

INVITED REVIEW

What can genetics tell us about population connectivity?

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Abstract

Genetic data are often used to assess 'population connectivity' because it is difficult to measure dispersal directly at large spatial scales. Genetic connectivity, however, depends primarily on the absolute number of dispersers among populations, whereas demographic connectivity depends on the relative contributions to population growth rates of dispersal vs. local recruitment (i.e. survival and reproduction of residents). Although many questions are best answered with data on genetic connectivity, genetic data alone provide little information on demographic connectivity. The importance of demographic connectivity is clear when the elimination of immigration results in a shift from stable or positive population growth to negative population growth. Otherwise, the amount of dispersal required for demographic connectivity depends on the context (e.g. conservation or harvest management), and even high dispersal rates may not indicate demographic interdependence. Therefore, it is risky to infer the importance of demographic connectivity without information on local demographic rates and how those rates vary over time. Genetic methods can provide insight on demographic connectivity when combined with these local demographic rates, data on movement behaviour, or estimates of reproductive success of immigrants and residents. We also consider the strengths and limitations of genetic measures of connectivity and discuss three concepts of genetic connectivity that depend upon the evolutionary criteria of interest: inbreeding connectivity, drift connectivity, and adaptive connectivity. To conclude, we describe alternative approaches for assessing population connectivity, highlighting the value of combining genetic data with capture-mark-recapture methods or other direct measures of movement to elucidate the complex role of dispersal in natural populations.

Keywords: adaptation, demographic connectivity, drift, emigration, *F*-statistics, gene flow, genetic connectivity, immigration, inbreeding, population dynamics, source–sink, spatial ecology

Received 7 October 2009; revision received 21 April 2010; accepted 26 April 2010

The ecological paradigm remains challenging for evaluations using genetic markers, because the transition from demographic dependence to independence occurs in a region of high migration where genetic methods have relatively little power.

Waples & Gaggiotti (2006)

Introduction

Dispersal can contribute significantly to population growth rates, gene flow and, ultimately, species persistence. Therefore, assessing the effects of dispersal is crucial to understanding population biology and evolution

in natural systems (Wright 1951; Hanski & Gilpin 1997; Clobert *et al.* 2001). Likewise, effective protection of endangered species and management of economically important species often rely on estimates of 'population connectivity' (Mills & Allendorf 1996; Monkkonen & Reunanen 1999; Drechsler *et al.* 2003), a concept based on the dispersal of individuals among discrete populations, but which can have very different meanings and implications depending on how it is measured.

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Genetic methods are frequently used to assess population connectivity because it can be difficult to measure dispersal directly at scales that are relevant to basic and applied questions (Koenig *et al.* 1996; Leis 2002; Palumbi 2003; Hedgcock *et al.* 2007). But in most applications, genetic methods provide information on genetic connectivity, which we define as the degree to which gene flow affects evolutionary processes within populations. Although many questions can be answered with data on genetic connectivity, genetic methods alone provide little information on demographic connectivity, which we define as the degree to which population growth and vital rates are affected by dispersal. Demographic connectivity is of central importance to basic population biology (Gotelli 1991; Nichols *et al.* 2000; Runge *et al.* 2006) and to species persistence in human-modified systems (Kauffman *et al.* 2004; Griffin & Mills 2009; Peery *et al.* 2010).

Genetic indices of connectivity are invaluable for assessing gene flow and the evolutionary consequences of dispersal (e.g. Rieseberg & Burke 2001; Postma & van Noordwijk 2005). We are concerned, however, about important misconceptions associated with the use of genetic indices to provide information about population connectivity, which can lead to misinterpretation of patterns of genetic connectivity to make inferences about demographic connectivity. Our goals are to clarify the difference between genetic and demographic connectivity so that misinterpretation can be avoided and to suggest methods for assessing the demographic effects of dispersal for cases when that information is needed. Current misconceptions may cause scientists to undervalue these other methods for measuring dispersal and demographic connectivity, such as capture-mark-recapture (CMR) approaches, and to underestimate the cumulative insight that comes from combining these approaches with genetic analyses.

For this discussion, we define dispersal as (i) movement of individuals between spatially discrete populations, and (ii) permanent or long-term settlement in the new population. This definition is consistent with the use of 'migration' in the population genetics literature, where it implies both the movement of individuals between populations and residence for enough time to contribute to the gene pool of the new population (Wright 1951; Crow & Kimura 1970). Genetic and demographic effects of dispersal can occur without permanent settlement in the new population, but some minimum residence time is necessary to distinguish dispersal from temporary movements associated with foraging and other daily activities (Clobert *et al.* 2001; Delgado & Penteriani 2008; Peery *et al.* 2010). Our definition distinguishes dispersal from 'migration' as that term is used in ecology and population biology, where it describes

movements of animals in large numbers from one place to another and is usually restricted to regular, periodic movements of populations (Begon *et al.* 1990).

We have three specific objectives in this paper. First, we hope to clarify the distinction between genetic and demographic connectivity, drawing on general theory and specific examples to do so. Second, we consider the strengths and limitations of genetic measures of connectivity in order to encourage careful interpretation of these measures. Third, we describe other approaches for assessing dispersal and population connectivity, highlighting the value of combining genetic measures with these complementary approaches to assess the overall role of dispersal in natural populations.

