Conservation Genetics (2005) 6:665–682
DOI 10.1007/s10592-005-9026-4

Does time since colonization influence isolation by distance? A meta-analysis

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Received 9 September 2004; accepted 7 December 2004

Key words: dispersal, gene flow, glaciation, migration, equilibrium

Abstract

Isolation by distance (IBD) is a phenomenon characterized by increasing genetic divergence and decreasing gene flow with increasing geographic distance. IBD is often used in conservation biology to infer the extent of gene flow among populations. An assumption inherent to this approach is equilibrium between genetic drift and gene flow, which may take thousands of years to achieve. This implies that empirical IBD studies of recently colonized areas, such as postglacial systems, should be concerned with whether or not equilibrium has been reached. Short of equilibrium, IBD should increase with the length of time since a geographical area was colonized. We test the prediction that IBD increases with increasing time since colonization through a meta-analysis based on a diverse range of empirical systems. P and r^2 values from published IBD studies were analyzed with respect to time since colonization (in generations and years), taking into account variation in sample sizes, molecular markers, divergence metrics (genetic distance, F_{st}, Nm), and dispersal patterns (one or two dimensional). Overall, we found weak evidence for associations between time since colonization and IBD. Sample sizes, molecular markers, divergence metrics, and dispersal patterns did not appreciably influence IBD. We propose that the expected relationship between IBD and time since colonization is obscured by the influence of other factors, such as dispersal ability, geographical barriers, and proximity to glacial refugia. The possible effects of time since colonization should continue to be evaluated in empirical studies, but other potential factors should also be thoroughly explored.

Introduction

Wright (1943) coined the term "isolation by distance" (IBD) in reference to increasing genetic differences among populations separated by increasing geographic distances. IBD theory has since been substantially refined and used to develop methods for inferring gene flow among natural populations (e.g., Wright 1946; Kimura and Weiss 1964; Maruyama 1971; Nagylaki 1976; Slatkin 1993; Rousset 1997). Currently popular empirical applications employ pair-wise comparisons among populations to test for positive relationships between genetic divergence and geographic distance (e.g., Rousset 1997) or negative relationships between gene flow and geographic distance (e.g., Slatkin 1993). These methods are frequently used in conservation biology to infer the extent of gene flow among populations. For example, an absence of IBD is commonly interpreted to mean that gene flow is very high over large distances (e.g., Seppä and Laurila 1999) or very low, even over short distances (e.g., Gold et al. 1999; Kark et al. 1999; Koljonen et al. 1999; McLean et al. 1999; Shaffer et al. 2000; Caizergues et al. 2001; de Innocentiis et al. 2001; Costello et al. 2003; Olsen et al. 2003). Such conclusions might then be used by managers to make decisions about which populations should be considered distinct (and therefore eligible for protection), and whether or not gene flow should be artificially manipulated. However, inferring gene flow from IBD depends critically on several assumptions inherent in the application of IBD theory to natural systems. We here assess whether empirical biologists need to be concerned about one of these assumptions: equilibrium between genetic drift and gene flow.

IBD should reflect a balance between genetic drift and gene flow, with the former increasing and the latter decreasing genetic divergence (Hutchison and Templeton 1999). Moreover, IBD should be maximal at equilibrium between genetic drift and gene flow, which may take a considerable length of time to develop. Slatkin (1993) explored a "radiation model", wherein a single ancestral population gives rise to all descendent populations at time τ in the past. He found that when τ is small (radiation is recent), only nearby populations will show a signature of IBD. For example, populations more than 10 steps away from each other (i.e., 10 intervening populations) will only exhibit IBD after 10N generations, where N is the number of individuals in each population. If $N = 1000$, populations more than 10 steps away from each other should therefore fail to manifest IBD, even after 10,000 generations. Empirical studies of IBD often survey widely separated populations which may thus lead to considerable bias in gene flow estimation if equilibrium has not been reached.

Acknowledging the possibility of non-equilibrium conditions generates several testable predictions. First, the relationship between pair-wise gene flow (*Nm*) and pair-wise geographic distance should become more negative with increasing time since colonization (Slatkin 1993). Second, the relationship between pair-wise genetic divergence and pair-wise geographic distance should become more positive with increasing time since colonization. Individual empirical studies can be cited in support of these predictions: IBD is often found in long-established populations but is sometimes lacking in recently established populations (e.g., Rafiński and Babik 2000; Knutsen et al. 2001; Castric and Bernatchez 2003; Costello et al. 2003). Exceptions do, however, occur (e.g., Green et al. 1996; Kinnison et al. 2002). Individual studies thus do not allow general conclusions about the role of non-equilibrium conditions on IBD. Thus, we here aim to detect general patterns of decreasing IBD with increasing time since colonization, through a meta-analysis of IBD in vertebrates. Specifically, we ask whether the strength and significance of IBD relationships is affected by the time since colonization.

The amount of elapsed evolutionary time since the colonization of a particular geographical area should be positively correlated with the number of years since the area became habitable and negatively correlated with the generation length of the colonizing species. For most species in temperate regions, the number of years since an area became habitable can be determined by the last retreat of continental glaciers. During the height of the Pleistocene glaciation (20,000 to 18,000 years ago), ice covered most of northern North America and northern Europe (Hewitt 1993, 1996, 1999, 2000). Populations now found in areas that were formerly covered by ice must have colonized these areas after the glacial retreat (Hewitt 1993). These populations may not have reached equilibrium between drift and gene flow. If so, IBD should increase with an increase in the number of years since the most recent retreat of ice sheets. IBD in these areas should also be influenced by generation lengths because species with shorter generations experience more evolutionary time for a given number of years.

