

## Notes and Comments

### Invertebrate Eggs Can Fly: Evidence of Waterfowl-Mediated Gene Flow in Aquatic Invertebrates

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**ABSTRACT:** Waterfowl often have been assumed to disperse fresh-water aquatic organisms between isolated wetlands, but no one has analyzed the impact of this transport on the population structure of aquatic organisms. For three cladocerans (*Daphnia ambigua*, *Daphnia laevis*, and *Sida crystallina*) and one bryozoan (*Cristatella mucedo*), we estimated the genetic distances between populations across North America using sequences of several mitochondrial DNA genes and genotypic frequencies at allozyme and microsatellite loci. Waterfowl movements across North America (estimated from band recovery data) explained a significant proportion of the gene flow occurring between populations across the continent for three of the four species, even after controlling for geographic distances between localities. The fourth species, *S. crystallina*, has propagules less likely to survive desiccation or ingestion by birds. Differences in the capacity to exploit bird-mediated transport are likely to have important consequences for the ecology of aquatic communities and the spread of invasive species.

**Keywords:** dispersal in fragmented habitats, gene flow, habitat colonization, passive dispersal, phylogeography.

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The wide distribution of fresh-water plants and of the lower animals ... apparently depends in main part on the wide dispersal of their seeds and eggs by animals, more especially by fresh-water birds, which have great powers of flight, and nat-

urally travel from one piece of water to another. (Charles Darwin 1859)

The capacity of aquatic plants and invertebrates to colonize new habitats and distribute themselves over large geographic ranges has long fascinated naturalists (Lyell 1832). Such ubiquity has often been ascribed to the potential for waterfowl to transport propagules of such organisms (Darwin 1859; Avise 2000). Waterbirds can carry plant and animal propagules both externally (attached to plumage or feet) and internally (after surviving digestion; Figuerola and Green 2002), but no one has found a way to quantify the direction and distance in which propagules are moved or their capacity to establish new populations after dispersal. Although gene flow between invertebrate populations in different watersheds has sometimes been attributed to bird flyways (Taylor et al. 1998; Freeland et al. 2000), bird movements have not been quantified. Transport potentially could be caused by other dispersal mechanisms such as wind (Brendonck and Riddoch 1999), rain, or human activities (Havel and Shurin 2004). As yet, there is no solid evidence that waterfowl-mediated long-distance dispersal leads to the establishment of invertebrate populations or to gene flow between them (De Meester et al. 2002).

We hypothesized that if waterfowl are important vectors for invertebrate dispersal, waterfowl movements should be a better predictor of invertebrate genetic structure than geographical distances between populations. In this study, we used molecular estimates of population differentiation for four aquatic invertebrates and banding data for waterbirds in North America to obtain strong evidence that aquatic invertebrates can disperse effectively via waterfowl. North America is traditionally divided into four waterfowl flyways. However, this concept is a major simplification because birds frequently move between flyways (Bellrose 1980), and their migrations can best be described by probability matrices of movements between one area and another. We used band recoveries to produce a matrix of distances based on waterfowl movements and tested its

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**Table 1:** Relationships between genetic, geographical, and bird movement matrices for mtDNA

Description of the test	<i>Cristatella mucedo</i>		<i>Daphnia ambigua</i>		<i>Daphnia laevis</i>		<i>Sida crystallina</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Genetic vs. kilometers	.38	.06	.25	.04	.24	.05	.34	.002
Genetic vs. bird	.49	.04	.43	.006	.38	.007	.32	.006
Genetic vs. bird, controlling for kilometers	.34	.03	.36	.005	.31	.04	.13	.11
Genetic vs. kilometers, controlling for bird	.00	.47	-.01	.56	.05	.35	.17	.06
Number of haplotypes		53		31		20		40
Number of localities		20		33		20		44
Number of states		9		15		10		16
Number of bird recoveries used		310,668		359,586		301,320		251,123
Evolutionary model		K81uf + I + G		TrN + I		GTR + I		HKY + I + G