Demographic connectivity

Demographically connected populations are those in which population growth rates (λ , r) or specific vital rates (survival and birth rates) are affected by immigration or emigration (Hanski & Gilpin 1997; Runge *et al.* 2006; Mills 2007). Demographic connectivity is generally thought to promote population stability (e.g. $\lambda \geq 1.0$) and this stabilizing effect can occur at two different scales. In individual populations, demographic connectivity can promote stability by providing an immigrant subsidy that compensates for low survival or birth rates of residents [i.e. low local recruitment (Fig. 1); Pulliam 1988; Runge *et al.* 2006;]. Demographic connectivity can also promote the stability of metapopulations by increasing colonization of unoccupied patches (i.e. discrete subpopulations), even when the extinction rate of occupied patches is high (Levins 1970; Gotelli 1991; Hanski 1998).

Unlike genetic connectivity, which is primarily a function of the absolute number of dispersers (see below), demographic connectivity is a function of the relative contribution of net immigration (i.e. immigration–emigration) to total recruitment in a focal population (Figs 1 and 2). Total recruitment is the number of 'new' individuals at time $t + 1$ that were not present at time t because they were born in the intervening interval without being offset by deaths, or immigrated

$$N_{t+1} = N_t + \underbrace{\text{Births} - \text{Deaths}}_{\text{Local recruitment}} + \underbrace{\text{Immigrants} - \text{Emigrants}}_{\text{Net immigration}}$$

Total recruitment

Fig. 1 Components of λ , the discrete population growth rate, where N_t is the number of individual in the population at time t , N_{t+1} is the number of individual at time $t + 1$ and $\lambda = N_{t+1}/N_t$.

during that time without being offset by emigrants. Therefore, information on the extrinsic contribution of dispersal and the intrinsic demographic rates of the focal population are required to assess demographic connectivity, and conclusions about the importance of demographic connectivity should be qualified with information on those intrinsic rates.

In rapidly growing populations ($N_{t+1} \gg N_t$), net immigration can be very high in absolute terms, but represent a small proportion of total recruitment. Likewise, low net immigration values may represent a large proportion of total recruitment when populations are near extinction (e.g. the 'rescue effect'; Brown & Kodric-Brown 1977) or when population growth rates are low ($N_{t+1} > N_t$). Net immigration can compensate for negative local recruitment in stable populations ($N_{t+1} = N_t$; Fig. 1) and can have this same compensatory effect in declining population ($N_{t+1} < N_t$), slowing the rate of decline. More generally, demographic connectivity (like genetic connectivity) is highly sensitive to non-equilibrium population dynamics (Kareiva 1990; Harrison 1991). If net immigration or local recruitment varies over time, then demographic connectivity will also vary and any broad conclusions about the demographic importance of dispersal must acknowledge this temporal variability.

In the absence of other disturbances or strong outbreeding depression, increasing demographic connectivity is unlikely to destabilize local populations and metapopulations, but this does not mean that demographic connectivity is required for stability. Directional bias has been documented repeatedly in empirical studies of animal movement (e.g. Skalski & Gilliam 2000; Pe'er *et al.* 2004; Macneale *et al.* 2005; Bonebrake & Beissinger 2010). Directionally-biased movement can produce asymmetrical rates of interpopulation dispersal, where, according to the broad definitions used by Kawecki & Holt (2002), 'sources' are net producers of emigrants and 'sinks' are net recipients of immigrants. Sinks are commonly assumed to benefit from immigration (reviewed in Runge *et al.* 2006), but uncertainties about the demographic consequences of asymmetrical dispersal challenge this assumption.

Immigration can be critical to the persistence of sinks by compensating for low local recruitment. However, Watkinson & Sutherland (1995) showed that this is not the case in 'pseudo-sinks', where local recruitment is density dependent and immigration causes it to drop below the replacement level. Like 'true sinks', net immigration is a significant component of total recruitment in pseudo-sinks, but unlike true sinks, it is not necessary for persistence. In a related scenario, the demographic contribution of immigrants may be low when local density and competition for recruitment are high, and increase as local density and competition decrease

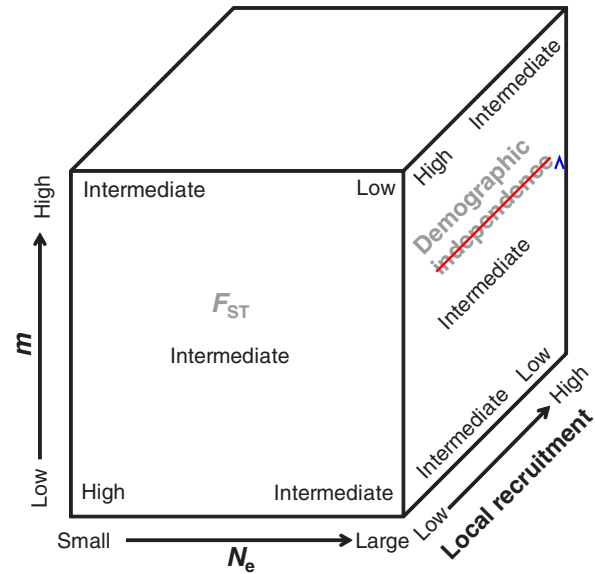


Fig. 2 Combinations of migration rate (m), effective population size (N_e) and local recruitment resulting in different expected values of genetic divergence (F_{ST}) and demographic independence. Local recruitment is determined by births and deaths of resident individuals (Fig. 1). Genetic divergence is primarily a function of Nm , while demographic connectivity is primarily a function of m relative to local recruitment.

(Kumar *et al.* 1993; Gomulkiewicz *et al.* 1999). Consequently, the same immigration rate may have very different demographic implications as species density and related interactions fluctuate in recipient populations. These cases illustrate the central importance of information on local demographic rates and the mechanisms regulating those rates for assessing demographic connectivity (Fig. 2).

