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OPINION ARTICLE

Cross-species transfer of nuclear microsatellite markers: potential and limitations

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Abstract

Molecular ecologists increasingly require 'universal' genetic markers that can easily be transferred between species. The distribution of cross-species transferability of nuclear microsatellite loci is highly uneven across taxa, being greater in animals and highly variable in flowering plants. The potential for successful cross-species transfer appears highest in species with long generation times, mixed or outcrossing breeding systems, and where genome size in the target species is small compared to the source. We discuss the implications of these findings and close with an outlook on potential alternative sources of cross-species transferable markers.

Keywords: animals, cross-species amplification, DNA sequencing, fungi, microsatellites, plants

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Nuclear microsatellites are currently one of the most popular types of genetic markers for molecular ecology studies. However, molecular ecologists increasingly require universal markers that can readily be transferred between species. Such transferable markers facilitate comparisons among closely related taxa for addressing the mechanisms involved in population divergence and speciation (Noor & Feder 2006), and comparisons among multiple co-occurring species for studying how patterns of diversity at the genetic and community levels interact (Whitham *et al*. 2006).

Ongoing research on the genetic effects of habitat fragmentation in a biodiversity 'hotspot', the Atlantic Rainforest of Brazil (Myers *et al*. 2000), has confronted us with an issue well known to readers of this journal: many species need to be studied in a comparative way while time to do so is running out, in our case due to logging and urban development which reduce remaining forest fragments at a rapid pace. This has prompted us to utilize the potential of cross-species transfer of microsatellite loci in our ongoing studies (Palma-Silva *et al*. 2006; Barbará *et al*. 2007). It has also led us to investigate its potential in other taxa to inform molecular ecologists in similar situations, and the results of our literature search are discussed here. We do *not* focus on interspecific differences in microsatellite mutation rates, constraints on microsatellite evolution, or homoplasy, as these issues have been dealt with elsewhere (e.g. Estoup & Cornuet 1999; Amos 1999). Rather, we focus on the likelihood of successful cross-species transfer measured as the proportions of amplified and polymorphic markers in a large number of animals, fungi, and plants. In doing so, we expand earlier studies by Schlötterer *et al*. (1991), Primmer *et al*. (1996, 2005), Rosetto (2001), and Primmer & Merilä (2002) on the conservation of microsatellite loci in specific groups of taxa. To our knowledge, this is the first comprehensive evaluation of microsatellite cross-species transfer potential across three kingdoms.

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Review of the success of cross-species marker transfer in animals, plants, and fungi

We reviewed 64 primer notes published in *Molecular Ecology*, *Molecular Ecology Notes*, and elsewhere between 1997 and mid-2006, representing a total of 611 cross-species encounters and matching with stringent quality criteria (Table 1). Each study reported cross-transfer results for at least 10 markers and five target taxa within a fully informative table (not just partial presentation in the text). In each original study, successful marker amplification was determined by comparison to expected fragment size and/

Table 1 Summary of the reviewed studies, including the total number of studies, total number of cross-species encounters, and number of cross-species encounters for different taxonomic categories and taxonomic ranges of molecular marker assays

Category	No. of items
Total studies*	64
Total cross-species encounters	611
Cross-species encounters per taxonomic category:	
Vertebrates	311
Invertebrates	114
Plants	155
Fungi	31
Taxonomic range of cross-species amplification†:	
Among species — within genus	301
Among genera — within family	190
Among families — within order	92
Among orders — within class	21

*Each article reported a cross-amplification table based on at least 10 markers and five target taxa. †Seven cases were difficult to classify and are thus not listed.

or direct sequencing of amplified fragments. For each cross-species encounter in each study, we scored the 'percentage of markers amplified' and, among those, the 'percentage of polymorphic markers' as surrogates of transfer success. Then we sought to explain variation in cross-species transfer success in a three-step procedure.