Here we test whether the strength and significance of IBD relationships (geographic distance versus genetic divergence or gene flow) are positively correlated with time since colonization, measured in years or generations. Specifically, P values (significance) associated with IBD relationships should decrease and r^2 values (strength) should increase as time since colonization increases. Any influence of time on IBD might be moderated by other factors. We therefore also consider possible effects of taxonomic group, pattern of dispersal, molecular marker type, and the genetic divergence metric used for IBD analyses. Our results will indicate whether concerns about equilibrium conditions should be paramount when interpreting IBD trends.

Methods

Data collection

Our analyses were based on published studies that examined IBD in 66 vertebrate species (see Appendix A). The studies were obtained by searching online databases: BIOSIS Previews, CAB Abstracts, Current Contents, Wilson Biological and Agricultural Index, and Wilson General Science Abstracts. Relevant studies were included in our database if they met several criteria. First, we used only the most recent article on any particular species, thus reducing pseudoreplication. Second, we excluded studies for which physical barriers clearly influenced gene flow. Third, we excluded studies wherein IBD results were reported for only a subset of the surveyed populations, thus avoiding situations where IBD analyses were based on *post hoc* criteria. When IBD statistics were reported for multiple subsets of loci within a single paper, we always selected those based on the maximum number of loci. All but one of the studies focused on systems established through natural colonization, with the exception involving an introduction by humans (rabbit, *Oryctolagus cuniculus*; Fuller et al. 1996). Inclusion or exclusion of this study did not influence our conclusions.

Whether individuals disperse in one dimension (e.g., fish along a river or coast) or two dimensions (e.g., birds across a landscape) should theoretically influence IBD (Maruyama 1970, 1971; Slatkin and Maddison 1990; Slatkin 1991, 1993; Rousset 1997). For each study, we therefore recorded the primary dispersal pattern (one or two dimensional), along with taxonomic group (mammals, birds, fish, reptiles, and amphibians), molecular marker type (microsatellite, allozyme, mitochondrial DNA), and divergence metric (gene flow, including *Nm* and transformations; F_{st}, including R_{st} and transformations; genetic distance). Dispersal pattern and taxonomic group were partially confounded and gave similar results, but dispersal pattern had more power because it had fewer groups and more data points per group. We therefore do not further consider the role of taxomonic group. We next recorded P and r^2 values for IBD relationships, which reflect their significance and strength, respectively. P values were typically from Mantel (1967) tests, but were sometimes from regression analyses. Our analyses were based on P and r^2 values rather than slopes and intercepts because analysis methods varied among studies and because slopes and intercepts were often not reported. This decision greatly increased our sample sizes. Moreover, r^2 values are directly related to regression slopes: r is the correlation coefficient, which is the regression slope multiplied by the ratio of the standard deviations of the two variables (Sokal and Rohlf 1995, p. 566).

Specific P and r^2 values were chosen from each study according to the following criteria. First, if results based on more than one marker type or divergence metric were reported separately, we randomly chose (coin toss) values for one of the markers/metrics. If values were reported for more than one year, we calculated the average. When recording P values, we ignored "greater than" and "less than" signs (e.g., if $P<0.01$ was reported, we used $P=0.01$). The exception was $P>0.05$, in which case we excluded the values from our database. One P value was reported as $0.1>P>0.05$ (King and Lawson 2001), for which we used the mid-point ($P=0.075$).

For each study, time since colonization of the geographical area was recorded in years and generations. If years since colonization were explicitly stated in the paper from which the IBD data were obtained, we used that value. Failing this, we estimated years since colonization based on a minimum number of other sources (see Appendix A), thus reducing potential error caused by different dating methods. In most cases, years since colonization were the number of years since the most recent glacial retreat. For the single introduction by humans, we used the introduction date. If different populations in a single study had different colonization times, we used the average. In some cases, the geographical area had clearly been colonized long ago but the specific time was not known. For these, we simply used 20,000 years because equilibrium was likely to have been reached in a shorter time. The number of *generations* since colonization was estimated as the number of years divided by the generation length of the species in question, the latter obtained by personal communication from the authors or from other literature sources (see Appendix A).

Statistical analyses

We tested for associations between IBD (P and r^2 values) and time since colonization (years and generations) using two statistical methods: ANCOVA (to account for variation attributable to factors other than time) and weighted linear regression (to account for variation in sample sizes). ANCOVAs were performed in SPSS (version 11.0) and included time since colonization (covariate), dispersal pattern (fixed effect), molecular marker type (fixed effect), and divergence metric (fixed effect). We also considered second-order interactions between these fixed effect factors. For all ANCOVAs, P values were logit transformed ($\ln[y/(1\text{-}y)]$) and r^2 values were arcsine square-root transformed, which improved normality and linearity.

Weighted linear regressions were performed in MetaWin (version 2.1; Rosenberg et al. 2000), which converts test statistics to correlation coefficients weighted by their sampling variances: *variance* $= 1/(n-3)$, where n is the sample size within a study. As a result, studies with larger sample sizes (lower variances) are given greater weight. We used untransformed P and r^2 values for regressions because MetaWin analyzes proportions. For each combination of test statistic (P or r^2) and time metric (years or generations), we performed fixed-effect regressions based on three different weighting schemes: the number of populations per study, the total number of individuals per study, and the number of loci per study (studies that used mtDNA were excluded when weightings were based on the number of loci). Significance levels were obtained using 999 iterations in randomization tests. This is the preferred method because our data were not normally distributed and were obtained opportunistically rather than randomly (Quinn and Keough 2002, p. 46). MetaWin does not allow multiple predictor variables and thus cannot be used to simultaneously examine the effects of other factors, as in our ANCOVAs.