Demographic connectivity is likely to be sensitive to the attributes of dispersing individuals if vital rates vary with dispersal status, body size, age or life history stage. For example, juvenile dispersal is common in many species (Johnson & Gaines 1990; Clobert *et al.* 2001), yet juveniles often have low survival rates independent of dispersal status (Caswell 2001; Mills 2007). Dispersers may also have lower survival or reproductive rates than non-dispersers due to pre-dispersal factors, costs incurred during dispersal or negative interactions with residents after settlement (Stamps *et al.* 2005; Benard & McCauley 2008; Hall *et al.* 2009). The possibility that survival rate or reproductive potential varies with age, stage, dispersal status or other individual attributes reinforces the importance of assessing connectivity within the larger demographic context of the focal population. Without that context, measures of dispersal—whether from genetic or observational data—are descriptive and cannot tell us whether and by what mechanisms populations are linked.

Even when demographic connectivity is necessary for population persistence, benefits of connectivity to recipient populations must be weighed against the costs to donor populations, risks to dispersers themselves, and possible negative effects on other species. For example, when dispersal is limited to corridors of once-continuous habitat, resulting in dispersal rates that are high and asymmetrical, emigration may overwhelm local recruitment in donor populations (Cronin 2007; Fahrig 2007). Also, dispersers often experience increased mortality and negative interactions with other species (Johnson & Gaines 1990; Morris 1992; Stamps *et al.* 2005) and can be important vectors in the spread of disease (Mundt *et al.* 2009). The benefits of increasing demographic connectivity may generally outweigh these risks, but demographic connectivity is no different from genetic connectivity in its complexities and potential costs.

Delimiting demographic connectivity

If the elimination of immigration results in a shift from stable or positive population growth ($\lambda \geq 1.0$) to negative population growth ($\lambda < 1.0$), then the importance of demographic connectivity is clear (Pulliam 1988). Otherwise, thresholds of demographic connectivity are context-dependent. Leis (2006) has defined demographic connectivity as 'the movement of individuals between populations in numbers large enough to be demographically significant'. He also points out that 'significance' will depend upon the context. While we believe that a definition of demographic connectivity needs to acknowledge its continuity, as in the definition we propose in the introduction, the observation that it is context-dependent is also extremely important. A small contribution of net immigration to total recruitment may be of significance to someone interested in basic population ecology. However, much greater contributions of net immigration may be required for a manager to consider two harvested stocks demographically connected. A conservation biologist may have different criteria for demographic connectivity depending on the threats to a population or metapopulation of interest. Table 1 gives definitions for three types of demographic connectivity depending upon the context of use.

Waples & Gaggiotti (2006) have suggested based on Hastings (1993) that the transition from demographic dependence to independence generally occurs when the fraction of immigrants in a subpopulation falls below 10%. Hastings (1993) identifies the 10% threshold as the point where population dynamics in two patches transition from behaving independently to behaving as a single population, with similar population sizes and growth rates. This threshold influences demographic similarity and synchrony in the model, but not the demographic interdependence of the patches. Nevertheless, an assumption of demographic interdependence is often implicit when this threshold is cited. Also, as Hastings emphasizes, predictions are contingent on all model parameters. Therefore, any effect of the exchange parameter (D) on population dynamics in the two-patch system must be interpreted in the context of other model parameters, particularly intrinsic population growth rates (r). This is cause for extreme caution in applying the results of Hastings (1993) or other theoretical studies to real systems where other demographic parameters are unknown (Fig. 1).

Interpretation of demographic connectivity in genetic studies

Explicit and implicit definitions of demographic connectivity in the population genetics literature are consistent with the ecological definition of populations described by Waples & Gaggiotti (2006). This definition emphasizes 'co-occurrence in space and time so that individuals have the opportunity to interact demographically (competition, social and behavioural interactions, etc.)'. By extension, it implies that demographic connectivity is the degree to which dispersal promotes co-occurrence and interactions between individuals from different populations, independent of its effects on population growth or vital rates. For example, Howeth *et al.* (2008) contrast genetic and demographic connectivity in the endangered Coahuilan box turtle (*Terrapene coahuila*). Their measure of demographic connectivity, however, is based only on movement of individuals among populations. They do not consider the effects of immigration on population growth or vital rates.

Table 1 Definitions for three types of demographic connectivity depending upon the context of use. Criteria are for the minimum threshold for connectivity

	Ecological connectivity	Conservation connectivity	Harvest connectivity
Criterion	Elimination of dispersal reduces population growth rate	Elimination of dispersal decreases population viability	Elimination of dispersal decreases yield
<i>m</i>	low	medium	high

Changes in population growth or vital rates can be caused by direct interactions between dispersers and residents, but defining demographic connectivity based on the possibility of these interactions gives the concept a false murkiness, highlighting its symptoms as opposed to its ultimate consequences. This is not unlike defining genetic connectivity based on the behavioural and physical interactions associated with mating and not its ultimate evolutionary outcome: the incorporation of dispersers' genes into the local gene pool.

The use of interaction-based definitions of demographic connectivity has two primary effects on how we interpret and conduct research on spatial population processes. Most obviously, these definitions misrepresent the true meaning of demographic connectivity and the very basic importance of interactions among populations that affect population growth and vital rates. These definitions also promote misconceptions of the utility of genetic methods for assessing population connectivity. By emphasizing what genetic methods *can* quantify (the co-occurrence of immigrants and residents) and not what genetic methods alone *cannot* quantify (the contribution of dispersal to local population growth), they incorrectly imply that genetic methods reveal everything we need to and can know about population connectivity.

The secondary effects of nebulous definitions of demographic connectivity are equally detrimental. By encouraging reliance on genetic methods alone for assessing connectivity, they can misdirect management efforts through imprecise conclusions about the role of dispersal in population persistence and productivity. They also obscure the limitations of what we do know about the effects of dispersal, thereby discouraging novel approaches that could expand our understanding of this fundamental process.