In the *first* step, we used 'taxonomic grouping' and the 'taxonomic range' of cross-species transfer as predictor variables in linear models to inspect the taxonomic distribution of cross-species transfer success (see Table 2 for a key to these variables). The use of taxonomic variables rather than genetic distance based on DNA sequence data was necessary because there is currently no universal molecular 'barcode' across animals, fungi, and plants (Chase *et al*. 2005). The response of marker transfer success to taxonomic predictors was modelled using either least-squares analysis of variance (ANOVA) or a mixed model including 'source species' of microsatellites as a random factor. The latter approach takes into account the lack of independence in cross-species comparisons involving the same source species. In the *second* step, we added organismal and geographical predictor variables to refine the analysis and identify additional patterns. The following organismal and geographical variables were analysed: mating system, geographical distribution, distribution range, and generation time (see Table 2 for factor levels of these variables). We focused on organismal factors rather than molecular properties of individual loci, as the latter have been dealt with in a review of selected animal taxa recently (Primmer *et al*. 2005). The organismal factors we recorded may be related to rates of molecular evolution which are known to vary greatly between taxa (Zhang & Hewitt 2003). We did not include primer annealing temperature (T_a) in the analysis because lowering T_a in cross-species amplifications is now routine. Also, no contrast between anonymous and expressed sequence tag (EST)-derived markers was intended, as this topic has been addressed elsewhere (Pashley *et al*. 2006; Bouck & Vision 2007). Response to organismal and geographical factors was modelled by least-squares ANOVA, because the representation of some of the variables was not sufficiently balanced for running mixed models, and our earlier results showed that the results of both approaches are comparable. For graphical representation, means and standard errors of transfer success for different categories of organismal/geographical factors were plotted after adjusting for differences in the taxonomic range of marker transfer. Residuals from simple one-way ANOVA with taxonomic range as factor variable were used for this adjustment. In a *third* and final step, the effect of variation in genome size (*C* value) on cross-species transfer success was analysed using Pearson's correlation.

Distribution of cross-species transfer success

The results of our analysis contain information on the distribution of the effort invested by the molecular ecology community in testing the potential for cross-species marker transfer, the taxonomic distribution of cross-species transfer success that follows from these tests, and the relationship between transfer success and key organismal and geographical factors.

With respect to distribution of investment, it seems clear that the potential of cross-species marker transfer has been utilized the least where it is needed most: in narrowly endemic and tropical taxa. Our review of 64 informative primer note articles published over a 10-year period revealed only 88 cross-species encounters for tropical target taxa vs. 243 for temperate ones (Table 2 — second column from the left), despite the fact that approximately half of the source species in the reviewed studies were tropical. Likewise, our review revealed only 42 cross-species encounters for narrow endemics vs. 250 for widespread and 96 for regionally distributed taxa (Table 2). The under-representation of endemic taxa is surprising, as endemics should be of great interest to conservation biologists. We suspect that failure to test the transferability of markers in narrow endemics is primarily due to the difficulty of obtaining samples from suitable specimens for the necessary laboratory tests at short notice.

With respect to taxonomic distribution of transfer success, we found a significant effect of 'taxonomic group' and, as expected from previous reports (e.g. Primmer *et al*. 1996; Steinkellner *et al*. 1997), 'taxonomic range of marker assay' on the proportions of amplified and polymorphic markers (Table 3). Reptiles, birds, mammals, and invertebrates other than arthropods clearly fared best within

Table 2 Percentages of amplified and polymorphic markers by taxonomic group, taxonomic range of cross-species amplification, mating system, geographical distribution, distribution range, and generation time