We performed all analyses on three different subsets of the data. The first included all studies in the database. The second included the entire database except for two extreme outliers, the yellow pygmy rice rat (*Oligoryzomys flavescence*; Chiappero et al. 1997) and the rice rat (*Oryzomys capito*; Patton et al. 1996), both of which had very high P values despite long times since colonization. The third dataset included only studies of systems colonized less than 20,000 years ago. The reason for using this last dataset is that we could not accurately estimate the time since colonization for populations not influenced by the last ice age, which may confound our results if a longer time is required for genetic equilibrium to be reached.

Meta-analyses should test for publication bias. In general, papers with non-significant results may be less likely to be submitted or accepted than papers with significant results (Jennions and Møller 2002). In our case, this might lead to a bias because IBD studies that examined recently colonized populations may be less likely to be published, if they show less IBD as predicted. This publication bias, if present, should be reflected in P values that increase and r^2 values that decrease with increasing sample size (Jennions and Møller 2002). We used Spearman rank order correlations (SPSS version 11.0) to examine our database for these signatures of publication bias. We performed three analyses for each test statistic, one using the number of populations per study, one using the total number of individuals per study, and one using the number of loci per study.

Results

P values

ANCOVA found no significant relationship between P values and time since colonization (in years or generations) (Table 1; Figure 1). ANCOVA also did not detect any effects of dispersal pattern, marker type, or divergence metric, nor were any interactions among these factors significant (Table 1). Regressions weighted by the number of individuals or the number of loci did not, with a single exception, detect a significant relationship between P values and time since colonization (Table 2). The exception was a significant negative correlation for years since colonization in systems less than 20,000 years old when the number of individuals was used for weighting ($P = 0.005$; Table 2). Regressions weighted by the number of populations detected a significant negative correlation for all datasets when considering years since colonization but not generations since colonization (albeit only

Table 1. P values from ANCOVAs assessing the relationship between IBD P values and time since colonization, molecular marker type, divergence metric, and dispersal pattern

Variable	*df*	Time = years	Time = generations
All studies			
Time	1	0.177	0.323
Marker type	2	0.507	0.868
Divergence metric	2	0.449	0.463
Dispersal pattern	1	0.504	0.931
Marker*metric	4	0.277	0.169
Marker*dispersal	2	0.377	0.204
Metric*dispersal	2	0.857	0.415
Outliers removed			
Time	1	0.629	0.091
Marker type	2	0.567	0.685
Divergence metric	2	0.254	0.359
Dispersal pattern	1	0.719	0.954
Marker*metric	4	0.111	0.141
Marker*dispersal	2	0.247	0.181
Metric*dispersal	2	0.926	0.550
< 20,000 years			
Time	1	0.896	0.524
Marker type	2	0.271	0.229
Divergence metric	2	0.318	0.161
Dispersal pattern	1	0.388	0.357
Marker*metric	3	0.139	0.067
Marker*dispersal	0	n/a	n/a
Metric*dispersal	1	0.457	0.666

Results are presented for all studies, all studies minus two outliers, and the studies of systems colonized less than 20,000 years ago.

marginally significant for populations colonized less than 20,000 years ago ($P = 0.059$); Table 2).

r^2 values

ANCOVA found only marginally positive correlations between r^2 values and years since colonization for all datasets (Table 3; Figure 2). There were no significant relationships between r^2 values and generations since colonization when all studies, and all studies minus two outliers, were considered, but there *was* a significant positive relationship between these variables when only systems colonized less than 20,000 years ago were considered ($P = 0.041$; Table 3; Figure 2). ANCOVA found no effects of dispersal pattern, marker type, or divergence metric, nor were any interactions apparent (Table 3). Weighted regressions found no significant relationship between r^2 values and time since colonization for all datasets and weighting methods (Table 4).

Publication bias

P values were not correlated with the number of individuals sampled when all studies were included ($r_s = -0.010$, $P = 0.937$, n = 61), nor when the two outliers were removed ($r_s = 0.053$, $P = 0.691$, n = 59). Similarly, P values were not correlated with the number of loci when all studies were included ($r_s = 0.063$, $P = 0.672$, n = 48) nor when the two outliers were removed ($r_s = 0.013$, $P = 0.933$, n = 47). In contrast, P values decreased with increasing numbers of populations when all studies were included ($r_s = -0.339$, $P = 0.008$, n = 61) and when the two outliers were removed ($r_s = -0.320$, $P = 0.014$, n = 59), a result opposite to that expected if a publication bias was present. r^2 values were not correlated with the total number of individuals ($r_s = 0.044$, $P = 0.777$, n = 44), the number of populations ($r_s = 0.168$, $P = 0.277$, n = 44), nor the number of loci ($r_s = -0.059$, $P = 0.747$, n = 32). These results suggest that a publication bias was not present in our database.

Discussion

Contrary to theory (Slatkin 1993), our analyses found that time since colonization did not appreciably influence IBD. Most of the apparent exceptions to this generalization were only marginally significant, and visual inspection of the data revealed very low explanatory power (Figures 1, 2). Indeed, studies of populations colonized recently varied from very strong IBD to very weak IBD (Figures 1, 2). Studies of populations colonized more than 20,000 years ago also varied dramatically, although very weak IBD was perhaps less frequent. We conclude that time since colonization had weak (if any) effects on IBD in this broad-brush meta-analysis.