Genetic connectivity

We define genetic connectivity as the degree to which gene flow affects evolutionary processes within subpopulations. Researchers often use F_{ST} to assess gene flow, the standard measure of divergence at individual loci among subpopulations defined by Wright (1943), where

$$F_{ST} = \frac{\sigma^2}{\bar{q}(1 - \bar{q})}$$

and where \bar{q} and σ^2 are the mean and variance of allelic frequencies among subpopulations. Lower values of F_{ST} indicate less genetic divergence; see Holsinger & Weir (2009) for a recent review of defining, estimating and interpreting F_{ST} .

In the island model, Wright (1951) considered a large number of equal-size subpopulations in which genetic drift produces genetic divergence among the subpopulations at a rate inversely proportional to the local effective population size (N_e), which is assumed to equal the census size, N . A proportion m of the individuals in each subpopulation are immigrants from outside that subpopulation and the allele frequency in immigrant individuals is the average allele frequency in all subpopulations. This model leads to the surprisingly simple result that at equilibrium the amount of divergence among subpopulations for reasonably small values of m is approximately

$$F_{ST} \approx \frac{1}{4Nm + 1} \quad (1)$$

Note that because m is the proportion of immigrants and N is the local subpopulation size, Nm is the actual number of immigrants entering a subpopulation each generation. Therefore, the expected divergence among subpopulations is a function of the number of immigrants (Nm), rather than the proportion (m). For example, we expect the same amount of divergence among subpopulations of size 1000 with 2.5% migration as we do among subpopulations of size 50 with 50% migration; in both cases there are 25 immigrants per generation.

Delimiting genetic connectivity

Different amounts of dispersal are required to bring about 'genetic connectivity' depending upon the evolutionary consequences of interest (Table 2). The original concept of genetic connectivity is from Sewall Wright (1951) who concluded that very small amounts of gene flow are sufficient to avoid harmful effects of genetic drift and inbreeding which could lead to adaptive decline (Equation 1 and Fig. 3). Wright's (1951) observation that even Nm values of as low as one are sufficient to avoid harmful effects of genetic drift and inbreeding led to the one-migrant-per-generation rule (OMPG; Mills & Allendorf 1996), which has been used as a criterion for fragmentation in defining threatened species categories of the World Conservation Union (Mace & Lande 1991). There is no actual threshold at which there will be no harmful effects of local inbreeding. Rather the OMPG rule is based on the expectation that even as little as one immigrant per generation is sufficient for *inbreeding connectivity* – a significant reduction in the harmful effects of inbreeding (Table 2).

One immigrant per generation is sufficient to ensure that the same alleles will be shared among populations over long periods of evolutionary time. But one immigrant per generation is not sufficient to maintain nearly

Table 2 Definitions for three types of genetic connectivity. The values for m , Nm , and F_{ST} are the approximate values associated with each type of connectivity with the island model of migration. The actual values for each parameter will differ with other models of population structure

	Adaptive connectivity	Inbreeding connectivity	Drift connectivity
Criterion	Sufficient gene flow to spread advantageous alleles	Sufficient gene flow to avoid harmful effects of local inbreeding	Sufficient gene flow to maintain similar allele frequencies
m	?	?	?
Nm	>0.1	>1.0	>10
F_{ST}	<0.35	<0.20	<0.02

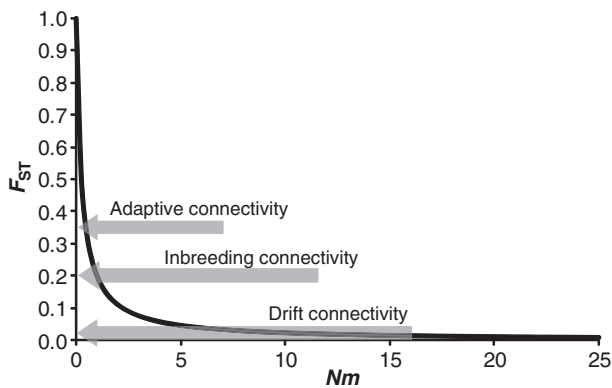


Fig. 3 Expected values of F_{ST} with the island model of migration (equation 1). Arrows indicate the F_{ST} values for the three types of genetic connectivity (Table 2).

identical allelic frequencies between populations. There has been some confusion in the literature about the effects of OMPG. Some have suggested that OMPG is sufficient to bring about similar allele frequencies in all populations (e.g. Leis 2002; Palumbi 2003). For example, 'migration at the rate of one immigrant individual per local population per generation is, generally, sufficient to obscure any disruptive effects of drift' (Spieth 1974). However, as pointed out by Wright (1969), 'a rather small value of F_{ST} may be associated with a very considerable amount of differentiation among the subpopulations'.

Subpopulations are expected to have equal allele frequencies only if they are panmictic (Waples & Gaggiotti 2006). That is, the absence of panmixia will result in significant allele frequency divergence among subpopulations if enough loci and individuals are sampled (Waples & Gaggiotti 2006; Palsbøll *et al.* 2007). Relative to inbreeding connectivity, considerably more exchange is required to bring about *drift connectivity* – nearly equal allele frequencies in subpopulations (Fig. 3). Wright (1969) pointed out that moderate allele frequency divergence will be expected even when Nm is an order of magnitude greater ($Nm = 10$, as in Table 2).

Rieseberg & Burke (2001) have presented a different concept of genetic connectivity. They argue that the spread of selectively advantageous alleles is crucial for maintaining genetic cohesiveness of species. As long as the selective advantage of an allele is fairly large (a selective advantage of 5% or greater), even small amounts of gene flow (an average of one immigrant every 10 generations) is sufficient to bring about *adaptive connectivity* – the potential for an advantageous allele to spread across the range of a species (Slatkin 1976; Table 2). Rieseberg & Burke (2001) conclude that the connectivity provided by the spread of highly advantageous alleles provides genetic integration for species.

