

# The geography of host and parasite invasions

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## 14.1 Introduction

This volume demonstrates that there can be strong geographic patterns for some parasite communities. For instance, one general prediction is that the similarity of parasite communities should decrease as a function of distance (Soininen *et al.* 2007; see also Chapter 9 of this volume). Species invasions are fundamental biogeographical processes that have occurred through geological time via long distance dispersal and through historical biotic exchange (Vermeij 2005). Now, the globalization of the world's economies is dramatically increasing the rate of invasions. Parasites can be lost, transferred, and gained when their hosts invade a new location. To what extent do these invasions affect parasite biogeography?

The 'Enemy Release Hypothesis' predicts that colonizing populations can benefit from a lack of natural enemies compared to populations within their original range (Elton 1958). Studies of contemporary species invasions indicate that most of the parasite species a colonist might bring with it are either left behind during the colonization process, lost shortly thereafter, or cannot survive in the new and different habitat (Dobson and May 1986; Torchin *et al.* 2003). The invasion process can 'filter out' parasites and pathogens that occur in an invading host's native range through several mechanisms (Keane and Crawley 2002).

Herein, we start with the general premise that the extent of enemy release in a host population should increase in distant, novel habitats where colonizing hosts face the greatest obstacles to establishment

(Blossey and Notzhold 1995; Keane and Crawley 2002; Torchin and Mitchell 2004). Host-specific parasites will not likely be awaiting a colonizer because they need to be brought in with the colonizing species. Escape from parasites should increase with the isolation of a new habitat because few infected colonists will reach isolated areas (or colonizing groups will arrive less frequently) and isolated areas will be more likely to differ environmentally from the colonist's native range. Perhaps, as a result of this, endemic species on islands often lack infectious diseases (Van Riper III *et al.* 1986; Fallon *et al.* 2005).

We first consider patterns of escape from natural enemies in the context of historical 'natural' invasions, asking whether the distribution of parasites of native mice on islands was affected by biogeography. We then use a model to illustrate how the biogeography of escape from natural enemies might increase host speciation rates. Finally, we consider escape from natural enemies in contemporary human-mediated invasions, asking whether biogeography influences the extent to which introduced species escape from natural enemies, namely, parasites.

## 14.2 Does island size or distance from mainland affect parasitism of island mice?

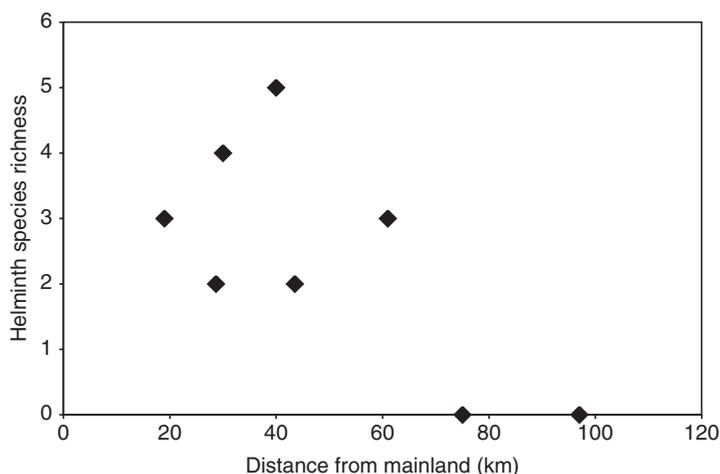
Smith and Carpenter's (2006) study, evaluating the transfer of helminth parasites from introduced black rats (*Rattus rattus*) to native deer mice (*Peromyscus maniculatus*) on the California Channel Islands, provides a good starting point for

understanding how geography can affect enemy release. Here, parasitological surveys of native mice were replicated across a single island archipelago. Each island has its own described subspecies of mouse that colonized the islands naturally, and with assistance from Native Americans over 1,000 years ago. The authors note that of the 40 genera of helminths known to affect deer mice in North America, only 5 genera occur in the Channel Islands. Introduced rats appear to have introduced one of these (*Trichuris muris*). Thus, we were able to ask whether the authors' measures of parasite richness and summed prevalence correspond to the geographic variables of island size and distance from mainland. We predicted that parasite richness and summed prevalence in mice should increase with island size and decrease with distance from the mainland.

Consistent with our prediction, helminth richness in mice declined with the distance from the mainland (Fig. 14.1, Table 14.1). In particular, the putatively introduced nematode was absent from the four most distant islands. However, there was no significant effect of island size on helminth richness. Summed prevalence also declined with distance from the mainland (Table 14.2). However, surprisingly, summed prevalence declined with island size, par-

ticularly on distant islands. These patterns were driven mostly by two species, *Hymenolepis* sp. and *Pterygodermatite peromysci*. Why did island size fail to have the predicted effect on parasite richness and prevalence? Larger islands could have more predators or competitors and this could reduce host density, making transmission less efficient on larger islands. Information on mouse density (not presently available) would be necessary to evaluate this hypothesis. In addition, large islands have more habitat diversity, increasing the likelihood of sampling locations with few parasites, assuming, as is usually the case, that parasites are spatially aggregated.