Also contrary to theory (Slatkin 1993; Rousset 1997), dispersal pattern (one or two dimensional) did not influence IBD. Dispersal in one dimension occurs when populations are arranged in a linear fashion, whereas dispersal in two dimensions occurs when populations are arranged in a radial

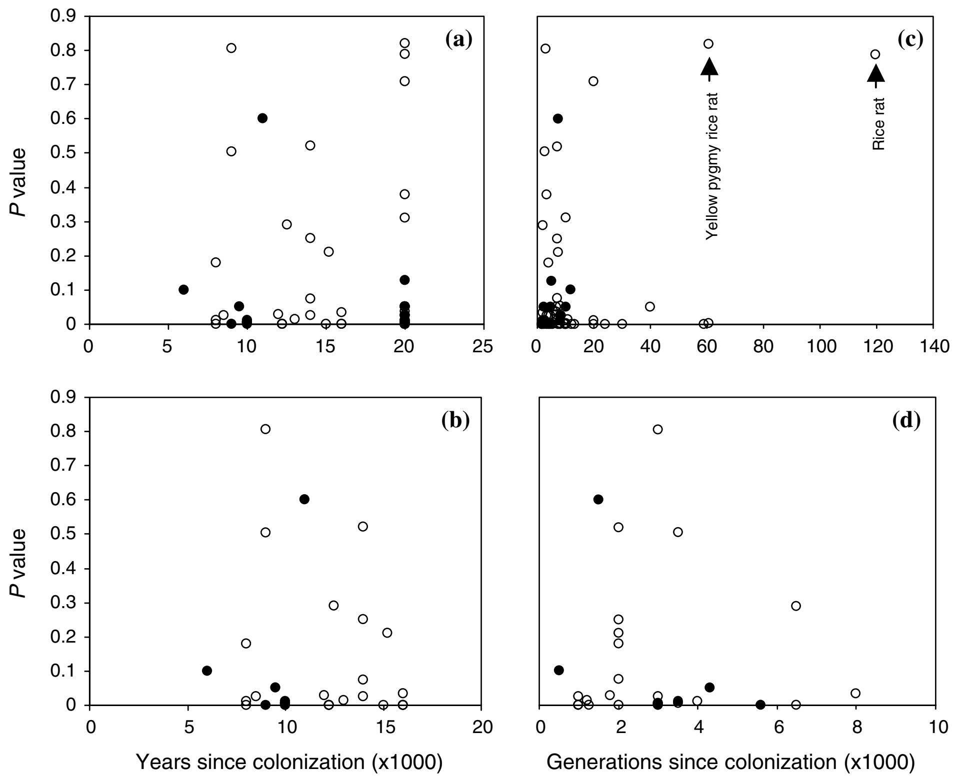

Figure 1. Relationships between time since colonization and *P* values of isolation by distance (IBD). The left-hand panels show results with respect to *years* since colonization: with all studies included (a), and with only studies of systems colonized less than 20,000 years ago (b). The right-hand panels show results with respect to *generations* since colonization: with all studies included (c), and with only studies of systems colonized less than 20,000 years ago (d). Black circles indicate one dimensional dispersal, open circles indicate two dimensional dispersal.

Table 2. P values from weighted regressions assessing the relationship between IBD *P* values and time since colonization

Sample size	n	Time = years	Time = generations
All studies			
Populations	61	0.013	0.863
Individuals	61	0.943	0.969
Loci	45	0.355	0.577
Excluding outliers			
Populations	59	0.015	0.942
Individuals	59	0.966	0.991
Loci	44	0.475	0.970
< 20,000 years			
Populations	30	0.059	0.785
Individuals	30	0.005	0.485
Loci	24	0.585	0.982

Weighting was based on the number of populations, the total number of sampled individuals, and the number of loci. Significance levels were calculated using randomization. Results are presented for all studies, all studies minus two outliers, and the studies of systems colonized less than 20,000 years ago.

pattern or across a surface. Theoretical models suggest that IBD should be more pronounced in the former case than in the latter (Slatkin and Maddison 1990; Slatkin 1991, 1993). Taking this prediction literally, IBD slopes in empirical studies have been used to infer whether dispersal is one or two dimensional (e.g., Baer 1998; Gavin et al. 1999; Koljonen et al. 1999; Shaffer et al. 2000; Baker et al. 2001; Hundertmark et al. 2003). Despite theoretical expectations, however, the effect of dispersal pattern on IBD has not been tested empirically. Our failure to find such an effect suggests that it is obscured by confounding factors, such as dispersal ability stemming from physical barriers or behavioral traits. For example, Peterson and Denno (1998) have shown that dispersal ability, regardless of dispersal pattern, influences IBD in at least some taxa.

One possible reason for our failure to detect an increase in IBD with time since colonization is that

Table 3. P values from ANCOVAs assessing the relationship between IBD r^2 and time since colonization values, molecular marker type, divergence metric, and dispersal pattern

Variable	*df*	Time = years	Time = generations
All studies			
Time	1	0.063	0.605
Marker type	2	0.101	0.262
Divergence metric	2	0.546	0.254
Dispersal pattern	1	0.528	0.782
Marker*metric	3	0.247	0.344
Marker*dispersal	2	0.947	0.898
Metric*dispersal	1	0.610	0.935
Excluding outliers			
Time	1	0.055	0.977
Marker type	2	0.128	0.303
Divergence metric	2	0.357	0.241
Dispersal pattern	1	0.694	0.858
Marker*metric	3	0.232	0.346
Marker*dispersal	2	0.914	0.909
Metric*dispersal	1	0.720	0.869
< 20,000 years			
Time	1	0.045	0.041
Marker type	2	0.091	0.091
Divergence metric	2	0.471	0.516
Dispersal pattern	1	0.276	0.813
Marker*metric	2	0.231	0.206
Marker*dispersal	0	n/a	n/a
Metric*dispersal	0	n/a	n/a

Results are presented for all studies, all studies minus two outliers, and the studies of systems colonized less than 20,000 years ago.

equilibrium between gene flow and genetic drift had been reached on shorter than expected time scales. Returning to theory (Slatkin 1993), small population sizes and few intervening populations should speed the rate at which IBD is achieved – perhaps the studies in our database were characterized by these properties. We cannot directly assess these possibilities because studies of IBD generally do not report population sizes or the number of populations separating those surveyed. Regardless, our results suggest that caution is necessary when inferring that populations are unlikely to display IBD solely because they have been colonized after the ice age.