	Amplification***			Polymorphism		
		%			%	
Variable	*n*†††	Mean ± SE	Median	*n*†††	Mean ± SE	Median
Taxonomic group						
Conifers*	5	71 ± 6	66	0	—	—
Monocots†	23	58 ± 7	64	9	27 ± 7	35
Eudicots‡	127	71 ± 2	80	49	48 ± 4	46
Mammals§	84	64 ± 4	82	68	52 ± 4	61
Birds¶	100	53 ± 3	59	38	44 ± 6	41
Reptiles**	5	85 ± 4	88	5	69 ± 11	76
Fishes††	122	57 ± 2	58	68	57 ± 3	57
Arthropods‡‡	95	61 ± 3	63	65	62 ± 3	65
Other invertebrates§§	19	72 ± 7	88	9	77 ± 7	83
Fungi¶¶	31	36 ± 7	20	0	—	—
Taxonomic range						
Between species/within genus	301	73 ± 1	82	175	65 ± 2	67
Between genera/within family	190	60 ± 2	59	96	43 ± 3	42
Between families/within order	92	33 ± 3	25	38	28 ± 6	0
Between orders/within class	21	6 ± 2	0	0	—	—
Mating system						
Primarily selfing	14	54 ± 9	55	5	69 ± 11	76
Mixed	162	65 ± 2	77	67	51 ± 3	49
Outcrossing	405	59 ± 2	62	238	54 ± 2	60
Unknown	30	60 ± 5	59	1	—	—
Geographical distribution						
Tropical	88	59 ± 3	56	39	41 ± 5	33
Tropical-temperate	143	62 ± 3	64	87	57 ± 3	63
Temperate	243	59 ± 2	62	112	58 ± 3	63
Temperate-polar	36	56 ± 5	61	22	56 ± 6	58
Tropical-temperate-polar	19	44 ± 7	46	9	25 ± 11	17
Unknown	82	70 ± 3	79	42	55 ± 4	48
Distribution range						
Narrowly endemic	42	69 ± 5	79	25	59 ± 6	64
Regional	96	58 ± 3	57	44	55 ± 5	56
Widespread	250	56 ± 2	58	123	50 ± 3	55
Unknown	223	65 ± 2	74	119	56 ± 3	57
Generation time						
Annual/semelparous	64	66 ± 3	67	31	63 ± 4	63
Perennial/iteroparous	436	59 ± 2	62	213	53 ± 2	57
Unknown	112	64 ± 3	74	67	53 ± 4	56

*Conifers: Chagne *et al*. 2004. †Monocots: Blum *et al*. 2004; Flanagan *et al*. 2006; Tostain *et al*. 2006. ‡Eudicots: Steinkellner *et al*. (1997); White & Powell (1997); Lanaud *et al*. (1999); Combes *et al*. 2000; Squirrell & Wolff 2001; Hale *et al*. 2002; Escribano *et al*. 2004; Jones *et al*. 2004; Morillo *et al*. 2004; Topinka *et al*. 2004; Perez *et al*. 2006; Porter *et al*. 2006; Terui *et al*. 2006; Salywon & Dierig 2006. §Mammals: Gemmell *et al*. (1997); Ortega *et al*. 2002; Williamson *et al*. 2002; Gaur *et al*. 2003; Dawson *et al*. 2004; Maudet *et al*. 2004; Gunn *et al*. 2005. ¶Birds: Richardson *et al*. 2000; Chbel *et al*. 2002; Martinez-Cruz *et al*. 2002; Maak *et al*. 2003; Dawson *et al*. 2005; Mcrae *et al*. 2005; Rubenstein 2005. **Reptiles: Sinclair *et al*. 2006. ††Fishes: Cairney *et al*. 2000; Iyengar *et al*. 2000; Farias *et al*. 2003; Keeney & Heist 2003; Rodriguez *et al*. 2003; Yue *et al*. 2003; Lippe *et al*. 2004; Rogers *et al*. 2004; Coulibaly *et al*. 2005; Feulner *et al*. 2005; Holmen *et al*. 2005; Perry *et al*. 2005; Vasemagi *et al*. 2005; Ovenden *et al*. 2006; Tonnis 2006. ‡‡Arthropods: Belfiore & May 2000; Mohra *et al*. 2000; Zhu *et al*. 2000; Daly *et al*. 2002; Flanagan *et al*. 2002; Huttunen & Schotterer 2002; Dawson *et al*. 2003; Funk *et al*. 2006; Mavarez & Gonzalez 2006; Schug *et al*. 2004; Shearman *et al*. 2006; Smith *et al*. 2005. §§Other invertebrates: Eackles & King 2002; McMullin *et al*. 2004. ¶¶Fungi: Slippers *et al*. 2004; Wadud *et al*. 2006. ***Successful marker amplification in individual studies was inferred by comparison to expected fragment size and/or direct sequencing of amplified fragments. †††Sample sizes (*n*) refer to the number of cross-species encounters assessed for marker amplification and, among those that amplified, for marker polymorphism. Sample sizes are generally smaller for marker polymorphism because they represent a subset of the samples assessed for amplification, and because not all reviewed studies tested for polymorphism. SE, standard error.