Note: Pairwise correlations between genetic distances and geographical distances (km) or similarity in waterfowl movements (bird) were calculated using a Mantel test (Legendre and Legendre 1998). Relative contributions of bird distances to explaining genetic distances while controlling for geographical distances were estimated using partial Mantel tests. Number of states and bird recoveries and the evolutionary model used to calculate genetic distances (see Posada and Crandall 1998 for notation) are shown.

effectiveness in explaining the genetic structure of three cladoceran crustaceans (*Daphnia ambigua*, *Daphnia laevis*, and *Sida crystallina*) and one bryozoan (*Cristatella mucedo*) estimated from markers with very different temporal resolution (mitochondrial DNA [mtDNA] sequences and allozymes/microsatellites). All four species have resting stages that may be suitable for internal or external transport by waterfowl and have been studied over a wide geographical range within North America.

### Material and Methods

Mitochondrial DNA sequences for the species were obtained from GenBank, as reported by Taylor et al. (1998; *Daphnia laevis*), Freeland et al. (2000; *Cristatella mucedo*), Cox and Hebert (2001; *Sida crystallina*) and Hebert et al. (2003; *Daphnia ambigua*). To calculate genetic distances we used the MODELTEST program (Posada and Crandall 1998) to select the evolutionary model best fitting the characteristics of the data based on the Akaike Information Criterion. See appendix for more details of mtDNA fragment characteristics and genetic distance calculations. The optimal model of evolution differed between species, and to rule out the possibility that differences in results between species were due to the model selected, all analyses were repeated using genetic distances calculated with the Kimura two-parameter model. Interstate differences were calculated as the mean distance between populations in different states minus the average of genetic distances between populations in the same state (Kumar et al. 2001).

Allozyme frequencies for *D. laevis* and *S. crystallina* and microsatellite frequencies for *C. mucedo* were obtained from the same sources as for mtDNA. Only mtDNA sequences were available for *D. ambigua*. Gene flow was

estimated using Wright's (1951) formula  $Nm = 0.25[(1/Fst) - 1]$ , where *Fst* was estimated based on Nei's coefficient of genetic variation, *Gst*. Calculations were made with the program used by Slatkin (1993). Because only allele frequency data were available, no other approximations based on individual genotypic composition (e.g., *Fst* or *Rst*) could be calculated. Only localities with the same number of individuals screened for all loci and with at least 20 individuals sampled were included in the analyses. Interstate differences were calculated as for mtDNA sequence data.

Recoveries from waterfowl in the United States and Canada between 1920 and 2000 were obtained from the Bird Banding Laboratory (U.S. Geological Survey). Matrices were constructed with the number of individuals banded and recovered in states where genetic information was available for invertebrates (tables 1, 2). This information was transformed into a matrix of distances measured as 1 minus the Steinhaus index and as the Canberra metric distance (Legendre and Legendre 1998) using the R-Package program (see appendix for more details of bird movement sources and distance calculations). Euclidean geographical distances (km) were log transformed before the analyses. With one exception, results are presented only for the Steinhaus index because there were no relevant differences in statistical significance between results obtained with alternative indices.

### Results

For mtDNA, the correlation between genetic and geographical distances among populations of a given invertebrate species ranged from  $r = 0.24$  to  $0.38$  ( $P$  from .06 to .002; see table 1), whereas the correlation of genetic

**Table 2:** Relationships between genetic, geographical, and bird movement matrices for microsatellites (*Cristatella mucedo*) and allozyme frequencies

Description of the test	<i>Cristatella mucedo</i>		<i>Daphnia laevis</i>		<i>Sida crystallina</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Genetic vs. kilometers	-.49	.04	-.35	.002	.05	.38
Genetic vs. bird	-.50	.02	-.63	.001	.12	.33
Genetic vs. bird, controlling for kilometers	-.29	.05	-.57	.001	.11	.34
Genetic vs. kilometers, controlling for bird	-.27	.18	.13	.25	-.02	.46
Number of loci	5		5		5	
Number of localities	10		20		28	
Number of states	7		9		10	
Number of bird recoveries used	186,628		233,094		128,602	

Note: Pairwise correlations between genetic distances and geographical distances (km) or similarity in waterfowl movements (bird) were calculated using a Mantel test (Legendre and Legendre 1998). The relative contributions of bird distances to explaining genetic distances while controlling for geographic distances were estimated using partial Mantel tests. The number of loci, states, and bird recoveries used in the analyses are shown for each species.