We also analysed data on the prevalence of hantavirus in mice from the same islands (Jay and Ascher, 1997). Unlike for helminths, viral prevalence was not affected by the distance to the mainland, but increased significantly with island size ( $F_{1,6}=9.5$ ,  $r^2=0.62$ , Estimate= $0.22\pm 0.07$ ,  $t$ -ratio=3.1,  $p=0.022$ ; Fig. 14.2). This pattern could result if life-time immunity strongly influences the dynamics of viral infections. On small islands viral infections, unlike helminth infections, are more likely to run out of susceptible hosts and go extinct. This is partly what leads to a strong association between viral diversity and landmass size in human populations (Constantin De Magny *et al.* 2009).



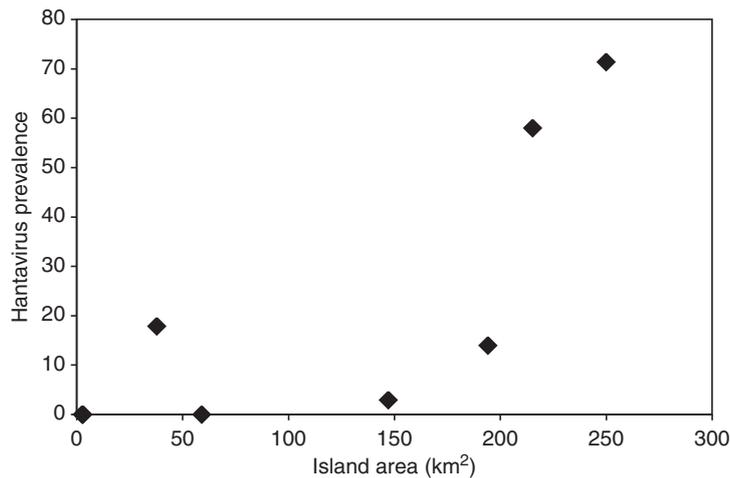
**Figure 14.1** A decrease in helminth species richness in native Channel Island deer mice with distance from mainland California using parasite data from Smith and Carpenter (2006). See Table 14.1 for statistics.

**Table 14.1** Species richness of mouse helminths in relation to island size (km<sup>2</sup>) and island distance from mainland (km) (islands: Anacapa [3 km<sup>2</sup>, 19 km], San Miguel [38 km<sup>2</sup>, 40 km], Santa Barbara [3 km<sup>2</sup>, 61 km], Santa Rosa [215 km<sup>2</sup>, 44 km], Santa Cruz [250 km<sup>2</sup>, 29 km], Santa Catalina [194 km<sup>2</sup>, 30 km], San Clemente [147 km<sup>2</sup>, 75 km], San Nicolas [60 km<sup>2</sup>, 97 km]) ( $r^2=0.71$ ,  $F_{3,4}=3.2$ ).

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	6.55	1.490	4.39	0.0117
Area	-0.01	0.006	-1.69	0.1672
Distance	-0.06	0.021	-2.97	0.0413
Area×Distance	-0.00	0.000	-1.04	0.3553

**Table 14.2** Summed prevalence of mouse helminths in relation to island distance and island size ( $r^2=0.87$ ,  $F_{3,4}=9.1$ ).

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	184.39	24.806	7.43	0.0017
Area	-0.31	0.101	-3.01	0.0395
Distance	-1.86	0.360	-5.17	0.0067
Area×Distance	-0.01	0.005	-2.82	0.0480



**Figure 14.2** Increase in Hantavirus prevalence in native Channel Island deer mice with island size, using data from Jay and Ascher (1997). See text for statistics.

### 14.3 The biogeography of enemy release and host speciation

Allopatric speciation, such as for the suite of island endemic mice species (or subspecies), described above, requires isolation from gene flow. This can be promoted by dispersal to remote locations and establishment of populations at those places. An obvious impediment to allopatric speciation is the rarity of colonists. If initial colonists are few,

demographic stochasticity and Allee effects can prevent establishment (Lande *et al.* 2003; Williamson 1996). Lack of adaptation to a new location (Holt *et al.* 2005; Peterson 2003) and/or low genetic diversity (Drake 2006; Briskie and Mackintosh 2004) make the establishment of colonists even less likely, particularly if they face competition from resident species already adapted to local conditions (Price 2008). However, an increased population growth rate resulting from enemy release might help

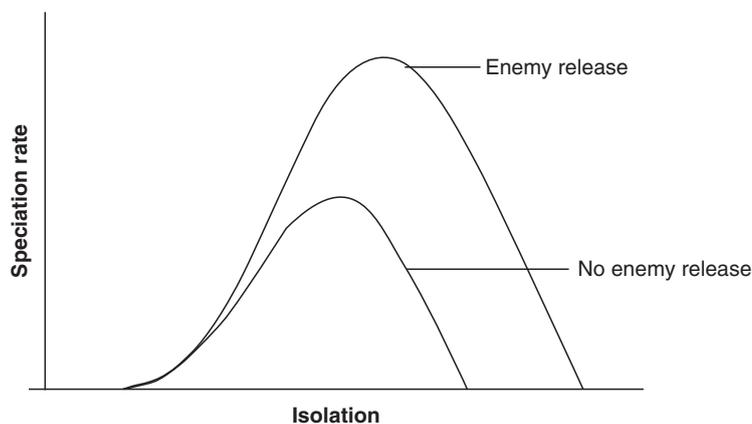
compensate for, and can theoretically exceed, the cost of demographic stochasticity resulting from a small initial population size (Drake 2003).