Table 3 ANOVA of the effects of taxonomic group, taxonomic range of marker assay, and interaction between these factors on the percentage of markers amplified (A) and the percentage of markers polymorphic (B) in cross-species amplification tests

A. Percentage markers amplified

	General linear model					Mixed model†	
Source of variation*	d.f.	SS	MS	*F*	*P* value	*F*	*P* value
Taxonomic group	9	126.41	14.05	5.89	**0.000**	13.07	**0.000**
Taxonomic range of marker assay	3	375.40	125.13	52.45	**0.000**	49.60	**0.000**
Taxonomic group × range of assay	11	58.33	5.30	2.22	**0.012**		
Error	580	1383.83	2.39				

B. Percentage markers polymorphic

	General linear model					Mixed model†	
Source of variation*	d.f.	SS	MS	*F*	*P* value	*F*	*P* value
Taxonomic group	7	97.77	13.97	5.71	**0.000**	5.63	**0.000**
Taxonomic range of marker assay	2	111.37	55.69	22.77	**0.000**	19.44	**0.000**
Taxonomic group × range of assay	8	53.13	6.64	2.72	**0.007**		
Error	291	711.55	2.45				

The residuals of both models were weighted by the number of markers assayed in each study. Significant factors at the 0.05 level are indicated with bold type. *For key to taxonomic predictor variables see Table 2. †In mixed models, taxonomic predictor variables were nested within the random factor 'microsatellite source species' and significance was tested using maximum-likelihood estimation. d.f.: degrees of freedom; SS: sums of squares; MS: mean squares.

genera in terms of 'per cent markers amplified' (Fig. 1A). The drop in transfer success to the next level (between genera/within family) was steeper for invertebrates and birds compared to reptiles and mammals, but in birds, an appreciable percentage of markers amplified successfully even between different families (Fig. 1A). The observed patterns are largely consistent with earlier observations by Schlötterer *et al*. (1991), Primmer *et al*. (1996, 2005), Rosetto (2001), and Primmer & Merilä (2002) on specific groups of taxa although, to our knowledge, cross-transferability has never been compared across taxa and kingdoms on this scale. A conspicuous pattern in plants is the greatly reduced chance of successful amplification in monocots compared to eudicots (Fig. 1A). Although observations for fungi were available only for the extremes of the taxonomic range of marker transfer, success rates appear to be intermediate and within the range of other groups of taxa (Fig. 1A). When transfer success was scored as 'per cent polymorphic markers', then birds, reptiles, mammals, fishes, and invertebrates other than arthropods fared best within and between genera (Fig. 1B). Plants clearly fared worse than animals, again with greater transfer success in eudicots than in monocots.

Can organismal or geographical attributes of each taxon predict cross-species transfer success? As visible from the ANOVA shown in Table 4, taxonomic range and taxonomic group clearly explained a greater proportion of the variation than any other factor. Nevertheless, we found a significant effect of mating system and generation time on the per cent of amplified markers (Table 4), with lower amplification success in primarily selfing and short-lived (annual or semelparous) species in our data set (Fig. 2A, D). Lower success rates in selfing species may be explained by a greater likelihood of selfers to accumulate mutations because of smaller effective population size (N_e) (Higgins & Lynch 2001; Lynch & Conery 2003). This may involve transposition, chromosomal rearrangements, local insertion/deletions, or point mutations, all of which could affect conservation of the markers. We note that modes and rates of genome turnover in flowering plants appear to be strikingly different from those observed in animals (Lim *et al*. 2007). Still, our result must be interpreted with care as sample sizes for this particular comparison were unbalanced (Table 2; Table 4). Lower amplification success in annual or semelparous species may be explained by the direct effect of generation time or by indirect effects of differences in metabolic rates (Gillooly *et al*. 2005). We also found a significant negative effect of genome size (*C* value) on cross-species amplification success (Fig. 3). Thus, genome size may not only affect the amplification of microsatellite markers in the source taxon (Garner 2002), but also the success of marker transfer between species. The great variation in amplification success at intermediate genome size ratios in the middle of the graph shown in Fig. 3 is primarily due to fishes (Salmonidae, Carcharhinidae, Clariidae, Scophthalmidae) and reflects large differences in the taxonomic range of cross-species marker transfer in this group.