Genetic indices of connectivity

Gene flow among populations can be estimated by both indirect and direct methods. Indirect methods estimate gene flow from the amount and pattern of genetic divergence among subpopulations. This approach is based upon population genetic theory and generally assumes that subpopulations have reached drift-gene flow equilibrium. If the subpopulations have not yet reached equilibrium, these methods will generally overestimate the current amount of gene flow. Direct methods use genotypic information to assign individuals to their subpopulation or parents of origin based upon their multiple-locus genotype. These direct genetic methods are analogous to non-genetic approaches for estimating exchange among populations.

Indirect genetic indices

The simplest approach to assess demographic connectivity with genetic methods was proposed by Bentzen (1998; see also Moritz 1994). Bentzen argued that if m is large enough to lead to demographic dependence, then Nm will be so large that genetic comparisons will not be able to reject the hypothesis of panmixia. He therefore concluded that if genetic analysis rejects panmixia,

then this provides strong evidence that the populations are demographically independent. However, Palsbøll *et al.* (2007) found that departures from panmixia can be detected consistently, even with migration rates as high as 20%, if many highly variable genetic markers are used. In general, dataset size and choice of statistical methods appear to strongly affect detection of departures from panmixia (Patterson *et al.* 2006; Reich *et al.* 2008). Although these findings are specific to the simulation parameters used, they suggest that departure from panmixia is, at best, subjective evidence of demographic independence. Departure from panmixia can also result from stochastic spatial and temporal variance in reproductive success and origin of recruits, further complicating interpretations of demographic connectivity using this method (Johnson & Black 1984; Gonzalez-Wanguemert *et al.* 2007; Arnaud-Haond *et al.* 2008).

Many papers have estimated gene flow using Equation 1 by rearrangement so that

$$Nm = \frac{(1 - F_{ST})}{4F_{ST}}.$$

There are a host of problems with this approach (Whitlock & McCauley 1999). First, it assumes that the subpopulations have reached drift-gene flow equilibrium. Second, it assumes the island model of migration in which gene flow is equally likely among all subpopulations which are of equal size. Moreover, as pointed out in the initial quote from Waples & Gaggiotti (2006), the transition between demographic dependence and independence is likely to occur in regions of high dispersal (Nm greater than 10) where the relationship between F_{ST} and Nm provides little power to estimate gene flow (Fig. 2).

Another indirect estimator of Nm is the private alleles method (Slatkin 1985). A private allele is one found in only one population. Slatkin (1985) showed that a linear relationship exists between Nm and the average frequency of private alleles at equilibrium. For example, if gene flow (Nm) is low, populations will have numerous private alleles that arise through mutation. The time during which a new allele remains private depends primarily on migration rates, such that the proportion of alleles that are private decreases as migration rate increases. Consequently, this method is not useful when dispersal is high ($Nm > 10$) because private alleles will be uncommon.

These indirect genetic methods estimate the number of immigrants (Nm). Therefore, they provide little insight into demographic connectivity, which depends upon m , not Nm (Fig. 2). Drawing inferences about demographic connectivity from indirect genetic models

requires, at least, estimating both Nm and effective population size (N). Furthermore, these indirect genetic analyses generally assume that the nominal immigration rate is also the effective immigration rate (e.g. Waples & Gaggiotti 2006). They do not assume, however, that all migrant individuals reproduce. The island model of genetic structure (Wright 1951) assumes that migrant individuals have the same fitness as local individuals. In random mating population with stable population size, approximately 12% of all individuals are expected not to contribute any progeny to the next generation (Allendorf & Luikart 2007, p. 153). In many cases, however, immigrants might have either greater or lower fitness than residents. Heterosis in matings between immigrants and residents, resulting from the accumulation of deleterious recessive alleles within local populations, can result in a much higher contribution of alleles carried by immigrants than expected under neutrality (Ebert *et al.* 2002; Roze & Rousset 2009). In contrast, natural selection can reduce effective gene flow when individuals move between divergent ecological environments (Hendry 2004; Nosil *et al.* 2005).

Recent progress in population genetics theory has led to the development of new methods that avoid many of the problems of the methods above, although they do have problems of their own. Coalescent approaches that use genealogical information have great promise to provide more reliable estimates of exchange among subpopulations. A maximum likelihood estimator of Nm and local population sizes was published by Beerli & Felsenstein (2001). Coalescent likelihood-based methods use all the data in its raw form, rather than a single summary statistic, such as F_{ST} . The statistic F_{ST} does not use information such as the proportion of alleles that are rare. Thus, the likelihood method potentially gives less biased and more precise estimates of Nm than classical moments-based methods (Beerli & Felsenstein 2001). Nevertheless, Abdo *et al.* (2004) concluded in their evaluation by simulation that this method does a poor job of estimating rates of migration and their confidence intervals when using mtDNA sequence data. However, it is possible that the poor performance observed by Abdo *et al.* (2004) resulted from lack of convergence of the Markov chain Monte Carlo (MCMC) algorithm in their analyses (Beerli 2006). This process can take many days, which makes it difficult to perform a thorough analysis comparing a variety of conditions. In addition, these approaches are sensitive to the presence of unsampled populations (ghost populations) that exchange dispersers with sampled populations (Beerli 2004). Slatkin (2005) concluded that there is no simple relationship between true and apparent migration rates with the occurrence of ghost populations and that it is

not possible to place an upper bound on the potential effects of ghost populations.

