting to note that the percentage of polymorphic SNPs appears to level off after *c.* 5 Myr divergence. Some level of shared polymorphism is to be expected; however, these shared sites are unlikely to be the result of retention of the same mutation because of selective advantage (Asthana *et al.* 2005) but more likely *de novo* mutations (Nowell *et al.* 2011).

Most of the SNPs discovered via commercial SNP chips are expected to be selectively neutral. For example, 65% of SNPs on the OvineSNP50 BeadChip are thought to be intergenic and not within 2.5 kb of a gene as loci were chosen to achieve approximately even spacing of SNPs across the sheep genome. This pattern is likely to be true for the other chips as well, where loci were also chosen based on spacing throughout the genome. However, an underlying issue with cross-species application of SNP arrays is that the SNPs discovered may be enriched for 'older' shared polymorphisms, and rare or novel variants are missed, introducing some level of ascertainment bias. However, ascertainment bias is inherent in any marker development (Clark *et al.* 2005; Rosenblum & Novembre 2007) and can be compensated for. Prior to formal analysis, loci can be subjected to preliminary screening, such as for deviation from neutrality or examining the distribution of minor allele frequencies, and removed or retained according to the focus of the study at hand. Alternatively, the discovery scheme can be directly factored into the analysis using various algorithms or models that can assess and correct the underlying allele frequency spectrum (e.g. Nielsen & Signorovitch 2003).

As more chips continue to be produced, it will be interesting to investigate what other factors may influence the patterns we observed, such as composition of the original SNP discovery panel or the intended goal of the chip. Although the three chips examined here had different discovery panels both in terms of number of individuals and SNP sources (Matukumalli *et al.* 2009;

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Kijas *et al.* 2012; McCue *et al.* 2012), they were developed with similar goals in mind: broadly, breed discrimination and assisting in targeted trait development through genome-wide association studies. Chips developed using data from multiple breeds or those based on species with different evolutionary histories may lead to different conversion rates (Satkoski Trask *et al.* 2011). An interesting point of comparison will come when chips derived from, and intended for, wild species are available and then applied to other wild relatives. A 'wild' SNP chip may have a larger amount of standing genetic variation to pull from during development, and without the history of artificial selection, polymorphisms may be more likely to be held in common across taxa.

We assessed the transferability of our results for nonungulates using data from two additional studies (Hacia *et al.* 1999; vonHoldt *et al.* 2011). Expected returns very closely parallel the observed results (Table S2, Supporting information), with the exception of higher than expected proportion of polymorphism retention in wolves and coyotes. However, this may be due to continuous interbreeding with domestic dogs, and inclusion of those taxa in the discovery panel (vonHoldt *et al.* 2011).

An alternative to cross-species application of SNP chips for marker discovery and genotyping are various genotype-by-sequencing (GBS) approaches (Davey *et al.* 2011; Elshire *et al.* 2011). These methods are likely to discover a multitude of species-specific SNPs, and avoid ascertainment bias caused by enriching for variants shared across species (though, rare SNPs are still likely to be underrepresented). However, there are some significant limitations when compared with SNP chips. First, error rates are likely to be higher with GBS than SNP chips. GBS approaches rely on pooling multiple individuals that have been labelled with unique barcodes into a single run on a next-generation sequencer. Sequencing reads are then partitioned across individuals and loci, which may result in low coverage for some individual/locus combination and hence genotyping errors, especially, as the number of individuals or loci increases. Sequencing each locus to a greater depth would prevent this problem, but that is only accomplished either by purchasing more time on a next-generation sequencer or by reducing the number of individual or loci examined. SNP chips, on the other hand, have built in redundancy where each locus is present multiple times, and a genotype is called by averaging over all of the individual calls leading to accurate genotypes (Oliphant *et al.* 2002; Steemers & Gunderson 2007). Second, it is more difficult to get a core set of loci genotyped in every individual. This is due to the fact that many GBS methods involve digestion with restriction enzymes that can lead to high variance between individuals on which loci are present in the sequencing library. Some of these limitations can be overcome by imputation of genotypes (Li *et al.* 2009; Pasaniuc *et al.* 2012), provided a reference panel of genotypes is available. In contrast, the same loci will always be present on a SNP chip. Lastly, the relative costs of each method also need to be considered, but these may vary depending on the application and questions addressed in a particular study. These limitations are further exacerbated if one wants to consider multiple species, which will hamper the use of GBS methods in phylogenetic analyses where having homologous regions of the genome is of the utmost importance (McCormack *et al.* 2012, in press).

In many cases, even if only 1% of loci on a 50k SNP chip are polymorphic, those 500 loci would represent a substantial increase in genetic resources available for a wild species. Beyond marker discovery, call rate decrease from Illumina technologies can provide a way to rapidly estimate the divergence time and evolutionary relationship among poorly studied species. In addition to the chips examined here, porcine (Ramos *et al.* 2009), chicken (Groenen *et al.* 2011) as well as various murine and human arrays are available. Thus, these technologies can provide resources in a vast and diverse array of wild species.

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J.M.M. conceived the study, conducted data analyses and drafted the original manuscript. J.W.K., M.P.H., J.C.M., and D.W.C. provided DNA samples and funded the collection of SNP genotypes using the OvineSNP50 BeadChip. All authors contributed analytical guidance

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and provided input to the manuscript throughout it's preparation.

Data Accessibility

All data used in this study can be found in the Tables S1 and S2 (Supporting information).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of species examined with their associated amplification success, percentage of polymorphic loci, and estimate of divergence time.

Table S2 List of taxa used to assess transferability of our results with their associated amplification success, percentage of polymorphic loci, and estimate of divergence time.

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