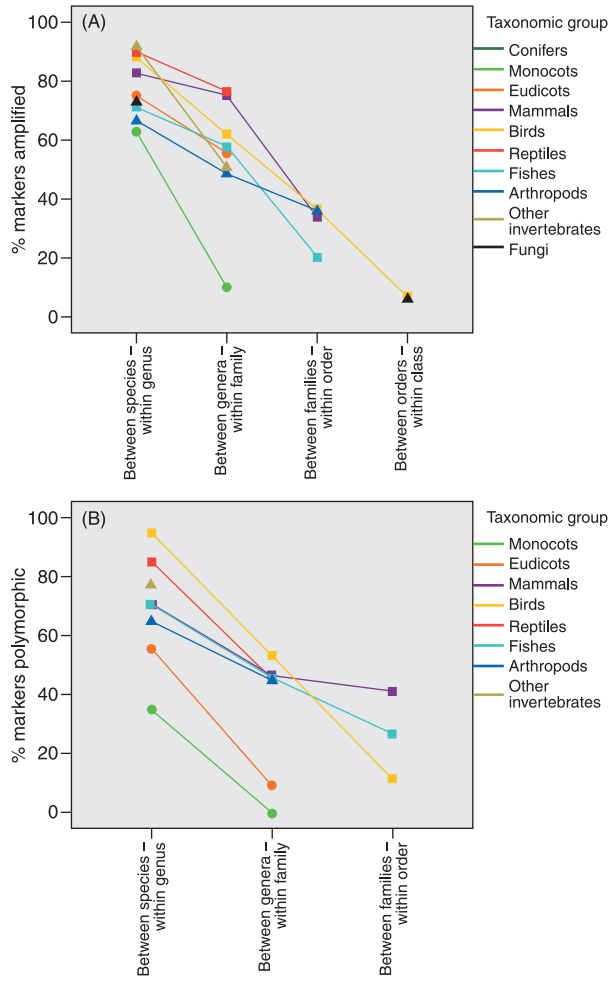

Fig. 1 Mean values for the percentage of markers amplified (A) and, among those that amplified, percentage of markers polymorphic (B) across different taxonomic groups and taxonomic ranges of molecular marker assays for a total of 611 cross-species encounters from 64 studies. The taxonomic groups considered in the analysis are indicated by different colours. In addition, the following symbols help distinguish between major groups of taxa: filled circles for plants, filled rectangles for vertebrates, and filled triangles for invertebrates and fungi. The only mean value available for conifers ('between species-within genus' category) is not visible as it overlaps exactly with the values for fishes and fungi.

All our observations on organismal/geographical variables are for transfer success in terms of marker amplification — no significant effect on polymorphism was found. This suggests that differences in polymorphism upon cross-species transfer are either due to factors not included in our review, or to multiple factors with individual effects too small to be detected here. Reduced marker polymorphism upon cross-species transfer has often been attributed to 'ascertainment bias' whereby a microsatellite chosen to be maximally long in the source species is then likely to be shorter in a new target species (Ellegren *et al*. 1995). It is thought that ascertainment operates in part via a restriction in microsatellite length, such that occasional deletions or internal point mutations lead to shorter and less polymorphic loci upon cross-species transfer (Vowles & Amos 2006). In a previous study of molecular properties recorded for a large number of microsatellites cross-amplified in birds, only the repeat number in the source species had a significant effect on cross-species polymorphism success (Primmer *et al*. 2005).

Conclusions

Our results indicate that cross-species transferability of microsatellite markers is unevenly distributed across taxa (Fig. 1A, B). High amplification success within and between genera in many groups of animals and plants indicates a great potential to use microsatellites and their flanking regions as a source of single- or low-copy nuclear sequences, as suggested by Zhang & Hewitt (2003). Of course, the likelihood of orthology vs. paralogy of cross-amplified loci will have to be evaluated on a case-by-case basis, e.g. based on the evolutionary information inherent in the growing number of complete genomic sequences available (Vision *et al*. 2000; Lynch & Conery 2003; Tuskan *et al*. 2006).

Variation between taxa is even greater when cross-species transfer success is evaluated in terms of marker polymorphism, the ultimate criterion for the direct use of microsatellite length polymorphisms as markers (Fig. 1B). In effect, tests for cross-species transferability of polymorphic markers can be expected to yield returns in most groups of animals within and between genera and even across different families in some cases (> 40% transfer success in mammals, > 25% in fishes, and > 10% in birds at this level; Fig. 1B). By contrast, transferability of polymorphic markers in plants is likely to be successful mainly within genera (success rate close to 60% in eudicots and close to 40% in the reviewed monocots). Between genera, transfer rates are approximately 10% for eudicots, and students of monocots such as orchids or grasses are very unlikely to get away without isolating novel markers from the genomes of new target genera. An exception, in our experience, are large adaptive radiations with low levels of DNA sequence divergence such as Bromeliaceae, where polymorphic markers are readily transferred between species of the same subfamily and beyond (Palma-Silva *et al*. 2006; Barbará *et al*. 2007).