Our models (see Appendix) indicated that enemy release could increase the probability of speciation several fold because species that dispersed to an isolated habitat were more likely to establish if they left some of their natural enemies behind (Fig. 14.3). A higher probability of establishment in isolated locations increased the probability of the persistence of isolated populations, which was a prerequisite for allopatric speciation in the model. To a certain extent, these results derive from simple logic. Any factor that aids the establishment of arriving colonists in isolated areas should increase the potential for speciation. Escape from natural enemies may be transient on evolutionary time scales, but it may buy invaders needed time to colonize and adapt to novel environments.

The magnitude of the effect of natural enemies in speciation, expressed by the differences in the curves in Fig. 14.3, depends chiefly on the extent that parasites negatively affect demographic performance. Although ecologists historically viewed parasites as benign (Lack 1954), recent models (Anderson and May 1978; May and Anderson 1978), field studies (Canter and Lund 1948; Fenner and Ratcliffe 1965; Lemly and Esch 1984; Lafferty 2004) and experiments in the laboratory (Park 1948; Keymer 1981; Scott and Anderson 1984) and field

(Dobson and Hudson 1992; Lafferty 1993; Fitze *et al.* 2004) indicate that some parasites can greatly affect host density (Tompkins and Begon 1999). For instance, the nematode *Heligmosomoides polygyrus* increases host mortality and can reduce lab mouse densities 20 fold (Scott 1987) and native populations of the European green crab infected with a castrating parasitic barnacle (*Sacculina carcini*) have, on average, one third the crab biomass of uninfected populations (Torchin *et al.* 2001).

In addition to facilitating colonization and establishment, a lack of parasites and pathogens presents a shift in selective forces that shape evolution. Faced with fewer enemies initially and different suites of enemies over time, rapid diversification of founding populations can also influence rates of speciation (Ricklefs and Bermingham 2008). While a lack of natural enemies might foster genetic differentiation and eventual speciation, losing the legacy of past enemies also puts a species at risk if parasites eventually catch up with their hosts. In particular, if selection for defences is relaxed (Wolfe *et al.* 2004), and if genetic variation is low in isolated populations (Lyles and Dobson 1993), then susceptibility to both new and former pathogens may increase. The current susceptibility of native island endemics to mainland pathogens (Warner 1969) is a good example of a process that, in geological time, has been called the taxon cycle (Ricklefs and Cox 1972). In addition, local natural enemies might eventually



**Figure 14.3** Relationship between speciation and isolation for no enemy release ( $b=0$ ) and enemy release ( $b=1$ ) in the full model. All model parameters set to 1 except  $p$  and  $q$ , which were set to 0.5.

evolve to be able to use new hosts, particularly if those hosts become abundant (Tabashnik 1983; Zietara and Lumme 2002). Therefore, while our model uses the rate of species creation, it does not consider the extent to which new species will persist over time as conditions change. However, under natural conditions, invasions of competitors or natural enemies that could lead to extinction of island endemics seem to be sufficiently infrequent at isolated locations, promoting a relatively long persistence for island endemics (Price 2008).

Often, allopatric speciation events probably do not involve dispersal and establishment processes. Rather, the genetic isolating mechanisms are geological, including stream capture, orogeny, rifting, and the formation of new barriers such as the Isthmus of Panama (a barrier to marine species). Populations separated by these processes likely retain a substantial part of their original parasitofauna and enemy release is probably less important in influencing diversification.

#### **14.4 The biogeography of enemy release and human-mediated biological invasions**

Globalization of the world's economies is dramatically increasing the rate of biological invasions and homogenizing the earth's biota on a global scale. Escape from the effects of parasites is a common explanation given for the success of introduced species. Although invaders can also accumulate natural enemies from the communities they invade, accumulation does not generally make up for escape, and invaders often have fewer parasites than where they are native (Torchin and Mitchell 2004). To what extent does biogeography affect patterns of enemy release? First, it is conceivable that some or all of what appears to be enemy release is explainable through biogeographic processes. For instance, if species tend to invade from the tropics to temperate regions or from mainlands to islands, their parasite fauna could be reduced in accordance with general biogeographic patterns. If this were the case, differences in parasite communities among host populations would depend more on latitude, distance between populations, and landmass size than on whether a species was historically present

in a particular location. Clearly, enemy release and biogeography are not mutually exclusive hypotheses—each may contribute to the differences seen among parasite communities.