In contrast to the island model of migration, nearby individuals are more likely to mate with one another in isolation by distance models. In the original isolation by distance model (IBD; Wright 1943), individuals are continuously distributed across the landscape; neighbourhoods of individuals exist that are areas within which panmixia occurs and across which genetic differentiation occurs due to isolation by distance. The spatial scale over which IBD develops is proportional to the scale of gene flow. This approach has been used to estimate dispersal rate by examining the relatedness of individuals (Watts *et al.* 2007). We believe that such 'landscape genetics' approaches are even more difficult to combine with a demographic perspective. Other than cases where individuals can be assigned back to parents at a known location (discussed below), making the jump from individual relatedness to demographic connectivity seems like a huge stretch because relatedness is likely to be very sensitive to individual behaviours and chance breeding among individuals. It is a big step from here to conclude anything about what is happening at the demographic level.

Direct genetic indices

Analysis of many genetic loci makes it possible to assign individuals to their subpopulation of origin based upon their multiple-locus genotypes (assignment tests; Manel *et al.* 2005). Assignment tests use genotypic information to identify individuals who did not originate in the subpopulation in which they were sampled in a way that is analogous to non-genetic approaches for estimating immigrants among populations (e.g. marking individuals). Assigning individuals to the correct local population requires the presence of genetic divergence among subpopulations. Therefore, in general, assignment methods do not work well at high levels of gene flow. However, the amount of divergence required cannot be generalized because the power to identify immigrants also depends upon the sample size of individuals, as well as the number and variability of loci sampled. With large sample sizes and numbers of variable loci, individuals can be correctly assigned even with low genetic divergence (Paetkau *et al.* 2004; Hall *et al.* 2009). The standard assignment test approach has also been extended to identify individuals with immigrant ancestry within the last generation or two (Manel *et al.* 2005).

Assignment methods originally assumed Hardy-Weinberg proportions and gametic equilibrium among loci (Rannala & Mountain 1997; Pritchard *et al.* 2000), but a more recent approach uses multilocus genotype

data and gametic disequilibrium to estimate local inbreeding coefficients and contemporary migration rates among subpopulations (e.g. BAYESASS; Wilson & Rannala 2003). A thorough simulation evaluation of the performance of this approach (Faubet *et al.* 2007) has concluded that it can provide accurate estimation of migration rates (m) even when m is fairly high ($m = 0.10$) if genetic differentiation is not too low ($F_{ST} > 0.05$). This scenario is most likely when N is low. When N is high, m must be lower than 0.10 for accurate estimation. Faubet *et al.* (2007) conclude that BAYESASS is unlikely to be useful for identifying demographically independent subpopulations for borderline cases when m is near 10%. However, we believe that any assessment of demographic independence is risky without information on local demographic rates, regardless of m .

Single-generation dispersal distances can also be estimated using multi-locus genotypes to identify the parents of individuals, assuming that offspring were born at or near the location of the parents when sampling occurred (Blouin 2003). This approach does not depend upon the presence of genetic divergence among local populations to identify immigrants. However, it does require sampling all, or almost all, of the potential parents, or the use of resampling simulations to estimate the true diversity of parental genotypes from a subsample. Parentage analysis has been used to estimate dispersal distances and distribution of raccoons (*Procyon lotor*; Cullingham *et al.* 2008), large-scale dispersal in water voles (*Arvicola terrestris*; Telfer *et al.* 2003), and precapture dispersal in banner-tailed kangaroo rats (*Dipodomys spectabilis*; Waser *et al.* 2006).

In an innovative application, Peery *et al.* (2008) used parentage analysis and population simulation to assess demographic connectivity in marbled murrelets (*Brachyramphus marmoratus*). Specifically, they compared the observed number of parent-offspring dyads in a subpopulation to the number expected by chance assuming a closed population to estimate the annual effective (breeding) immigration rate. With information on local demographic parameters, λ was then estimated with and without effective immigration to assess its impact on population growth. Estimates of effective immigration are not as informative as estimates of net immigration because they do not account for emigration or direct numerical effects of immigrants (Fig. 1). Nevertheless, it is clear from Peery *et al.* (2008) that effective immigration rates can provide important insight on demographic connectivity.

Hall *et al.* (2009) used a combination of assignment tests and parentage analysis to show that immigrants were less likely to breed than residents in a population of marbled murrelets. This finding illustrates the

potential disconnect between numerical and breeding effects of immigration. Like the approach of Peery *et al.* (2008), it also underscores the value of combining genetic and demographic information to assess population connectivity. In cases like the one described by Hall *et al.* (2009), count-based demographic estimates might show a stable population supported by immigration, whereas genetic data would show an isolated population with small N and at risk of inbreeding depression. In addition to these demographic and genetic implications, assessing the relative fitness of immigrants vs. residents is crucial to understanding how dispersal is maintained in natural populations (Johnson & Gaines 1990; Ronce 2007; Lowe *in press*).

Other approaches for assessing dispersal and population connectivity

In the last decade there have been important advances in tracking dispersal directly (Holden & Blackburn 2006; Wikelski *et al.* 2006; Ovaskainen *et al.* 2008) and in methods for linking those data to population-level processes (Nichols *et al.* 2000; Cooch & White 2001; MacKenzie *et al.* 2006). Here we provide an overview of direct approaches to assessing demographic connectivity and dispersal, with particular emphasis on how information gained from these approaches can complement data on genetic connectivity. We recognize that there are many taxa for which direct estimates of demographic connectivity are not feasible (e.g. many plants, invertebrates, marine fishes) and we conclude this section with a discussion of non-genetic approaches for assessing dispersal in these groups.

