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GRADE / DEGREE

Department of Biology
FACULTÉ, ÉCOLE, DÉPARTEMENT / FACULTY, SCHOOL, DEPARTMENT

Diversity investigations from the micro- to the macro- scale

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Diversity investigations from the micro- to the macro- scale

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Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
In partial fulfillment of the requirements
For the MSc. degree in Biology

Department of Biology
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ISBN: 978-0-494-49277-2
Our file Notre référence
ISBN: 978-0-494-49277-2

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Abstract

Macroecology and experimental evolution are two disparate sub-disciplines with contrasting approaches to the study of biological diversity. First I use macroecology and the Global Invasive Species Database to determine the best predictors of diversity patterns of invasive species around the globe. I show that economic factors account for more of the variance in invasive species richness among countries than typical ecological variables used to explain broad-scale species diversity patterns. I then use a microecological approach in which experimental evolution is performed with the soil bacterium *Pseudomonas fluorescens* to evaluate the idea that selection in environments varying in productivity will impact the degree of ecological specialization and maintenance of diversity. The results show that although ecological specialization increases with productivity, diversity does not. Both disciplines can be used to inform each other with the aim of explaining the abundance and distribution of species in nature through space and time.

Résumé

La macro-écologie et l'évolution expérimentale sont deux disciplines bien distinctes dont les approches dans l'étude de la diversité biologique sont contrastées. Premièrement, j'utilise la macro-écologie et la Base de Données Globale sur les Espèces Invasives pour déterminer les meilleurs prédicteurs des patrons de diversité des espèces invasives à travers le monde. Je montre que les facteurs économiques expliquent plus la variance de richesse en espèces invasives parmis les pays que les variables écologiques typiquement utilisées pour expliquer les patrons de diversité d'espèce à grande échelle. J'utilise alors une approche en micro-écologie dans laquelle l'évolution expérimentale de la bactérie du sol *Pseudomonas fluorescens* est effectuée pour évaluer l'idée que la sélection dans des environnements qui varient en productivité aura un impact sur le degré de spécialisation écologique et sur la maintenance de la diversité. Les résultats montrent que bien que la spécialisation écologique augmente avec la productivité, la diversité elle n'augmente pas. Les deux disciplines peuvent être utilisées pour se compléter l'une l'autre afin d'expliquer l'abondance et la distribution des espèces dans la nature à travers l'espace et le temps.

Acknowledgements

I would like to thank everyone from the Kassen lab who has helped me out when experiments became too large or by allowing me to run ideas off of them. In particular, Jean-Nicolas with his not always constructive criticism but constant willingness to spend time talking about anything related to science. Justin and Sijmen for helping me work out many different problems, and always being up for Friday afternoon beer club. Also to Rees for giving me deadlines.

Thank you to my family and friends for all the support they have given me over the past few years, especially the Rundle lab, my parents and Michael.

Introduction

Why are there so many species? Understanding the vastness of biological diversity has baffled biologists since long before Darwin. Over 900 plant species with a diameter greater than 10 cm at breast height can coexist within one hectare of forest in Queensland, Australia (Phillips & Gentry, 1994). According to the competitive exclusion principle put forward by Gause (1934), two species competing for the same resources cannot stably coexist. Eventually one of the two competitors will use the resources more efficiently causing the elimination of the second competitor. So how can so many species coexist within one hectare of forest where light intensity and soil nutrients are likely similar? Explaining the diversity, distribution and abundance of species is a central goal of ecology and evolution. It has led to the fractioning of the field into many sub-disciplines, often differing in their epistemological basis. Two disparate but common approaches are macroecology and experimental evolution, a technique I will refer to as microecology.