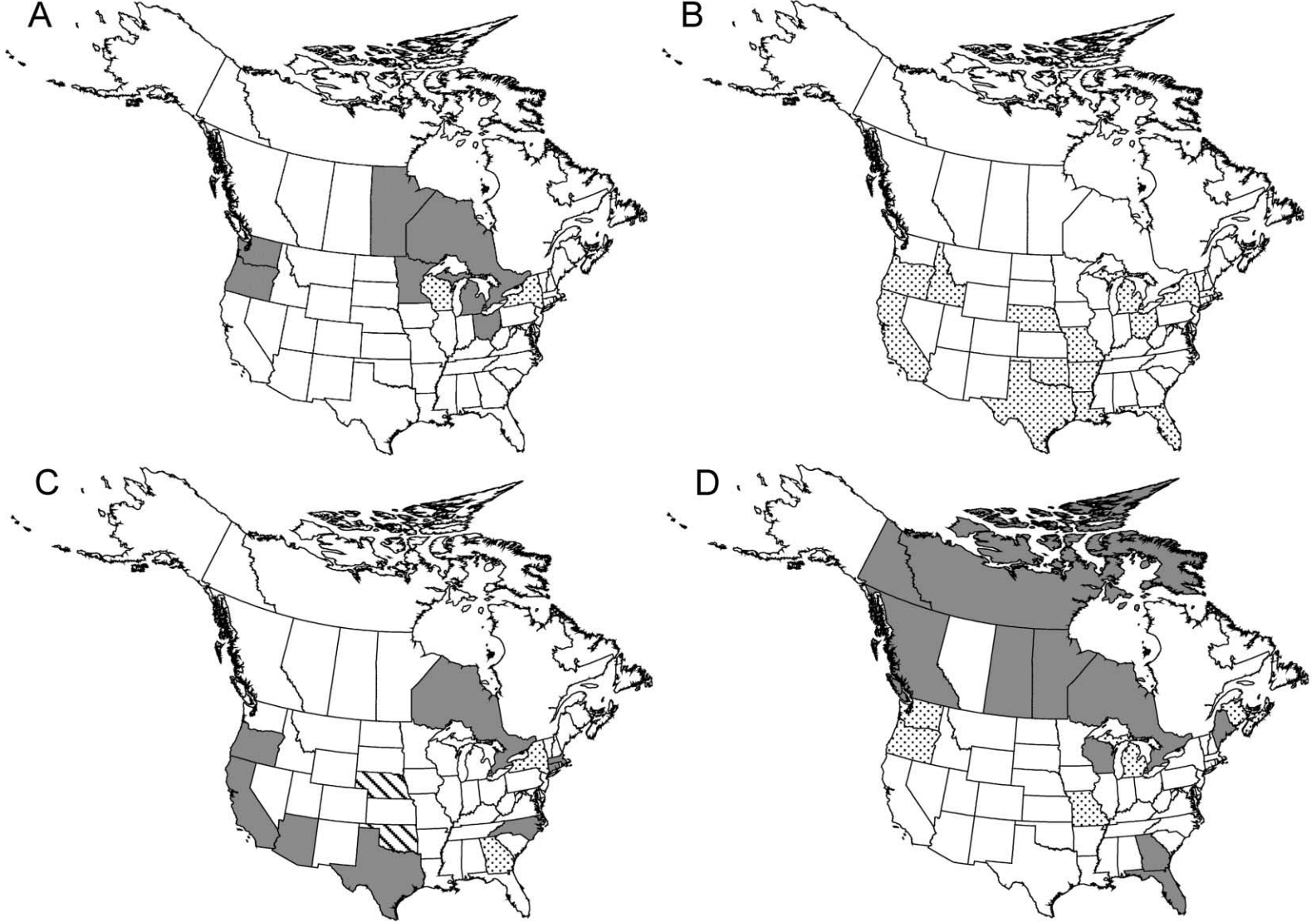
distance with our indices of waterfowl movements ranged from  $r = 0.32$  to  $0.49$  ( $P$  from .04 to .006). Waterfowl movements explained a greater amount of variance in genetic distance than in geographical distance for three of the species analyzed (*Daphnia ambigua*, *Daphnia laevis*, and *Cristatella mucedo*), and the opposite occurred for *Sida crystallina* (table 1). After controlling for geographical distance, waterfowl movements still explained a significant fraction of variation in genetic distance for *D. ambigua* (partial  $r = 0.36$ ,  $P = .005$ ), *D. laevis* (partial  $r = 0.31$ ,  $P = .04$ ), and *C. mucedo* (partial  $r = 0.34$ ,  $P = .03$ ). For *S. crystallina*, waterfowl movements were unrelated to genetic distance after controlling for geographical distance (partial  $r = 0.13$ ,  $P = .11$ ). The partial correlations between genetic and geographical distances while controlling for waterfowl movements were consistent with the above results because relationships between geography and genetics were no longer significant for *D. ambigua*, *D. laevis*, and *C. mucedo*. For *S. crystallina*, they were significant when using the Canberra metric (partial  $r = 0.24$ ,  $P = .01$ ) but not significant when using the Steinhaus index (partial  $r = 0.17$ ,  $P = .06$ ).