Despite encouraging aspects, it is clear that the potential for cross-species transfer of microsatellites is more limited than molecular ecologists would wish for. Although EST-derived microsatellites may be conserved over larger evolutionary distances, their transfer beyond the genus level often appears to be limited too (Pashley *et al*. 2006; Bouck & Vision 2007). Also, molecular ecology studies increasingly aim at comparing genetic, demographic, behavioural, and breeding system parameters among related species or multiple species co-occurring in the same community. This

Table 4 ANOVA of the effects of taxonomic group, taxonomic range of marker assay, mating system, geographical distribution, distribution range, and generation time, on the proportion of markers amplified across species

	General linear model				
Source of variation*	d.f.	SS	MS	*F*	*P* value
Taxonomic group†	7	151.02	21.57	7.97	**0.000**
Taxonomic range of marker assay	3	279.67	93.22	34.42	**0.000**
Mating system	2	25.05	12.53	4.63	**0.011**
Geographical distribution	4	10.23	2.56	0.95	0.438
Distribution range	2	4.10	2.05	0.76	0.470
Generation time	1	17.01	17.01	6.28	**0.013**
Error	298	807.04	2.71		

The residuals were weighted by the number of markers assayed in each study. Percentage of variation explained by the entire model (R^2) = 36%. Interaction effects were not tested. Significant main effects at the 0.05 level are indicated with bold type. *For factor levels of predictor variables see Table 2. †Reptiles and fungi were excluded from this analysis because of missing data for some of the variables. d.f.: degrees of freedom; SS: sums of squares; MS: mean squares.