Macroecology blends together ecology, biogeography and evolution in order to get above the case specific issues with studying community or local processes. It searches for major statistical patterns among the type, distribution, abundance and richness of species from a local to global scale while attempting to develop and test theoretical explanations for the emerging patterns (Lawton, 1999). Often times the specific details of an ecological interaction can be determined, but due to inter- and intra-specific effects as well as species-environment effects through space and time, a generalized pattern is nearly impossible to define unless the details are ignored (Lawton, 1999). Therefore, a fundamental assumption of macroecology is that any pattern that emerges at a global level must be governed by a general process, and is not due to a collection of special circumstances. The goal of macroecology is to identify a few very strong predictors of ecological patterns, primarily species distribution through space and time, by creating models that explain large amounts of variance (Currie et al. 1999). The success of a study is judged by how much predictive power is gained. For example, species diversity across space can be predicted using a few highly correlated climatic or energetic variables (see Hawkins et al. 2003 for a review), a pattern Hawkins pointed out was first observed by Von Humboldt in 1808. Although there has been much progress identifying macroecological patterns that hold across taxa and geographic regions much less progress has been made in identifying the underlying mechanisms (Brown & Maurer, 1989). This is particularly true for the species diversity/climate pattern, where at least nine hypotheses exist to explain this highly studied pattern (Evans and Gaston, 2005). Disentangling the hypothesis is difficult due to predictions for one hypothesis overlapping with other hypothesis (Gaston and Blackburn 1999) as well as several independent variables correlating with each other (Hawkins et al 2003). The field of macroecology itself makes it difficult to test mechanistic explanations due to the inability of performing manipulative experiments. Despite these drawbacks, the promise of macroecology to identify broad-scale patterns that are governed by universal general mechanisms is alluring and could aid in determining the appropriate actions to help conserve dwindling biodiversity.

In Chapter 1 of this thesis, I will use macroecological methods in order to gain an understanding of what factors are most important for explaining broad scale invasive species diversity patterns. Previous work by Lonsdale using various collections of local data sets suggests that site invasion potential is highly dependent upon the number of native species, whether the site is an island or mainland and whether or not the site is a reserve (Lonsdale 1999). Two larger analyses focusing on the United States (Taylor & Irwin 2004) and 10 European or North African countries (Vila & Pujadas 2001) found that economic indices explained much of the variation in invasive species diversity implicating the importance of economics. Other factors previously studied with respect to invasive species patterns include latitude (Sax 2001, Stohlgreen et al. 2005), climate (Pauchard et al. 2004, Evans et al. 2005), measures of anthropogenic disturbance (Mack 1989, Didham et al. 2007), population (Vila & Pujadas 2001, Taylor and Irwin 2004) and tourism (Vila & Pujadas 2001, Taylor & Irwin 2004) . The novelty of Chapter 1 is the use of the Global Invasive Species Database to study invasive species patterns of all species (except marine) across the entire globe. Although previous broad scale studies have been performed (Vila & Pujadas 2001, Taylor & Irwin 2004), none are at the same geographic level or include as many taxa. The final database consists of 158 countries and over 400 species deemed invasive by experts reporting to the Global Invasive Species Database. Incorporating biotic and abiotic factors, including various socio-economic indices, I conclude that Gross Domestic Product (GDP), a measure of economic status, is the best predictor of global invasive species patterns. Here I suggest that this pattern is due to the important role trade plays in transporting invasive species around the planet. An increase in trade likely increases propagule pressure, the term used to encompass both the number of species released per event and the number of release events. Propagule pressure is one of the few factors known to increase success of invasion (Cassey et al. 2004, Lockwood et al. 2005). This study steps away from the traditional approach used to study invasive species, one that focuses on the properties of species that predispose them as potential invaders (Kolar & Lodge 2001, Rejmanek & Richardson 1996) or specific properties of habitats that make them easily invaded (Fargione & Tilman 2005, Knops et al. 1999, Levine et al. 2004). Looking at global patterns may also help us develop a global solution to one of the largest threats to current levels of biodiversity (Mack & Lonsdale 2001, Vitousek et al. 1996).

Microecology, on the other hand, attempts to determine how evolutionary change affects ecological processes by reducing the complexity of the system so mechanistic processes can be determined and tested, typically with microbial model systems (Rainey et al. 2000). Through the use of microbial model systems, control can be exerted over environmental variables and one can watch the evolutionary process as it unfolds. This approach allows for more rigorous testing of an evolutionary hypothesis than would otherwise be possible. Microbial systems are ideal for many reasons: their ease in propagation, large population sizes, asexual life cycle, readily manipulated environmental variables, availability of molecular tools and a short generation time allowing for selection to occur over several hundreds of generations (Elena & Lenski 2003). A major assumption in microecology is that mechanisms determined at the simplest level are fundamental to ecological and evolutionary patterns, and therefore apply at larger scales and more complex systems than the experimental one (Jessup et al. 2004). The microecological approach is often used to study the emergence and maintenance of diversity (Kassen & Rainey 2004, Rainey et al. 2000), particularly the role of environmental heterogeneity (Bell 1997, Rainey & Travisano 1998, Kassen 2002, Barret et al. 2005). This work has found that the genetic variation in fitness is maintained more readily in heterogeneous than homogeneous environments, often through negative frequency dependent selection (Kassen 2002). This is not surprising since heterogeneous environments contain more niches into which species can specialize. The interaction between environmental heterogeneity and productivity – the rate of flow of organic matter through a community – remains unexplored, however, and constitutes a second focus of the work here.