Similar results were obtained when analyzing  $Nm$  based on  $Gst$  estimates for allozyme (*D. laevis* and *S. crystallina*) and microsatellite (*C. mucedo*) data. Waterfowl movements explained a larger amount of variance in  $Nm$  than did geographical distance in both *C. mucedo* and *D. laevis*, while the opposite occurred in *S. crystallina* (table 2). After controlling for geographical distance, waterfowl movements were still related to  $Nm$  in *C. mucedo* (partial  $r = -0.29$ ,  $P = .05$ ) and *D. laevis* (partial  $r = -0.57$ ,  $P = .001$ ) but not in *S. crystallina* (partial  $r = 0.11$ ,  $P = .34$ ). For all three species, geographical distance and  $Nm$  were unrelated after controlling for waterfowl movements (table 2).

## Discussion

Our results show that quantitative estimates of waterfowl movements provided a better fit to genetic population structure than geographical distances for three of four invertebrate species, and this may explain previous studies reporting high levels of gene flow between invertebrate populations (Weider et al. 1996; Weider and Hobæk 1997; Taylor et al. 1998; Freeland et al. 2000). Furthermore, our results suggest that waterfowl transport propagules effectively during migration, or at least with enough frequency to affect genetic patterns of geographical variation in the transported species. Although gene flow between established populations may be limited by priority effects and adaptation to local conditions, reducing effective migration rates (De Meester et al. 2002), the direction of ongoing effective invertebrate dispersal detected with allozymes and microsatellite data agrees with that predicted from waterfowl movements, even when controlling for isolation by distance effects.

There are several biases associated with banding data, mainly because of spatial heterogeneity in banding effort and recovery probabilities (Webster et al. 2002). Furthermore, birds may not move directly between the banding and recovery localities but rather are likely to stop at other wetlands with little hunting activity (and thus low chance of band recovery). In addition, we combined banding data for a list of waterfowl species that vary both in their movement patterns and probably also in their relative importance as dispersers of different invertebrates (Green et al. 2002). All these factors make our tests more conservative (making Type II errors more likely and Type I less so) because there is no a priori reason to expect an association between genetic distances of aquatic organisms and such biases in banding data. The relatively low amount of var-



**Figure 1:** States of the United States and provinces from Canada with only mtDNA samples (*dotted*), only allozyme or microsatellites data (*hatched*), or with both kinds of data (*gray*) for different invertebrate species: A, *Cristatella mucedo*; B, *Daphnia ambigua*; C, *Daphnia laevis*; D, *Sida crystallina*.