Another alternative is that time since colonization does indeed influence IBD but that its effects are masked by other factors not controlled for in a broad-brush meta-analysis such as ours. These factors might include barriers to dispersal, variation in dispersal ability, glaciation patterns, and distances among populations. First, barriers to dispersal, and hence gene flow, are likely to disrupt IBD (e.g., Pfau et al. 2001; Taylor et al. 2003). Although we excluded studies with obvious barriers, undocumented partial barriers may still influence gene flow. Second, dispersal abilities vary among species and are known to influence IBD in at least some taxa, with lower levels of IBD observed in species with either very high or very low dispersal (Peterson and Denno 1998). Third, the historic distribution of glacial refugia and colonization routes (Castric et al. 2001; Castric and Bernatchez 2003; Costello et al. 2003), as well as patterns of ice sheet expansion and contraction (Rowe et al. 2004) should influence IBD. Unfortunately, these factors are poorly known and difficult to quantify. Fourth, the maximum geographic distance between populations may influence IBD because this influences dispersal. An additional factor, not usually considered, is that ecological gradients may cause barriers to gene flow that do not correlate obviously with any sort of physical barrier (e.g., Smith et al. 1997; Ogden and Thorpe 2002). Finally, errors in the estimation of parameters used (e.g., time since deglaciation, generation length, dispersal pattern) could also have influenced our results.

Many authors consider one or more of the above factors when interpreting IBD in their study systems. When IBD is not found, authors most often consider the effects of barriers to dispersal, either physical (e.g., Piertney et al. 1998; Barber 1999; Gavin et al. 1999; Gold et al. 1999; van Hooft et al. 2000; Castric et al. 2001; Pfau et al. 2001; Burton et al. 2002; Lugon-Moulin and Hausser 2002; Costello et al. 2003) or behavioral (e.g., Gold et al. 1999; Goossens et al. 2001; Ellis et al. 2002). If no such barriers appear likely, some authors conclude that populations not exhibiting IBD have been too recently colonized or have been influenced by Pleistocene glaciers (e.g., Patton et al. 1996; Chiappero et al. 1997; Holder et al. 2000; Rafiński and Babik 2000). Other factors sometimes taken into consideration include dispersal ability (e.g., Chiappero et al. 1997; King and Lawson 2001), effective population sizes (e.g., Baer 1998; Turgeon and Bernatchez 2001), colonization routes (e.g., McLean et al. 1999;

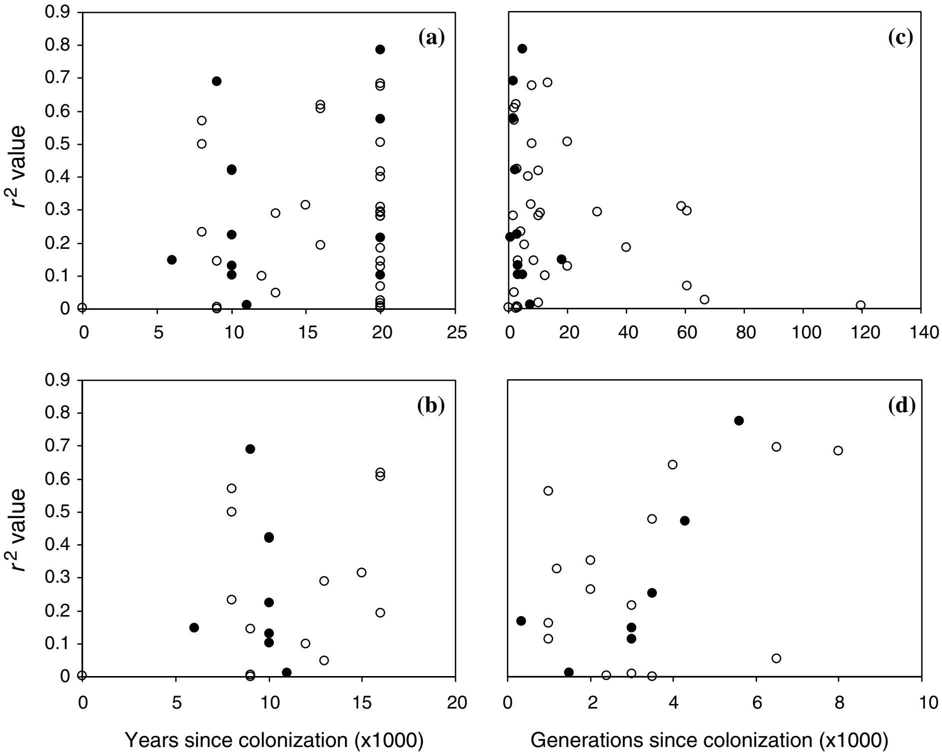

Figure 2. Relationships between time since colonization and r^2 values of isolation by distance (IBD). See the caption for Figure 1 for more details.

Table 4. P values from weighted regressions assessing the relationship between IBD r^2 values and time since colonization

Sample size	n	Time = years	Time = generations
All studies			
Populations	44	0.872	0.066
Individuals	44	0.403	0.173
Loci	30	0.332	0.122
Excluding outliers			
Populations	42	0.921	0.237
Individuals	42	0.430	0.190
Loci	29	0.388	0.184
<20,000 years			
Populations	22	0.841	0.167
Individuals	22	0.623	0.328
Loci	17	0.947	0.077

Weighting was based on the number of populations, the total number of sampled individuals, and the number of loci. Significance levels were calculated using randomization. Results are presented for all studies, all studies minus two outliers, and the studies of systems colonized less than 20,000 years ago.