In Chapter 2 I use the microecological approach to study the evolutionary response of populations to selection in environments varying in productivity. From broad scale species studies the relationship between productivity and species richness remains controversial, although for vascular plants it is predominately hump shaped at scales smaller than continents and for animals a positive relationship is most common (Mittelbach et al 2001). The mechanisms to explain these patterns are as numerous as the observed relationships, making the microecological approach potentially useful. As well, current effort to understand the role of evolution in producing these patterns is lacking. In this chapter I perform a microbial evolution experiment that manipulates environmental heterogeneity by delivering two carbon sources either alone or as a mixture (to mimic spatially coarse-grained and fine-grained environments) at different productivities achieved by varying the concentration of total carbon available for growth. Although I found that the average amount of environmental variance among genotypes after selection in the mixture increased with productivity, diversity did not. Furthermore, the mixture lines increased in fitness markedly compared to the ancestor during growth in the mixture itself, but not in the individual components suggesting the evolution of phenotypic plasticity.

Both the microecological and macroecological approach are useful in studying species diversity and have their benefits and drawbacks. In Chapter 1 I use the macroecological approach to look at invasive species from a global perspective with the aim of identifying key factors to explain the variation in exotic species diversity and to develop a hypothesis to interpret this relationship. The microecological approach is used in Chapter 2 to test directly how productivity can affect the outcome of selection in a heterogeneous environment, the aim being to evaluate the prediction that diversity should increase with productivity. Overall both approaches are useful for each particular study, and without statistical broad scale methods, or experimental manipulation, ecology would not be where it is today. Despite the differences between each field there exists a unifying theme to seek explanations for diversity by employing complementary approaches.

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Chapter 1

Trade and global patterns of invasive species diversity

Abstract

The invasion of species into non-native environments represents a serious threat to world biodiversity. Here I show that, on a global scale, economic factors such as gross domestic product account for more of the variance in invasive species richness among countries than many ecological variables typically used to explain broad-scale patterns of species diversity. Furthermore, I show that trade is likely to be the driving force underlying the relationship between invasive species richness and gross domestic product by documenting (1) a positive relationship between invasive species richness and the number of free trade agreements held by a country; (2) that the slope of the relationship between the number of invasive small-bodied, cryptic species and gross domestic product is steeper than for larger, more conspicuous invasive species; (3) a positive relationship between species native to a particular country and invasive elsewhere and gross domestic product. Given that trade provides repeated opportunities for introduction of invasive species, my results suggest that propagule pressure, the effective number of individuals introduced into a region, is a possible mechanism governing global patterns of invasive species richness.

Introduction

Invasive species constitute a redistribution of global biodiversity with manifold threats to ecosystem integrity, economic well-being, and human health (Vitousek et al. 1996; Mack et al. 2000). Understanding the causal factors underlying biological invasions has been a major goal of conservation biologists and policy-makers in recent years (Williamson & Fitter 1996*a*; Kolar & Lodge 2001) with attention focusing on the life-history characteristics of species that make them invasive and the properties of environments or communities that allow them to be invaded (Williamson & Fitter 1996*b*; Lonsdale 1999). The broader issue; namely, the factors associated with the global distribution of invasive species, has not been thoroughly addressed. Here I focus attention on these broad-scale patterns by testing the importance of a range of natural and anthropogenic factors for explaining the variance in the diversity of invasive species in countries around the world.

It has long been recognized that the exchange of goods and people represent the main avenues of non-native species dispersal (Mack & Lonsdale 2001; Taylor & Irwin 2005), suggesting that associated socioeconomic variables such as trade or tourism may account for much of the variance in invasive species richness. To test this hypothesis, I regressed the number of invasive species in countries around the world, reported by the Global Invasive Species Database (GISD), against socioeconomic factors indicative of the volume of trade in goods and people (GDP, volume of trade, number of tourists), ecological variables known to be important in governing broad-scale patterns of species diversity (latitude, area, temperature, precipitation, environmental heterogeneity, disturbance) and total population size (see Table 1). The known impact of invasive species on island ecosystems suggests that different factors govern the success of invasive species on islands and continents (Loope & Mueller-Dombois 1989, Lonsdale 1999) so I report them as separate analyses here.