To evaluate the extent to which biogeography explains parasite release, we used the data from Torchin *et al.* (2003) providing information on the parasites of 26 diverse animal taxa in native and introduced populations from around the globe. Here, since we were interested specifically in the phenomenon of enemy release (as opposed to community similarities), we consider two measures of the parasite communities; relative species richness and summed prevalence. We use a standard measure of parasite species richness since we compared measures across a diverse range of host taxa (which varied in their parasite richness). For this, we calculated richness as a proportion relative to the total number of parasite species found in all studies in the native range of that host species as per Torchin *et al.* (2003). Similarly, to provide an indication of the unweighted cumulative extent of parasitism (or potential impact of parasitism on a host population) that each host experiences, we used summed prevalence (sum of the prevalence of all parasite species for each host species; see Torchin *et al.* 2003). We took several approaches to investigating this question. We first examined whether species origin (native or introduced) and geographical factors (latitude and land area) explained the parasite load in a particular host population. We then evaluated whether there were differences in enemy release between terrestrial and aquatic invaders. We also considered how distance and landmass area influenced differences in parasitism between pairs of native and introduced populations.

##### **14.4.1 How do latitude, landmass area, and population origin (native or introduced) affect parasitism?**

We evaluated how origin (native or introduced), location (longitude, latitude), and land area explained relative parasite species richness and summed parasite prevalence. We expected that parasitism would be higher near the equator (due to latitudinal diversity gradients), higher on large landmasses (due to negative effects of isolation on

diversity), and higher for native populations than for introduced populations (due to enemy release). The factors we considered in a least squared general linear model were:

- (1) species;
- (2) taxonomic group (molluscs, crustaceans, fishes, amphibians and reptiles (=herps), birds, mammals);
- (3) latitude (absolute);
- (4) longitude;
- (5) landmass type (island or mainland); and
- (6) origin (native vs. introduced).

We nested species within taxonomic group. We also included the first order interactions among taxa, longitude, latitude, and landmass type. Assumptions of the general linear model were met after using the square root transformation for the sum of prevalence and the angular transformation for relative species richness.

The only hypothesis consistently supported was origin. Introduced populations had lower parasite species richness (back transformed LSqM=23.8±0.2%) than did native populations (LSqM=45.5±2%). Taxon and species were also significant main effects (note that due the standardization among species, the main effects for taxon and species indicate differences in the variance of species richness, which was not a hypothesis we were considering; Table 14.3). There were several significant interactions among the main effects. Unlike the other taxonomic

groups, parasite richness in herps and mammals was not affected by origin. Parasite richness decreased with latitude for birds, mammals, and molluscs, but increased with latitude for herps. Parasite richness tended to increase with land area for herps and mammals, but declined with land area for birds and freshwater fishes. Parasite richness declined, on average, with latitude for native populations (as theory predicted), but increased with latitude for introduced populations. The interaction between area and latitude indicated that the effect of land area on parasite richness was negative near the equator and positive at the poles (or alternatively that richness declined with latitude on islands but increased with latitude on continents).

Similarly, introduced populations had a lower summed prevalence of parasites (back transformed LSqM=50.8±0.8%) than did native populations (LSqM=118.4±0.4%). This form of enemy release varied among taxa, with herps, mammals, and molluscs showing weak effects in comparison to crustaceans, birds, and fishes (Table 14.4). Latitude and land area did not have a consistent significant effect on summed prevalence. Summed prevalence increased slightly with landmass area for crustaceans, fish, mammals, and herps, but decreased with landmass area for birds and molluscs. Just as for parasite richness, summed prevalence tended to decline with landmass area near the equator and increase with landmass area near the poles. The summed prevalence of parasites varied among taxa

**Table 14.3** Variation in relative species richness among populations ( $r^2=0.57$ ,  $F_{45,241}=7.02$ ,  $p<0.0001$ ).

Source	df	Sum of Squares	F	Prob>F
Origin	1	0.81	23.1	<0.0001
Abs Lat	1	0.00	0.1	0.8020
Area	1	0.03	0.9	0.3319
Taxon	5	0.43	2.5	0.0317
Species[Taxon]	19	2.55	3.9	<0.0001
Taxon×Origin	5	1.06	6.2	<0.0001
Taxon×Abs Lat	5	0.52	3.1	0.0109
Taxon×Area	5	0.48	2.8	0.0177
Origin×Abs Lat	1	0.08	2.3	0.1304
Origin×Area	1	0.15	4.5	0.0352
Abs Lat×Area	1	0.24	7.0	0.0085

**Table 14.4** Variation in summed prevalence among populations ( $r^2 = 0.70$ ,  $F_{45,232} = 11.8$ ;  $p < 0.0001$ ).

Source	df	Sum of Squares	F	Prob>F
Origin	1	212.7	19.8	<0.0001
Abs Lat	1	4.2	0.4	0.5312
Area	1	2.5	0.2	0.6271
Taxon	5	1388.6	25.8	<0.0001
Species[Taxon]	19	1022.8	5.0	<0.0001
Taxon×Origin	5	306.6	5.7	<0.0001
Taxon×Abs Lat	5	113.0	2.1	0.0664
Taxon×Area	5	171.4	3.2	0.0085
Origin×Abs Lat	1	19.1	1.8	0.1847
Origin×Area	1	4.9	0.5	0.5001
Abs Lat×Area	1	103.6	9.6	0.0022

with mammals; herps, birds, and fish having higher summed prevalence than crustaceans and molluscs. Whether a population was native or introduced was the best predictor for both measures of parasitism and while geographical effects were present, they were inconsistent among taxonomic groups.