Lugon-Moulin and Hausser 2002; Costello et al. 2003; Hundertmark et al. 2003), and scaling effects (e.g., maximum geographic distance among populations; Planes et al. 1996; Lougheed et al. 1999; Mossman and Waser 2001). In summary, many factors have the potential to influence IBD. Whether or not these factors are important and general in their effects, however, requires further study. We suggest that *all* of these factors, in addition to time since colonization, be considered when making management decisions based on IBD patterns.

In conclusion, time since colonization may influence the ability of populations to reach equilibrium between gene flow and genetic drift, and hence manifest IBD. However, any such effects appear weak in the context of other factors that might influence IBD. We conclude that the effects of time since colonization are likely context-dependent, and suggest that researchers continue to evaluate the possible influence of time, but also take a more comprehensive approach to the consideration of other factors. A lack of IBD may indeed reflect limited gene flow in a conservation context but it may also reflect other confounding factors, such as those listed above. Moreover, it is of critical importance in a conservation context to determine *why* gene flow is limited, which again necessitates consideration of these other factors.

Acknowledgements

We thank J. Correa for providing assistance with the statistics and K. Räsänen, S. A. Pavey, McGill Department of Biology graduate student discussion group members, and anonymous reviewers for providing comments. We also thank all individuals who provided information on generation lengths (see Appendix A). Financial support was provided by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to A. P. Hendry.

Appendix A

Studies used for data collection

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Appendix A. Data for each species used in the analyses, including sources of information

Species	Generations since colonization	Generation length (years)	Marker type	Divergence metric	r^2 value	P value	Source for IBD	Source for time since colonization	Source for generation length
Fish									
Atlantic salmon (*Salmo salar*)	1607	5.6	Allozyme	Nm	0.69	<0.001	Koljonen et al. 1999	Koljonen et al. 1999	Säisä et al. 2003
Australian barramundi (*Lates calcarifer*)	4706	4.3	mtDNA	Nm	0.787	<0.001	Chenoweth et al. (1998)	Flint (1971), p. 683	Merrick and Schmida (1984), p. 187
Australian bass (*Macquaria novemaculeata*)	4706	4.3	mtDNA	F_{st}	0.102	<0.05	Jerry and Baverstock (1998)	Flint (1971), p. 683	Harris (1986)
Brook charr (*Salvelinus fontinalis*)	3333	3.0	Microsatellite	F_{st}	–	<0.0005	Castric and Bernatchez (2003)	Flint (1971), p. 492, Figure 18.12	Scott and Crossman (1998), p. 211
Brown trout (*Salmo trutta*)	2209	4.3	Microsatellite	F_{st}	0.42	<0.05	Carlsson and Nilsson (2000)	Kleman et al. (1997)	Hesthagen and Jonsson (2002)
Cichlid (*Eretmodus cyanostictus*)	8000	2.5	Microsatellite	Nm	0.676	0.0016	Taylor et al. (2001)	Flint (1971), pp. 698–699	Martin Taylor (pers. comm.)
Coho salmon (*Oncorhynchus kisutch*)	3333	3.0	Microsatellite	F_{st}	0.13	0.002	Olsen et al. (2003)	Flint (1971), p. 492, Figure 18.12; Pielou (1991), p. 11, Figure 1.4	Jeffrey Olsen (pers. comm.)
Common sole (*Solea vulgaris*)	8000	2.5	Allozyme	Genetic distance	–	<0.01	Kotoulas et al. (1995)	Flint (1971), pp. 594–595, Figure 23.1, pp. 662–663, Figure 25.1	Georgios Kotoulas (pers. comm.)
Eulachon (*Thaleichthys pacificus*)	2857	3.5	mtDNA	Genetic distance	0.224	0.012	McLean et al. 1999	Flint (1971), p. 492, Figure 18.12; Pielou (1991), p. 11, Figure 1.4	Jennifer McLean (pers. comm.)
European eel (*Anguilla anguilla*)	2000	8.0	Allozyme	Genetic distance	0.608	0.033	Maes and Volckaert (2002)	Hewitt (1999); Kleman et al. (1997)	Gregory Maes (pers. comm.)
Goodeid fish (*Chapalichthys encaustus*)	66,667	0.3	Allozyme	Genetic distance	0.0256	–	White and Turner (1985)	Flint (1971), p. 476	Matthew White (pers. comm.)
Goodeid fish (*Goodea atripinnis*)	40,000	0.5	Allozyme	Genetic distance	0.185	<0.05	White and Turner (1985)	Flint (1971), p. 476	Matthew White (pers. comm.)
Haddock (*Melanogrammus aeglefinus*)	3333	3.0	Allozyme	Genetic distance	–	0.006	Giæver and Forthum (1999)	Kleman et al. (1997)	Overholtz (1988)

Appendix A. (Continued)