Methods

Data Set

I downloaded the number of invasive species for each country from the Global Invasive Species Database (GISD, http://www.issg.org/database/welcome/) that reports exotic species known to pose a threat to native biodiversity based on expert submissions. For each country I collected economic and ecological variables from the most recent publicly accessible database and transformed appropriately to maintain normality (Table 1). The economic variables included gross domestic product, trade in goods as a share of GDP, number of tourists per year and free trade agreements. The number of free trade agreements for each country includes all bilateral and regional free trade agreements and custom union agreements that have been notified to the World Trade Organization as well as some that have not been notified but identified by the Center of International Business. Ecological variables were central latitude, area, mean annual precipitation, mean temperature, anthropogenic disturbance and environmental heterogeneity calculated from Holdridge life zones. Climatic and life zone data were extracted for each country using Arc GIS 9. Global maps were projected using an Eckert IV equal-area projection to preserve area relationships among countries and life zones. I attempted to account for potential variation in natural history research by collecting data on the number of researcher and development personnel and the number of individuals enrolled in tertiary

Table 1: Units, transformation, reason and source of all collected variables

Factor	Measured Variable (unit)	Transform	Reason	Source
Area	Area (km^2)	$\log_{10}$	Established species-area relationship	NRC, National Research Council Services, http://www.nrcs.usda.gov/intranet/rad/data.html#hold
Latitude	Central latitude (°)	None	Established gradients in species diversity	CIA, Central Intelligence Agency, The World Factbook, http://www.cia.gov/cia/publications/factbook/index.html
Environmental Heterogeneity	Inverse of Simpson's Index using the area of Holdridge life zones	√	Niches increase with heterogeneity	NRC
Anthropogenic Disturbance	agricultural land area/total country area	Arcsine	Reduced competition in disturbed areas	FAO, Food and Agriculture Organization, http://faostat.fao.org/
Climate	Mean temperature (°C)	none	More species in productive climates due to energy availability	Worldclim, http://biogeo.berkeley.edu/worldclim/worldclim.htm
	Mean precipitation (mm)	√		
Economic Activity	Gross Domestic Product (GDP) (US$)	$\log_{10}$	Larger economic intensity more transport	The World Bank, World Development Indicators (WDI) database, Country Profiles, http://www.worldbank.org/
Trade	Trade in goods as a share of GDP (US$)	$\log_{10}$	Trade transports species	The World Bank
	Number of free trade agreements	none		CIB, Center for International Business,Tuck Trade Agreements Database, http://cibresearch.tuck.dartmouth.edu
Tourists	Number of visitors/year	$\log_{10}$	Tourists transport species	Yearbook of Tourism, World Tourism Organization, 2003
Knowledge	Number of researchers	$\log_{10}$	More research more species reported	UNESCO, United Nations Educational, Scientific and Cultural Organization Institute for Statistics, http://www.uis.unesco.org/
	Number of students enrolled in tertiary education	$\log_{10}$	Increased knowledge in population to report species	UNESCO
	Number of publications	$\log_{10}$	Invasive species study intensity increases reporting	Web of Science, ISI Web of Knowledge, http://www.thomsonisi.com/
Population	Population	$\log_{10}$	Humans as global transporters	The World Bank

education as well as the number of publications related to a country's flora and fauna by conducting an article search on Web of Science using the following keywords: flora, fauna, plant, animal, reptile, amphibian, mollusk, insect, bird or mammal and the country's name.

Analysis

I conducted a series of regression analyses with SAS 9.1 using the number of invasive species per country as the dependent variable and the ecological and economic variables listed above as independent variables. The final data set included 135 continental countries and 23 island countries. Preliminary examination of the data set indicated that GDP was highly correlated with number of tourists, volume of trade and indices of natural history research; therefore, to avoid-over fitting my model I used GDP in all further analyses (for all correlations see Appendix Table 1). I screened for collinearity among the independent variables included in each model by inspecting the variance inflation factors, all of which were <10 as long as trade, number of tourists and indices of natural history research were excluded. This result suggests that collinearity does not strongly affect the relationships I observed (SAS Institute 2004).