iance explained by our models ( $r^2 < 40\%$  in all the cases) is noteworthy. This moderate explanatory power may be partly associated with the problems discussed above in the estimation of waterfowl movements and also with the fact that the number of sampled invertebrates was often very low. For these reasons and because the localities sampled for this study were not selected on the basis of their use by waterbirds, our  $r^2$  values are likely to underestimate the extent of genetic exchange mediated by birds. In addition, the heterozygosity and number of markers analyzed set an upper limit for the relationship between genetic distance and any other distance measure that is well below 1.0 (see Slatkin 1993; Hellberg 1995).

The poor relationship between waterfowl movements and genetic distance in *Sida crystallina* is consistent with unusually high levels of genetic divergence between lineages in this species. This divergence previously has been suggested to be caused by a reduced capacity to disperse through waterfowl (Cox and Hebert 2001), as supported by our results. *Sida crystallina* propagules have a different structure from that of *Daphnia* eggs with less tolerance to desiccation (<24 h; Makrushin 1981) and appear less resistant to gut passage because of their softer coat. In contrast, resistance to ingestion by waterfowl has been demonstrated for several *Daphnia* species (Figuerola and Green 2002) and for *Cristatella mucedo* statoblasts (Charalambidou et al. 2003).

Dispersal of aquatic organisms across Canada is thought to have been greatly facilitated by the formation of great lakes during deglaciation (Pielou 1991), and this may have been an important factor shaping *S. crystallina* genetic structure, given its more northerly distribution than the other three species. However, waterfowl movements remained unrelated to *S. crystallina* genetic structure even when data from Canadian localities covered in ice during the last glaciation were excluded (results not presented).

The correlations observed between bird movements and genetic distance potentially could be due to other confounding variables shaping both waterfowl migration routes and invertebrate dispersal. However, given the large scale of our study, only coincidence of independent post-glacial expansions of both waterfowl and invertebrate distributions seems a plausible alternative explanation. The fact that the relationship between waterfowl migration and invertebrate population structure remains significant for taxa with both northern (*C. mucedo*) and southern (*Daphnia ambigua*) distributions (fig. 1) does not support this idea. In addition, we have used genetic markers with differing temporal scales of resolution (Avisé 2000). Mitochondrial DNA has low rates of change, and relationships between populations inferred from these data are usually interpreted as reflecting patterns of range expansion after the last glaciation (Taylor et al. 1998; Avisé 2000). This

probably reflects historical patterns in which waterfowl had a role in transporting invertebrates to new habitats available after glaciation. In comparison, allozymes and microsatellites are more variable than mtDNA, and allele frequencies in different populations are widely used to infer patterns of gene flow between populations based on *Fst* or *Gst* statistics (Slatkin 1985; Avisé 1994). Patterns inferred from these markers thus suggest a strong relationship between current waterfowl migratory movements and gene flow for *C. mucedo* and *Daphnia laevis* and the lack of such a relationship for *S. crystallina*. Consequently, while mtDNA data are compatible with historical colonization events of invertebrates mediated by waterfowl movements, patterns of allozyme and microsatellite diversity provide evidence of recent or contemporary gene flow associated with waterfowl migratory movements.

To obtain reliable estimates of *Nm* from *Fst*, populations must be in migration-drift equilibrium (Hutchison and Templeton 1999). This assumption is likely to have been violated for two of the species analyzed (*D. laevis* and *S. crystallina*), which showed strong phylogeographic structuring based on mtDNA sequences (Taylor et al. 1998; Cox and Hebert 2001). However, this was not the case for *C. mucedo*, which lacks a clear geographical structuring of populations (Freeland et al. 2000). Thus, we are confident that the strong association with bird movements we have reported is not just an artifact due to biased estimates of *Nm*. Furthermore, it is hard to imagine why violation of the migration-drift assumption should favor the waterfowl movements hypothesis over a model of isolation by distance.