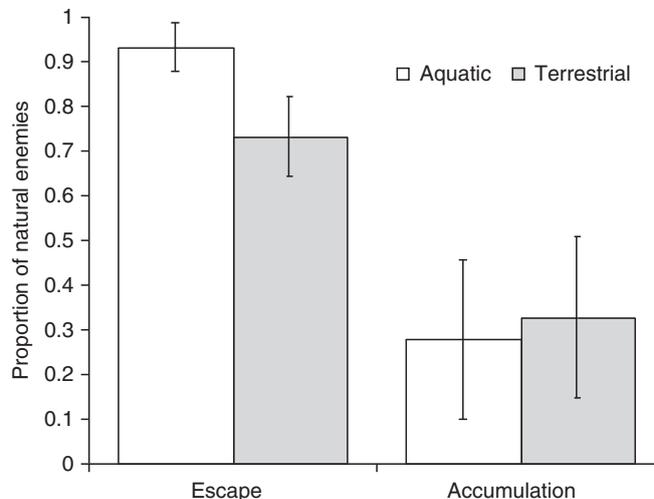
#### 14.4.2 Aquatic versus terrestrial invasions

Perhaps the most important aspect of biogeography is the interplay of land and water. Aquatic and terrestrial invasions might have different patterns of enemy release. Our analysis of data from Torchin *et al.* (2003) indicated that while there was no difference in accumulation of novel parasites by introduced species across habitats, a significantly higher extent of escape from natural enemies occurred in aquatic relative to terrestrial systems (Fig. 14.4). These results are consistent with Soininen *et al.* (2007) who demonstrate a greater similarity of ecological communities (i.e. initial similarity) in freshwater and marine communities relative to terrestrial systems. Another factor contributing to the aquatic-terrestrial differences may be a greater likelihood of multiple introductions for the terrestrial compared

to the aquatic species. Species such as rats and starlings were introduced multiple times with a much greater likelihood of successful transport and establishment of their native parasites (Torchin *et al.* 2003). While aquatic invaders are also introduced multiple times, they are often introduced as larval forms free from parasites (Torchin *et al.* 2001; Torchin and Lafferty 2008).

#### 14.4.3 How do distance and difference in landmass area affect enemy release in invasive species?

As predicted by island biogeography theory, dispersal of organisms to remote locations, especially islands, is infrequent (MacArthur and Wilson 1967). Similarly, parasite release should vary with distance from the source of invasion, where distant colonists to novel locations escape a greater proportion of natural enemies relative to those invading close to home. To further explore how biogeography might affect enemy release for introduced species, we evaluated how distances between populations and differences in landmass areas among populations correlated with differences in parasitism. For each



**Figure 14.4** Parasite release in aquatic and terrestrial habitats. In an analysis of 16 aquatic (white bars) and ten terrestrial (grey bars) animal taxa, aquatic animals escaped a higher proportion of their natural enemies from their native range (93 per cent), compared with terrestrial animals (73 per cent) ( $t=-4.02$ ,  $p=0.0005$ ). Error bars are 95 per cent confidence intervals. Aquatic and terrestrial animals did not differ in the proportion of natural enemies accumulated from their new range (expressed as a fraction of the parasites that they had in their home range). Enemy release is escape minus accumulation. Data from Torchin *et al.* (2003).

of the 26 species in Torchin *et al.* (2003), we constructed a matrix to pair each introduced site with each native site. Note that these pairings did not imply the source and target of an invasion, but were merely a comparison of introduced and native populations. For each pair of sites, we quantified two measures of 'release', first, the difference in relative species richness between the native location and the introduced location and second, the difference in the summed prevalence of parasitism between the native location and the introduced location. Our measures of isolation of introduced populations were the log distance between the sites in kilome-

tres, and the proportional change in log landmass area (a value only meaningful for species that invaded new landmasses). We expected that enemy release would increase with the distance between native and introduced sites and with a shift from large landmasses to small landmasses.

Full models of all species were dominated by strong interactions between taxon (or species) and biogeography, indicating no general effect of biogeography (distance and area) on enemy release. The large number of contrasting patterns in this analysis led us to analyse each species separately (Table 14.5). Limited numbers of replicate popula-

**Table 14.5** The contribution of distance and area and their interaction to the species richness and prevalence of parasites in introduced populations (Mc—mollusc, H—reptile/amphibian, C—crustacean, F—fish, Mm—mammal, B—bird).