King mackerel (*Scomberomorus cavalla*)	5000	4.0	Microsatellite	F_{st}	–	0.127	Broughton et al. (2002)	Hewitt (2000)	Finucane et al. (1986)
Lake cisco (*Coregonis artedi*)	2857	3.5	Microsatellite	F_{st}	0.423	0.005	Turgeon and Bernatchez (2001)	Turgeon and Bernatchez (2001)	Scott and Crossman (1998), pp. 240–241
Mosquitofish (*Gambusia affinis*)	12,000	0.5	Allozyme	Genetic distance	–	>0.1	McClenaghan et al. (1985)	Baer 1998a	Fernandez-Delgado 1989
Mosquitofish (*Heterandria formosa*)	18,182	0.3	Allozyme	Nm	0.149	–	Baer (1998a)	Baer (1998a)	Baer (1998b)
Orange roughy (*Hopostethus atlanticus*)	635	31.5	Allozyme	Nm	0.216	–	Smith and Benson (1997)	Flint (1971), p. 688, Figure 25.7	Peter Smith (pers. comm.)
Pink salmon (*Oncorhynchus gorbuscha*)	10,000	2.0	Allozyme	F_{st}	–	<0.05	Hawkins et al. (2002)	Flint (1971), pp. 662–663, Figure 25.1	Jeffrey Olsen (pers. comm.)
Red drum (*Sciaenops ocellatus*)	1645	12.2	Microsatellite	F_{st}	0.575	0.001	Gold and Turner (2002)	Hewitt (2000)	John Gold (pers. comm.)
Surgeonfish (*Acanthurus triostegus*)	13,333	1.5	Allozyme	Nm	0.684	<0.001	Planes and Fauvelot (2002)	Hewitt 2000	Randall (1961)
Westslope cutthroat trout (*Oncorhynchus clarki lewisi*)	3333	3.0	Microsatellite	F_{st}	0.102	0.005	Taylor et al. (2003)	Flint (1971), p. 492, Figure 18.12; Pielou (1991), p. 11, Figure 1.4	Eric Taylor (pers. comm.)
Mammals									
African buffalo (*Syncerus caffer*)	4000	5.0	Microsatellite	F_{st}	–	<0.00001	van Hooft et al. (2000)	Flint (1971), pp. 698–699	Sinclair (1977), pp. 167–168
African elephant (*Loxodonta africana*)	1509	13.3	mtDNA	Nm	0.281	–	Georgiadis et al. (1994)	Flint (1971), pp. 698–699	Sukumar (2003), pp. 92, 100
Alpine marmot (*Marmota marmota*)	4000	2.0	Microsatellite	Nm	0.234	0.18	Goossens et al. (2001)	Hewitt (1999)	Arnold (1990)
Brown long-eared bat (*Plecotus auritus*)	9800	1.3	Microsatellite	F_{st}	–	0.001	Burland et al. (1999)	Elverhøi et al. (1993)	Entwistle et al. (1998)
Common shrew (*Sorex araneus*)	8000	1.0	Microsatellite	F_{st}	0.499	0.001	Lugon-Moulin and Hausser (2002)	Hewitt (1999)	Jacques Hausser (pers. comm.)
Ground squirrel (*Spermophilus brunneus*)	10,000	2.0	Allozyme	Nm	0.28	<0.001	Gavin et al. (1999)	Dyke and Prest (1987)	Sherman (1989)
Koala (*Phascolarctos cinereus*)	6667	3.0	Microsatellite	Nm	–	0.037	Ellis et al. (2002)	Flint (1987), p. 683	Martin (1981)

Appendix A. (Continued)

Species	Generations since colonization	Generation length (years)	Marker type	Divergence metric	r^2 value	P value	Source for IBD	Source for time since colonization	Source for generation length
Moose (*Alces alces*)	1923	6.5	mtDNA	Genetic distance	0.0484	0.29	Hundertmark et al. (2003)	Hundertmark et al. (2003)	Kris Hundertmark (pers. comm.)
Noctule bat (*Nyctalus noctula*)	7600	2.0	Microsatellite	F_{st}	–	0.21	Petit and Mayer (1999)	Kleman et al. (1997)	Jiri Gaisler (pers. comm.)
Pine vole (*Microtus subterraneus, M. majori*)	58,824	0.3	Allozyme	Nm	0.309	<0.001	Macholán et al. (2001)	Hewitt (1999)	Zimová (1985)
Pygmy rice rat (*Oligoryzomys microtis*)	60,606	0.3	mtDNA	Nm	0.295	<0.002	Patton et al. (1996)	Flint (1971), p. 710	James Patton (pers. comm.)
Rabbit (*Oryctolagus cuniculus*)	60	2.4	Allozyme	Genetic distance	0.00325	–	Fuller et al. (1996)	Fuller et al. (1996)	Parer (1977); Gilbert et al. (1987)
Rice rat (*Oryzomys capito*)	119,760	0.2	mtDNA	Nm	0.00884	>0.788	Patton et al. (1996)	Flint (1971), p. 710	James Patton (pers. comm.)
Snowshoe hare (*Lepus americanus*)	8,500	1.0	Microsatellite	F_{st}	0.144	0.025	Burton et al. (2002)	Pielou (1991), p. 11, Figures 1.4 and 1.5; Flint (1971), p. 492, Figure 18.12	Cole Burton (pers. comm.)
Spiny tree rat (*Mesomys hispidus*)	10,000	2.0	mtDNA	Nm	0.416	<0.0001	Patton et al. (1996)	Flint (1971), p. 710	James Patton (pers. comm.)
Striped mouse (*Rhabdomys pumilia*)	30,303	0.7	Allozyme	Genetic distance	0.292	<0.001	Mahida et al. (1999)	Flint (1971), pp. 698–699	Neville Pillay (pers. comm.)
White-footed mouse (*Peromyscus leucopus*)	7000	2.0	Microsatellite	F_{st}	–	0.515	Mossman and Waser (2001)	Dyke and Prest (1987)	Catherine Mossman (pers. comm.)
White-tailed deer (*Odocoileus virginianus*)	10,000	2.0	Allozyme	Genetic distance	–	0.004	Purdue et al. (2000)	Hewitt (2000)	Nixon and Etter (1995)
Yellow pygmy rice rat (*Oligoryzomys flavescens*)	60,606	0.3	Allozyme	Nm	0.0676	0.82	Chiappero et al. (1997)	Flint (1971), p. 708	James Patton (pers. comm.)
Reptiles									
Black rat snake (*Elaphe obsoleta*)	2462	6.5	Microsatellite	F_{st}	0.662	0.0002	Lougheed et al. (1999)	Dyke and Prest (1987)	Blouin-Demers et al. (2002)
Brown snake (*Storeria dekayi*)	7000	2.0	Allozyme	Nm	–	0.1 >P >0.05	King and Lawson (2001)	Dyke and Prest (1987)	Richard King (pers. comm.)