The regression analyses proceeded as follows. I first obtained a minimal model by reducing a complete model for each dependent variable of interest that included all ecological factors, population and GDP using Akaike's information criterion (AIC) and adjusted R^2 values; both methods arriving at the identical reduced models presented in Table 2. To evaluate the importance of GDP, I contrasted the variance explained by the minimal model with and without GDP (Table 3). To isolate the effect of GDP I first calculated the residuals of the model of invasive species against all remaining factors in

Table 2: Reduced models used for regression analyses presented in Figure 1.

Fig. 1	Reduced Model
A	Invasives = heterogeneity latitude GDP (continental countries) Invasives = latitude precipitation temperature population GDP (island countries)
B	Invasives = heterogeneity latitude temperature population disturbance FTA
C	Plants and insects = heterogeneity latitude temperature GDP Aquatic animals = heterogeneity latitude precipitation temperature population area GDP Terrestrial animals = heterogeneity latitude precipitation population GDP
D	Native invasives = heterogeneity latitude precipitation temperature population disturbance GDP

the minimal model except GDP (model reported in Table 3). Secondly, I calculated the residuals of the model of GDP as an independent variable against these same remaining minimal model factors. Figure 1A shows the plot of the residuals of invasive species richness against all variables remaining in the minimal model except GDP regressed against the residuals of GDP on these same variables.

The trade analysis followed the same procedures as for GDP above but modifying the dependent and independent variables as identified below. For the free trade analysis, GDP was replaced by free trade agreements (FTA) as an independent variable. Invasive species were subdivided into three broad categories: plants and insects, aquatic freshwater animals (mollusks and fish) and large terrestrial animals (reptiles, amphibians, mammals and birds) for the taxonomic analysis and three separate regression analyses performed as described above for each of the taxonomic groupings acting as the dependent variable. Finally, for the native invasive species analysis the dependent variable utilized was the number of native species in a particular country that was reported to be invasive elsewhere in the world.

To test for spatial autocorrelation I produced Moran's I correlograms of the residuals from all regressions. In all cases, Moran's I values were not significantly different from zero

(α=0.05), even at the shortest lag distances, suggesting that spatial autocorrelation does not influence my results (Fortin & Dale 2005).

Results and Discussion

Contribution of economic factors

All studied ecological factors and population size account for 9% of the variance in invasive species richness on continents and 52% on islands. Adding GDP to the model increases the proportion of variance explained to 39% for continental countries and 63% for island countries (Table 3). Note that by eliminating outliers (USA and Australia) the variance explained by the model improved for continents from 39% to 56%. Thus for continental countries GDP (or its correlates) accounts for substantially more of the variance in invasive species richness than do all non-economic factors combined.

Figure 1A illustrates the relationship between invasive species richness and GDP after correcting for all other terms in the model. There is a clear positive relationship between these two variables that is highly significant for both continental (with USA and AUS: b=18.26, F=65.75, P<0.0001, r^2=0.33, without USA and AUS: b=11.19, F=136.81, P<0.0001, r^2=0.51) and island (b=19.00, F=7.38, P<0.013, r^2=0.26) countries. These results provide evidence that the economic wealth of a country, as measured through GDP, helps explain the success of invasive species in countries around the world. Ecological factors related to broad-scale patterns of species diversity do not appear to strongly influence the patterns of invasive species richness.