Group	Species	Release	N	r <sup>2</sup>	Distance	Area	Interaction
Mc	<i>Batillaria</i>	Richness	60	0.19	NS		NS
	<i>Batillaria</i>	Prevalence	60	0.29	NS		NS
H	<i>Bufo</i>	Richness	12	0.78	NS	NS	*(+)
	<i>Bufo</i>	Prevalence	12	0.37	NS	NS	NS
Mc	<i>Bythinia</i>	Richness	12	0.95	NS	*(-)	NS
	<i>Bythinia</i>	Prevalence	12	0.75	NS	NS	NS
C	<i>Carcinus</i>	Richness	204	0.02	NS	NS	NS
	<i>Carcinus</i>	Prevalence	204	0.05	NS	NS	NS
Mc	<i>Dreissena</i>	Richness	96	0	NS		NS
	<i>Dreissena</i>	Prevalence	96	0.03	NS		NS
F	<i>Gambusia</i>	Richness	14	0.5	NS	NS	*(-)
	<i>Gambusia</i>	Prevalence	14	0.4	NS	NS	NS
Mc	<i>Ilyanassa</i>	Richness	11	0.04	NS		
	<i>Ilyanassa</i>	Prevalence	11	0.27	NS		
H	<i>Lepidodactylus</i>	Richness	20	0.12	NS	NS	NS
	<i>Lepidodactylus</i>	Prevalence	20	0.35	NS	NS	NS
Mc	<i>Littorina lit</i>	Richness	32	0.2	NS		*(-)
	<i>Littorina lit</i>	Prevalence	32	0.03	NS		NS
Mm	<i>Oryctolagus</i>	Richness	108	0.17	*(+)	NS	NS
	<i>Oryctolagus</i>	Prevalence	108	0.2	NS	NS	NS
F	<i>Poecilia latipinna</i>	Richness	16	0.14	NS	NS	NS
	<i>Poecilia latipinna</i>	Prevalence	16	0.27	NS	NS	NS
Mc	<i>Potamopyrgus</i>	Richness	30	0.22	*(+)	*(+)	NS
	<i>Potamopyrgus</i>	Prevalence	30	0	NS	NS	NS
Mm	<i>Rattus</i>	Richness	36	0.14	NS	NS	NS
	<i>Rattus</i>	Prevalence	36	0.06	NS	NS	NS
B	<i>Sturnus vulgaris</i>	Richness	18	0.24	NS	NS	NS
	<i>Sturnus vulgaris</i>	Prevalence	18	0.32	NS	NS	NS
Mm	<i>Trichosurus</i>	Richness	14	0.02	NS		NS
	<i>Trichosurus</i>	Prevalence	14	0.93	***(+)		
Mm	<i>Vulpes</i>	Richness	24	0.28	NS	NS	NS
	<i>Vulpes</i>	Prevalence	24	0.57	NS	NS	NS

tions of some species (*Anas platyrhynchos*, *Cancer novaeseelandiae*, *Hemigrapsus sanguineus*, *Melanoides tuberculata*, *Passer domesticus*, *Perca fluviatilis*, and *Rana catesbeiana*) and insufficient variation in biogeography of another (*Onchorynchus mykiss*) prevented separate analyses for some species. Again, the species-level results did not provide strong evidence for an effect of biogeography on enemy release (Table 14.5). Neither did a similar taxon-level analysis. Of the 16 species analysed, 2 (*Oryzotolagus cuniculus* and *Potamopyrgus antipodarum*) showed positive associations between release (in terms of richness) and distance. One species (*Trichosurus vulpecula*) showed a positive association between release (in terms of summed prevalence) and distance. And one species (*Potamopyrgus antipodarum*) showed a positive association between release (in terms of richness) and reduction in landmass. Counter to expectations, *Bythinia tentaculata* showed a negative association between release (in terms of richness) and reduction in landmass. Given the large number of independent tests in our analysis, it is questionable whether any of these effects are biologically meaningful. These results indicate that there are no general geographical patterns for enemy release in our global dataset. Thus, for contemporary biological invasions, simply moving far away from the native range, or from a mainland to an island, may not lead to release. Instead, enemy release probably results from local host-specific interactions, which can be easily broken simply by transport to a location just outside the native range.

## 14.5 Conclusion

Geography is likely an important factor explaining the current distribution of natural parasite communities. Distance between populations might be directly related to propagule pressure in some instances. In particular, our analysis of parasites in mice across a small archipelago is consistent with island biogeography because we expect that, here, distance from the mainland relates to declining propagule pressure of hosts and parasites. Landmass size, on the other hand, may be more important for infectious agents like viruses that provoke life-time immunity because island populations may be able

to escape such parasites if susceptible hosts quickly become limited. Enemy release, in addition to shaping variation in parasitism, particularly in remote locations, may have played an important part in generating biodiversity by increasing the chance that hosts could become established in remote locations. We may see similar evolutionary responses in contemporary human-mediated invasions (Huey *et al.* 2005).

The main factor explaining enemy release in our invasions database was whether a species was native or introduced. Geographical factors explained little of the variation in parasite release for a particular host species in our study. We emphasize that our comparison controls for the effect of species and taxon, so it is not necessarily at odds with other studies that find parasite communities among species to vary with geography. For instance, it is conceivable that parasites of herps as a group could decline with latitude while the parasites of a single frog species might not strongly vary with latitude. Our results strongly indicate that any study of parasite biogeography needs to control for the origin of the host populations. Whether host populations are native or introduced may override other geographical factors commonly used to evaluate parasite community similarity.