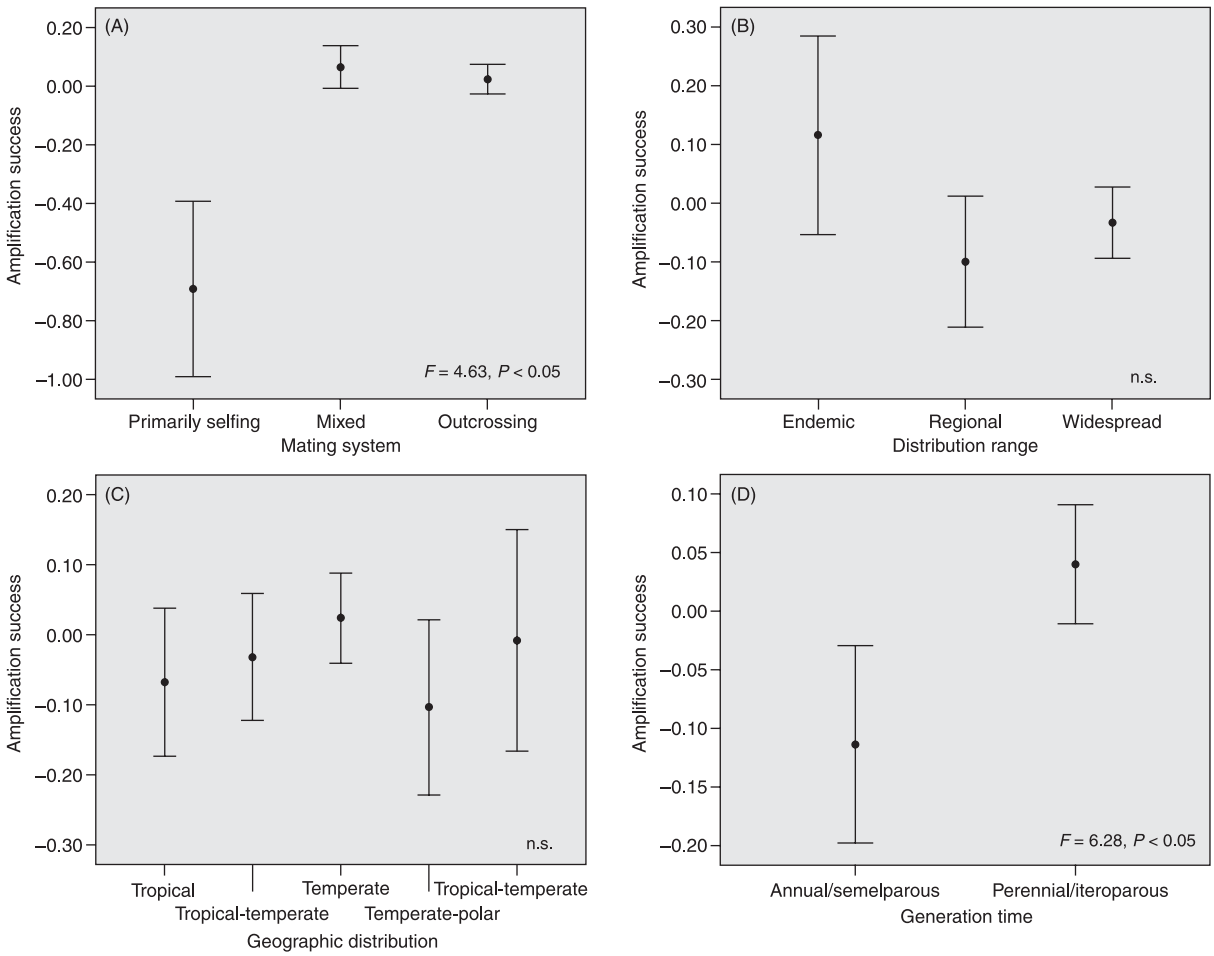

Fig. 2 Effects of four different organismal or geographical factors on the proportion of markers amplified (means ± SE), adjusted for differences in the taxonomic range of cross-species transfer. *X*-axes, from top to bottom panel: mating system (primarily selfing, mixed, or outcrossing), geographical distribution (tropical, tropical-temperate, temperate, temperate-polar, or tropical-temperate-polar), distribution range (narrowly endemic regional), or widespread and generation time (annual/semelparous, or perennial/iteroparous). *Y*-axes: amplification success adjusted for differences in the taxonomic range of cross-species transfer.

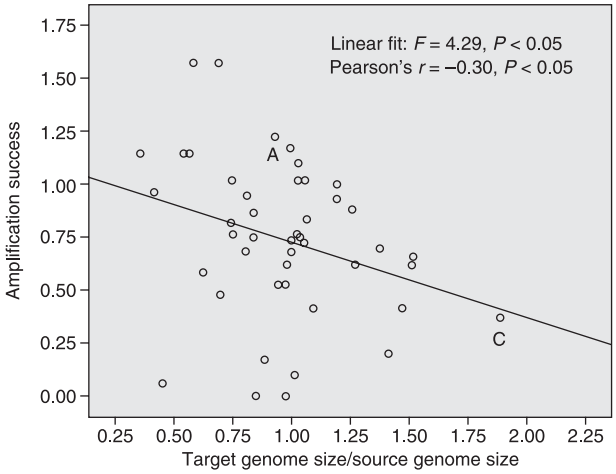

Fig. 3 The relationship between amplification success and the ratio of genome size (*C* value) between target and source species in 45 cases for which genome size estimates were available for both target and source, including plants, fishes, one bird and one insect. Amplification success decreases with increasing genome size in the target species relative to the source. *X*-axis: genome size ratio. *Y*-axes: arcsine-transformed percentages of amplified markers. 'A' and 'C' denote the only available entries for birds (Anatidae) and insects (Culicidae), respectively.

raises issues of interspecific differences in mutation rates, constraints on microsatellite evolution, and homoplasy (Estoup & Cornuet 1999; Amos 1999). Several alternative sources of nuclear markers which may be more easily transferable are currently under development. These include EST-derived single nucleotide polymorphisms and exon-primed, intron spanning markers (Bouck & Vision 2007), single-copy nuclear polymorphisms identified from whole genome sequences or genomic libraries (Zhang & Hewitt 2003), and nuclear DNA 'barcodes' potentially applicable across entire kingdoms (Chase *et al*. 2005). These developments, in combination with the increasing efficiency and decreasing costs of DNA sequencing, raise the hope that molecular ecologists will soon have an upgraded 'toolbox' of transferable markers from which to choose.

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