Arguably, the most significant advances in our understanding of the details of demographic exchange have come from improvements in capture-mark-recapture (CMR) models and the software for implementing those models. In particular, multistate models (Brownie *et al.* 1993; Schwarz *et al.* 1993) allow the estimation of survival (S) and recapture probabilities (p) in multiple populations and transition probabilities among populations (Ψ). Estimates of S and Ψ can then be used to calculate survival/transition probabilities (ϕ), representing the probability of an animal surviving from time t to $t + 1$ and either moving to another population or remaining in the same population. Recapture probability is the probability that a marked animal at risk of capture at time t is captured at t , and thus controls for differences in detection probabilities among populations or over time. By combining parameter estimates from multistate models with estimates of population growth rates from other CMR models (Pradel 1996), one can determine the relative contributions of net immigration and local recruitment to population growth (e.g. Lowe 2003).

Reverse-time CMR analysis have further advanced this area of research by providing a single modelling framework for simultaneous estimation of net immigration and local recruitment (Nichols *et al.* 2000). Reverse-time analysis uses multistate estimation methods on the reverse capture histories of individuals to simultaneously estimate net immigration and local recruitment in each of the linked study populations. Here again, estimates of recapture probability (p) for each population are crucial for minimizing detection bias, and these approaches are evolving rapidly to address other potential sources of error in parameter estimation (e.g. temporary emigration, uncertain species identification; Bailey *et al.* 2004; Runge *et al.* 2007). Several software options are available for implementing basic and reverse-time analyses using multistate models, including program MARK (White & Burnham 1999), MSSURVIV (Hines 1994) and M-SURGE (Choquet *et al.* 2004). Sandercock (2006) provides a thorough review of current CMR models and assumptions, and Runge *et al.* (2006) provide a useful conceptual framework for classifying sources and sinks using parameters estimated by these models. Peery *et al.* (2006) used reverse-time CMR analysis and matrix population models to estimate the contribution of immigration to λ in marbled murrelets, and Grant *et al.* (2010) used multistate CMR analysis and metapopulation simulation to show that overland dispersal is important to population stability in stream salamanders.

Rigid, spatially and temporally extensive sampling regimes are necessary to meet the assumptions and data requirements of multistate CMR models. For example, if sampling is not spatially extensive enough to encompass the majority of source populations, immigrants from unsampled 'ghost' populations will be misclassified as local recruits, and emigrants to unsampled populations will be misclassified as local mortalities. Also, it is difficult to incorporate population stage or age structure into reverse-time CMR analyses. Despite these limitations, there is no better way to assess the contribution of dispersal to local population dynamics, other than experimentally eliminating dispersal (Diffendorfer 1998). Given the complexities of demographic connectivity, the power of CMR approaches to minimize bias in parameter estimates, and rapid improvements in the flexibility of multistate models, it is reasonable to expect that, in the future, conclusions regarding the demographic importance of dispersal will be supported by CMR analyses. When it is not possible to implement multistate models at the scale of interest, traditional CMR methods can provide insight on λ and local recruitment (Fig. 1) that, by inference, elucidate the importance of demographic connectivity in the larger system.

We are aware of no case where multistate CMR estimates of demographic connectivity and data on genetic connectivity are available for the same system, yet such a study could provide valuable insight on whether and under what conditions these two metrics of population connectivity are correlated. Although F_{ST} is expected to be insensitive to variation in demographic connectivity beyond a low threshold (Fig. 2; Waples & Gaggiotti 2006), multistate CMR analyses could elucidate the specific factors influencing the position of that threshold (e.g. relative rates of local recruitment vs. net immigration, or of immigration vs. emigration; Fig. 1). It will always be easier to assess genetic connectivity at large scales; therefore, better understanding of the conditions under which pairwise F_{ST} values are correlated with demographic connectivity would expand the inferential scope of genetic data. As importantly, evidence that demographic connectivity is consistently insignificant despite variation in pairwise F_{ST} values would have the opposite effect, forcing us to narrow our interpretations of genetic connectivity. Genetic and demographic measures of connectivity may differ for reasons discussed throughout this paper. When this is the case, population simulations based on species attributes (generation time, number of offspring, mating system) may be useful for isolating the cause of this difference (e.g. non-equilibrium population dynamics, the time lag in the genetic data, unsampled populations; Hastings & Harrison 1994; Whitlock & McCauley 1999).

There are many taxa for which direct, CMR methods are not feasible due to large population sizes that result in low recapture rates, small body sizes that preclude direct marking, the production of many highly-dispersive propagules, and the logistical difficulties of sampling long-distance dispersal events. These taxa include many plants, terrestrial invertebrates and both marine and freshwater invertebrates, and fish with pelagic larvae. Below we discuss methods for assessing demographic connectivity and dispersal in these taxa. Also, please refer to the section on direct measures of genetic connectivity for other approaches combining genetic and demographic data that may be applicable in these taxa.

Data on patch occupancy (i.e. presence/absence) has been used extensively to understand how colonization and extinction rates of populations are affected by attributes of habitat patches (e.g. size, isolation) and the intervening landscape (e.g. specific barriers, human activity; Hanski & Gilpin 1997; Moilanen 1999). These occupancy-based, metapopulation approaches have been especially useful in systems where direct, CMR-based estimates of demographic connectivity would be impossible, including plants (Husband & Barrett 1996; Honnay *et al.* 2005), terrestrial invertebrates (Harrison

et al. 1995; Schooley & Wiens 2005), marine invertebrates (Ellien *et al.* 2000; Foggo *et al.* 2007), and marine fishes (Man *et al.* 1995; Kritzer & Sale 2004). Recent improvements in occupancy models and related software have expanded the applicability of these models to demographic questions (MacKenzie *et al.* 2006; Royle & Dorazio 2008). Harrison & Hastings (1996) concluded that the high turnover rates of classical metapopulations (Levins 1970) should generally be associated with low levels of among-population genetic differentiation. However, network theory and microsatellite data were used to identify subpopulations critical for maintaining genetic connectivity in a metapopulation of the threatened seagrass *Posidonia oceanica* (Rozenfeld *et al.* 2008).