For introduced species, distance and landmass area were generally not strong indicators of enemy release from parasites. Unlike natural dispersal, where isolation is a direct function of distance, human mediated invasions break normal dispersal barriers and provide corridors for rapid and often frequent invasion. For instance, ships regularly and frequently transport species long distances between different biotic provinces (Carlton and Geller 1993; Cohen and Carlton 1998). As a result, propagule pressure or the number of individuals and number of times a species is introduced to a novel location by humans (Williamson 1996; Lonsdale 1999), may be less dependent on distance and other geographical factors. Placing parasite communities in a biogeographical context has deepened our understanding of the ecology and evolution of host-parasite interactions. Now, as humans continue to homogenize the earth's biota, insights generated from species invasions will be key to further this understanding.

## Appendix

We used mainland-island models (one simple and one more complex, hereafter called the full model) where allopatric speciation results from long-distance dispersal, establishment, and subsequent isolation. In the models, a source population exists on a mainland with associated islands that vary in distance from the mainland. Assuming no island-to-island dispersal (an assumption often violated in nature), the probability of dispersal from the mainland declines with the isolation of the island from the mainland. Some islands may be so isolated that dispersing species never reach them. For closer islands, a dispersal event from the mainland has four potential outcomes over geological time: failure to establish, persistence without speciation, allopatric speciation, and extinction. As a result, whether an island supports the mainland species, a derived species, or no species, should correspond to the degree of isolation. A hump-shaped relationship between isolation and speciation will result if individuals rarely or never colonize the most isolated islands and gene flow prevents divergence on islands near the mainland.

The models track the probability, in an arbitrary unit of time, that an island will experience a colonization of individuals destined to become a new species. For simplicity, we refer to this as the 'probability of speciation'. In the models, the probability of speciation is a product of the probabilities of dispersal,  $D$ , establishment (including persistence),  $E$ , and the probability,  $B$ , that barriers to gene flow will allow speciation to occur, or  $S=DEB$ .

One possible way to describe a probability of dispersal to a new location is  $e^{-x}$  (MacArthur and Wilson 1967), where  $x$  is a measure of isolation from the mainland (which itself is a function of distance, and dispersal ability). The models assume that rates of speciation are not constrained by an initially small population size.

The initial number of colonizers,  $n$ , and the initial instantaneous growth rate in the new location,  $r$ , will determine the success of a dispersal event, such that a simple model for the probability of establishment is  $E=1-e^{-rn}$ . One way to isolate the effects of enemy release or establishment is to describe population growth rate as  $r=m-p$ , where  $p$  is the extent

that natural enemies depress population growth, and  $m$  is the residual growth rate of the species without natural enemies. Note that  $m>p$  is a condition necessary for speciation.

Even if a species colonizes a new location, it needs time in isolation from gene flow for drift, natural selection, and/or random mutations to lead to enough genetic differentiation that reproductive barriers to the parent species evolve (i.e. reproductive isolation). We express these complex and little-known functions in a single term,  $z$ , which represents the time needed for a successful colonist to speciate. The probability of speciation is a function of speciation rates in isolation and the probability of isolation, or  $B=(1-e^{-x})^z$ .

A simple model for the probability of speciation is, therefore,  $S=DEB$ , or

$$e^{-x}(1-e^{-x})^z(1-e^{n(p-m)}) \quad (\text{Eq. 14.1})$$

To find the level of isolation,  $x^*$ , that results in the maximum amount of speciation, we set  $\delta S/\delta x$  to zero and solved for  $x$ . Substituting  $x^*$  for  $x$  and then solving for  $S$  indicated the height of the peak in the relationship between speciation and isolation. We then investigated the sign of  $\delta S/\delta p$  to determine how speciation was affected by natural enemies,  $p$ , under the expectation that natural enemies would reduce  $S$  by reducing establishment/persistence.

Several parameters in this simple model might co-vary with isolation and lead to interactions that are more complex. For this reason, we created an expanded model to model enemy release explicitly.

Because species may be less physiologically adapted to areas far from where they are native, the residual growth rate in the new habitat without natural enemies,  $m$ , might decline with isolation,  $x$ , where  $a$  is a measure of the association between isolation and habitat suitability, such that residual growth rate is  $me^{-ax}$ . Such an effect of distance on reduced suitability could be ameliorated by a lack of competitors (or biotic resistance) at remote locations. A reduction in biotic resistance with isolation (Darwin 1872), while not explicitly treated in this chapter, might have an effect on speciation similar to an increase in enemy release with isolation (Mack 1996).

Because few individuals are likely to simultaneously colonize remote areas, the initial population size,  $n$ , might decline with isolation (due to the rarity of colonization),  $x$ , where  $N$  is the size of the source population and  $c$  is the strength of the association between  $N$  and  $x$  such that initial population size is  $Ne^{-cx}$ .