In order to understand how aquatic organisms can react to environmental change (Higgins and Richardson 1999) or to predict the expansion of invasive aquatic aliens (Williamson 1996), we need to improve our understanding of their mechanisms of dispersal. Our study suggests that birds disperse organisms effectively over large distances, and it provides a novel way to analyze interspecific differences in the success of bird-mediated dispersal. To assess the role of bird-mediated dispersal in generating and maintaining the structure and diversity of aquatic communities, there is a need to establish whether the relationship between bird movements and gene flow reported here is widespread and how bird-mediated transport interacts with the strong founder and local adaptation effects that may limit effective dispersal in many zooplanktonic invertebrates (Crease et al. 1997; Gómez et al. 2000; De Meester et al. 2002). Studies to address that question should be complemented by comparative analyses of the resistance of different propagules to ingestion by waterfowl (important for internal transport) and their adhesive capacity and resistance to desiccation (important for external transport).

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### APPENDIX

#### Details of the Calculations of Matrix of Distances Based on mtDNA Sequences and Bird Band Recovery Data

##### *Calculation of Genetic Distances between Populations*

For *Daphnia laevis*, sequences corresponded to a 569-bp fragment of mitochondrial 12S rRNA (Taylor et al. 1998; GENBANK accession numbers AF064152–AF064189; see table 1 for number of haplotypes, localities, and states sampled). *Daphnia ambigua* sequences were from a 640-bp fragment of the cytochrome c oxidase subunit I (COI; Hebert et al. 2003; AF523684–AF523713 and an additional sequence provided by the authors). *Sida crystallina* sequences were from a 614-bp fragment of COI (Cox and Hebert 2001; AF277849–AF277888), and those of *Cristatella mucedo* from a 363-bp fragment of cytochrome b (Freeland et al. 2000; AF260014–AF260066).

To calculate genetic distances, we used the MODELTEST program (Posada and Crandall 1998) to select the evolutionary model best fitting the characteristics of the data among 56 different models of molecular evolution, with different assumptions about the process of DNA substitution. Model selection was based on the Akaike Information Criterion that favors models with good fit to the data in relation to the number of parameters in the model. Because the model selected for *Daphnia laevis* resulted in nonestimable distances (due to extreme parameter estimates in the model), the model with the next lowest Akaike Information Criterion was used.

##### *Calculation of Bird-Mediated Distances between Populations*

Birds of the family Anatidae, ducks in particular, are likely to be the most important dispersers of aquatic invertebrates between inland wetlands because of their high concentrations in wetland habitats, their aquatic feeding habits, and their ability to travel over great distances during a relatively short period of time (Green et al. 2002). The genera included in the analyses were *Aythya* (five species:

*A. affinis*, *A. americana*, *A. collaris*, *A. marila*, and *A. valisineria*), *Anas* (nine species: *A. acuta*, *A. americana*, *A. crecca*, *A. clypeata*, *A. cyanoptera*, *A. discors*, *A. platyrhynchos*, *A. rubripes*, and *A. strepera*), and *Fulica* (*F. americana*).

Overall, 1,517,976 recoveries were available for these species. Matrices were constructed with the number of individuals banded and recovered in states where genetic information for the invertebrates was available (see tables 1, 2). We produced a symmetrical matrix by adding together the number of birds banded in state A and recovered in state B and the number of birds banded in state B and recovered in state A. This information was transformed into a matrix of distances measured as 1 minus the Steinhaus index (Legendre and Legendre 1998) using the R-Package program. The Steinhaus index is widely used in ecological research (Legendre and Legendre 1998). It compares two localities on the basis of the minimum number of recoveries at each of the sites. The similarity coefficient is close to 1 (i.e., the distance used in our analyses approaches 0) when more birds are banded in one state and recovered in another state but also when birds from each state use a third state in common during migration. This is a desirable quality of this index because most of the birds used in the analyses will have used many different localities through their life, between banding and being recovered (usually by hunting). All our analyses were repeated using the Canberra metric distance (Legendre and Legendre 1998), which weights the impact of each comparison between states as a function of the number of recoveries used in the comparison.

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