Even when analyses of demographic connectivity are not possible, marked individuals can provide information on movement behavior that is valuable for interpreting patterns of genetic connectivity (e.g. Boulet *et al.* 2007; Milot *et al.* 2008). With information on movement behavior from marked individuals of two sympatric stream salamanders, Lowe *et al.* (2008) were able to predict opposing patterns of genetic and phenotypic divergence along New Hampshire headwater streams. Without direct data on movement, inference about the mechanism underlying these divergence patterns would likely have been incorrect. These movement data can come from assignment tests and parentage analyses, in addition to non-genetic marking methods, underscoring the value of combining direct and indirect genetic methods to assess genetic connectivity.

Stable isotopes have been useful for assessing dispersal in species producing large numbers of propagules that cannot be individually marked (Thorrold *et al.* 2001; Macneale *et al.* 2005; Carlo *et al.* 2009; Williamson *et al.* 2009) and in species that disperse especially long distances (Kennedy *et al.* 1997; Graves *et al.* 2002; Sepulveda *et al.* 2009). Isotopes and other mass-marking methods cannot alone reveal the demographic context of dispersal, but they can complement measures of genetic connectivity by providing information on contemporary dispersal patterns. Specifically, they allow for explicit testing of the temporal resolution of genetic data (Bossart & Prowell 1998; Zellmer & Knowles 2009) and can serve as an empirical foundation for generating *a priori* predictions of broader patterns of divergence and phylogeography (Kelly *et al.* 2005; Buckley 2009; Templeton 2009). The combination of mass-marking methods and genetic analyses has been especially valuable for evaluating the importance of connectivity in marine systems, where many species produce large numbers of small propagules that cannot be individually marked (Jones *et al.* 2005; Cowen & Sponaugle 2009; Weersing & Toonen 2009).

Conclusion

Our central message is simple: the concepts of genetic and demographic connectivity are fundamentally different and they require different, but potentially complementary methods of assessment. We should not simply think of demographic connectivity in terms of the dispersal of individuals. Instead, we need to consider the effects of dispersal on population growth and vital rates. Genetic methods alone provide little information on demographic connectivity, but this limitation is only a problem when genetic data are misinterpreted to make inferences about demographic connectivity. Many research questions can be answered with data on genetic connectivity, and we are not suggesting that demography should be incorporated in all connectivity studies. When information on demographic connectivity is needed, genetic methods can be combined with data on population growth rates, occupancy, movement behaviour or individual reproductive success to address this need. Amazing advances in the accessibility and resolution of population genetic data in the last decades have led us to push these data as far as possible to make ecological inferences. This effort is crucial to scientific advancement, but should be balanced by clear understanding of the limitations of the data and openness to ways of addressing those limitations.

Acknowledgements

This article is based partially on work supported by the US National Science Foundation Grant DEB 074218 to F.W.A, who was partially supported by a Fellowship from the Australian Commonwealth Scientific and Industrial Research Organisation during the writing of this manuscript. We thank Phillip England, Jim Nichols, Mark Bravington, Blake Hossack, Adam Sepulveda, Matt Wilson, Robin Waples, Paul Sunnucks, and Jonathan Ebel for helpful comments on this manuscript, Jeff Leis for sending us copies of his papers, Alan Hastings and Monty Slatkin for answering our questions, and Louis Bernatchez, Oscar Gaggiotti, Steve Beissinger, and two anonymous referees for their helpful comments.

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Corrigendum

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We wish to bring attention to the following correction to Lowe & Allendorf (2010). Figure 2 shows combinations of migration rate (m), effective population size

(N_e), and local recruitment resulting in different expected values of genetic divergence (F_{ST}) and demographic interdependence, not demographic independence. Here we provide a corrected version of Fig. 2 where the term ‘demographic independence’ has been replaced with ‘demographic interdependence’.

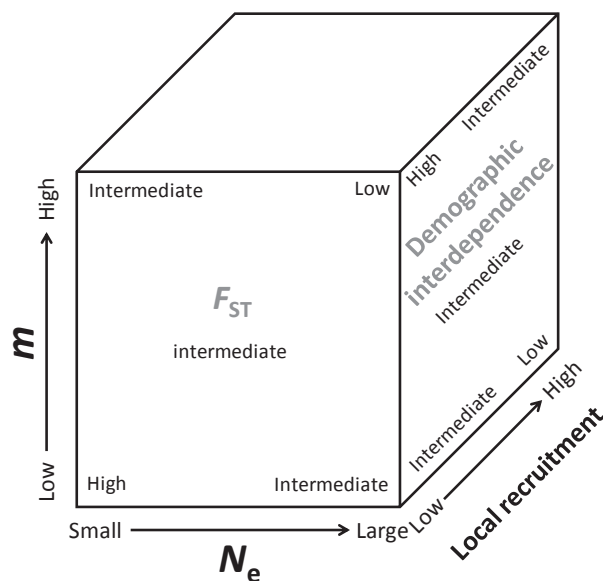


Fig. 2 Combinations of migration rate (m), effective population size (N_e), and local recruitment resulting in different expected values of genetic divergence (F_{ST}) and demographic interdependence. Local recruitment is determined by births and deaths of resident individuals. Genetic divergence is primarily a function of Nm , while demographic connectivity is primarily a function of m relative to local recruitment.

Reference

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