*Enemy release as a function of isolation:* The sampling effect (fewer colonists bring a smaller proportion of the available natural enemies) (Drake 2003), was represented as the probability of an infectious disease accompanying a set of colonists  $= (1 - q^{e^{-cx}N})^b$ , where  $q$  is the proportion of uninfected individuals in the native population and  $b$  is a measure of enemy release (e.g. for  $b=0$ , natural enemies always accompanied dispersers, for  $b=1$ , the probability of a natural enemy dispersing depended directly on the sampling effect). There are two other mechanisms for enemy release with isolation. Distant environments may be unsuitable for natural enemies; for instance, they might lack necessary intermediate hosts for parasites. In addition, few colonizers may be below the host threshold density needed for parasite transmission. Because, like the sampling effect, unsuitability and the initial number of colonizers should tend to decrease with  $x$ , these distinct mechanisms could have an additive effect on the extent to which isolation interacts with escape from natural enemies to promote speciation.

Because distant (especially different) habitats may foster more rapid genetic change through adaptation, time to speciation in isolation,  $z$ , might decline with isolation,  $x$ , where  $f$  is a measure of the extent that time to speciation decreases with isolation from the source population, such that time to speciation is  $ze^{-fx}$ . A full model of the probability of speciation,  $S$ , is, therefore:

$$e^{-x} \left( 1 - e^{-e^{-cx}N(1 - e^{-ax}m + p(1 - q^{e^{-cx}N})^b)} \right) (1 - e^{-x})e^{-fxz} \quad (\text{Eq. 14.2})$$

Calculating partial derivatives indicated the conditions for which speciation increased or decreased with the different variables (evaluated for conditions where  $r > 0$ ). We then used second-order mixed derivatives to determine how other variables ( $a$ ,  $c$ ,  $f$ ) influenced the effect of enemy release on speciation. For simplification, we only report non-trivial results. We also used numerical simulations to graphically

explore how release affected the relationship between speciation and isolation.

In the simple model, the relationship between speciation,  $S$ , and isolation,  $x$ , was hump-shaped with a peak (for non-trivial values) at  $x = \text{Log}(1+z)$ . The peak resulted from gene flow preventing speciation in areas that were not isolated because isolated areas were only rarely colonized. Because  $p$  was missing from the solution, the location of the speciation peak was unaffected by natural enemies (so long as  $p < m$ ). However, the height of the speciation peak was  $(1 - e^{-m+p})nz^z(1+z)^{1+z}$  and, therefore, decreased with the effects of natural enemies,  $p$ . In the simple model,  $\delta S / \delta p$  was always negative for  $x > 0$ , indicating that natural enemies always decreased the probability of speciation. In other words, natural enemies in the new location decreased the probability of speciation (by decreasing the chance of a successful colonization) but would not shift the distance at which the probability of speciation was maximal. Consequently, these results indirectly suggested that enemy release would increase the height of the speciation curve.

In the full model, just as for the simple model,  $\delta S / \delta p$  was negative, indicating that enemies decreased speciation rates. Simulations of the full model exhibited a strong hump-shaped relationship between isolation and speciation that was consistent with the analytical results of the simple model. However, in the full model, an increase in the impact of natural enemies shifted the peak to the left along the isolation axis, indicating that natural enemies inhibited speciation in more isolated locations. These results suggested that enemy release could affect both the height (increasing it) and the location of the speciation curve (shifting it to the right).

In the full model,  $\delta S / \delta b$  was always positive for  $x > 0$ , showing that release from natural enemies always increased the probability of speciation. In addition, enemy release shifted the peak of the speciation curve to the right, indicating that enemy release differentially facilitated speciation in isolated locations (Fig. 14.3). The shift resulted from the compensatory effect of enemy release decreasing the probability of host establishment in distant areas that were otherwise ideal for speciation. Not surprisingly,  $\delta S / \delta b \delta p$  was always positive. Hence,

the effect of enemy release on speciation increased with the impact of natural enemies.

The partial derivatives of the full model showed how other variables affected the probability of speciation, while the second order mixed derivatives indicated how these other variables affected the relationship between enemy release and speciation.  $\delta S/\delta a$  was negative, demonstrating that if isolated habitat were less suitable, the probability of speciation decreased (because unsuitable habitat reduced establishment).  $\delta S/(\delta b \delta a)$  was positive, indicating that the strength of the negative association between habitat unsuitability and speciation increased the extent to which enemy release increased speciation.  $\delta S/\delta f$  was positive, suggesting that a decrease in time to speciation with isolation (due to natural selection in novel environments) increased the probability of speciation (rapid rates of evolution allowed reproductive isolation to outpace gene flow).  $\delta S/(\delta b \delta f)$  was also positive, indicating that faster speciation in more distant habitats increased the extent that enemy release increased speciation (because enemy release increased establishment in isolated areas).  $\delta S/\delta c$  was positive for larger values of  $p$  and negative for smaller values of  $p$ . This partial derivative represented the trade-off between the value of large population sizes for establishment (if parasites had low pathology) and the value of small population sizes for leaving parasites behind (if parasites were highly pathogenic).  $\delta S/(\delta b \delta c)$  was positive because a reduction in the number of colonists with isolation increased the contribution of enemy release to speciation.

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