Appendix A. (Continued)

Garter snake (*Thamnophis sirtalis*)	7000	2.0	Allozyme	Nm	–	>0.25	King and Lawson (2001)	Dyke and Prest (1987)	Richard King (pers. comm.)
Marine iguana (*Amblyrhynchus cristatus*)	2500	8.0	Microsatellite	F_{st}	–	<0.008	Rassman et al. (1997)	Rassman et al. (1997)	Martin Wikelski (pers. comm.)
Prickly skink (*Gnypetoscincus queenslandiae*)	4000	5.0	Microsatellite	F_{st}	–	0.026	Sumner et al. (2001)	Flint (1971), p. 683	Michael Cunningham (pers. comm.)
Water snake (*Nerodia sipedon*)	4667	3.0	Allozyme	Nm	–	<0.025	King and Lawson (2001)	Dyke and Prest (1987)	Brown and Weatherhead (1999)
Amphibians									
Canyon tree frog (*Hyla arenicolor*)	20,000	1.0	mtDNA	Nm	0.127	0.00015	Barber (1999)	Hewitt (2000)	Paul Barber (pers. comm.)
Common frog (*Rana temporaria*)	3000	3.0	Allozyme	F_{st}	0.0064	0.805	Seppä and Laurila (1999)	Koljonen et al. (1999)	Ryser (1988)
Common toad (*Bufo bufo*)	2571	3.5	Allozyme	F_{st}	0.000729	0.504	Seppä and Laurila 1999	Koljonen et al. (1999)	Hemelaar (1988); Reading (1988)
Moor frog (*Rana arvalis*)	5333	3.0	Allozyme	Nm	0.192	0.0014	Rafiński and Babik (2000)	Kleman et al. (1997)	Jon Loman (pers. comm.)
Streamside salamander (*Ambystoma barbouri*)	8000	2.5	Allozyme	F_{st}	–	0.026	Storfer (1999)	Hewitt (2000)	Andrew Storfer (pers. comm.)
Wood frog (*Rana sylvatica*)	6667	1.8	Microsatellite	F_{st}	–	0.029	Squire and Newman (2002)	Dyke and Prest (1987)	Berven (1990)
Yosemite toad (*Bufo canorus*)	6667	3.0	mtDNA	Nm	0.4	<0.05	Shaffer et al. (2000)	Hewitt (2000); Flint (1971), p. 475, Figure 18.4	Howard Shaffer (pers. comm.)
Birds									
Australian magpie (*Gymnorhina tibicer*)	10,000	2.0	Allozyme	Nm	0.017	0.311	Baker et al. 2001	Flint (1971), p. 683	Carrick (1963)
Black grouse (*Tetrao tetrix*)	2000	4.0	Microsatellite	F_{st}	0.57	<0.01	Caizergues et al. (2001)	Hewitt (1999)	Alain Caizergues (pers. comm.)
Chukar partridge (*Alectoris chukar*)	24,096	0.8	Allozyme	Nm	–	<0.001	Kark et al. (1999)	Flint (1971), pp. 662–663, Figure 25.1	Creighton (1988)
Florida scrub jay (*Aphelocoma coerulescens*)	3333	6.0	Microsatellite	Genetic distance	0.144	0.026	McDonald et al. (1999)	Hewitt (2000)	McDonald and Caswell (1993)
Gray-breasted jay (*Aphelocoma ultramarina*)	8000	2.5	Allozyme	Genetic distance	–	0.052	Peterson (1992)	Hewitt (2000); Flint (1971), p. 476	Li and Brown (2000)

Appendix A. (Continued)

Species	Generations since colonization	Generation length (years)	Marker type	Divergence metric	r^2 value	P value	Source for IBD	Source for time since colonization	Source for generation length
Great spotted cuckoo (*Clamator glandarius*)	20,000	1.0	Microsatellite	Genetic distance	0.477	0.008	Martinez et al. (1999)	Kleman et al. (1997)	Juan Soler (pers. comm.)
Magpie (*Pica pica*)	7500	2.0	Microsatellite	Genetic distance	0.325	<0.001	Martinez et al. (1999)	Kleman et al. (1997)	Juan Soler, Manuel Soler (pers. comm.)
Red grouse (*Lagopus lagopus*)	12,250	1.0	Microsatellite	F_{st}	0.1	<0.001	Piertney et al. (1998)	Elverhøi et al. (1993)	Stuart Piertney (pers. comm.)
Rock ptarmigan (*Lagopus mutus*)	7333	1.5	mtDNA	Nm	0.01	0.6	Holder et al. (2000)	Holder et al. (2000)	Robert Montgomerie (pers. comm.)
Swainson's warbler (*Limnothlypis swainsonii*)	20,000	1.0	Allozyme	Genetic distance	–	0.71	Winker et al. (2000)	Hewitt (2000)	Kevin Winker (pers. comm.)
Western scrub jay (*Aphelocoma californica*)	3333	6.0	Microsatellite	Genetic distance	0.0016	0.378	McDonald et al. (1999)	Hewitt (2000)	McDonald and Caswell (1993)
Yellow warbler (*Dendroica petechia*)	10,833	1.2	Microsatellite	F_{st}	0.29	0.013	Gibbs et al. (2000)	Dyke and Prest (1987)	Lisle Gibbs (pers. comm.)

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