Trade and invasive species richness

It is tempting to interpret the relationship between GDP and invasive species as

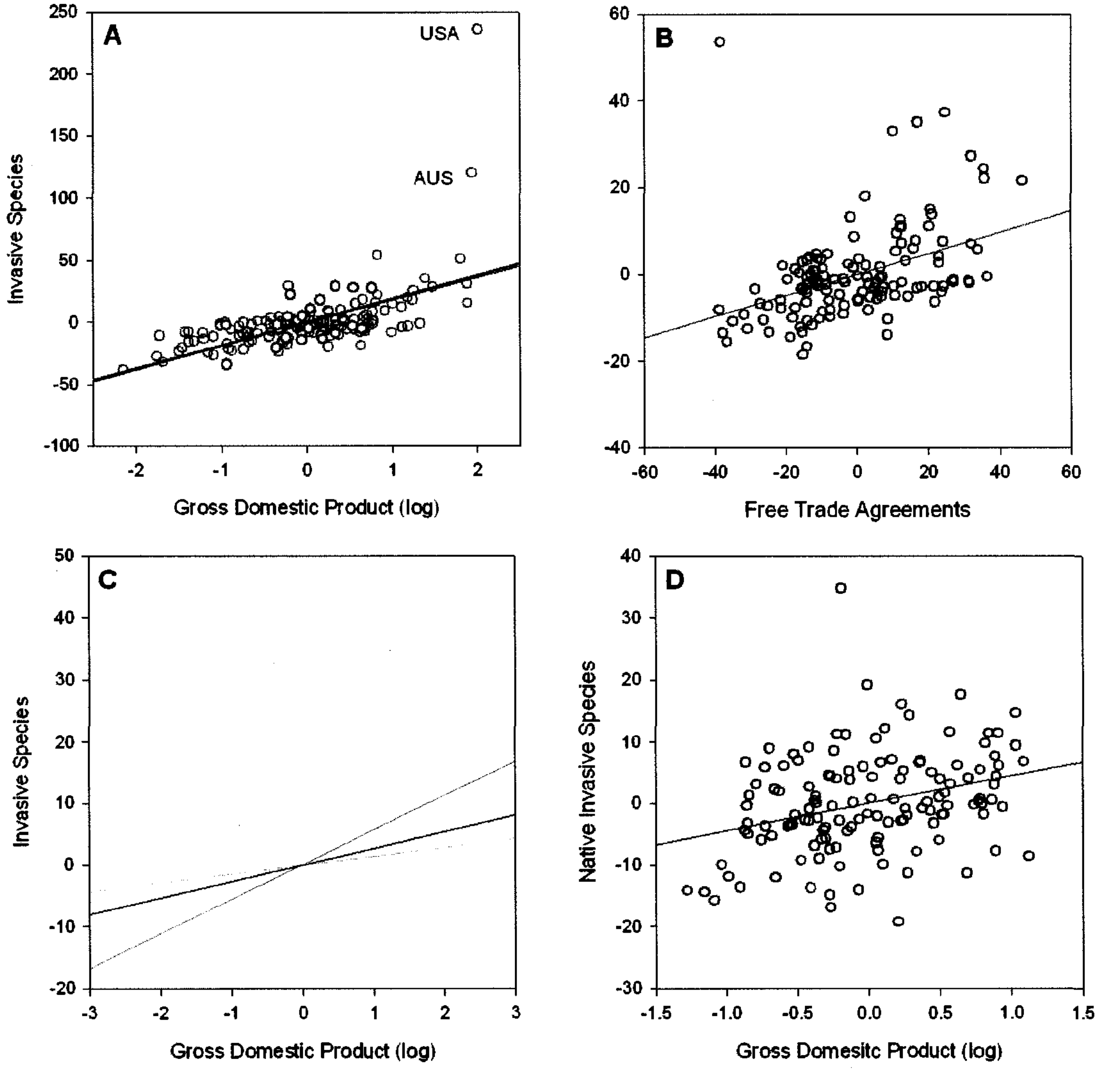

Figure 1. (A) Residuals of model of invasive species richness against all factors left in minimal model reported in Table 3 on the y axis plotted against the residuals of the model of GDP against all of these same factors, for continental (red; b=18.26, F=65.75, P<0.0001, r^2=0.33) and island (blue; b=19.00, F=7.38, P<0.013, r^2=0.26) countries (B) Residuals of model of invasive species richness against all relevant variables (found in Table 3) versus the residuals of the model of the number of free trade agreements against these same relevant variables (b=0.24 , F=27.13, P<0.0001, r^2=0.17); (C) Analysis of covariance between species group and GDP (plants/insects: red; aquatic animals: black; large terrestrial animals: green); (D) Relationship between residuals of model of species native to a country but invasive elsewhere (native invasives) against all remaining variables reported in Table 3 against residuals of the model of GDP against these same variables (b=4.49, F=14.39, P=0.0002, r^2=0.10).

Table 3: Comparison of Adjusted R^2 and AIC values for continental and island countries before and after the removal of GDP.

Model	Adj R^2	AIC	*F*	*P*
Continental Countries				
Including USA and AUS (n=135)				
Invasive species = latitude heterogeneity GDP	0.389	841.2	29.5	<.0001
Invasive species = latitude heterogeneity	0.094	893.4	8.0	0.0005
Excluding USA and AUS (n=133)				
Invasive species = latitude heterogeneity precipitation temperature GDP	0.563	590.0	35.0	<.0001
Invasive species = latitude heterogeneity precipitation temperature	0.113	683.1	5.2	0.0006
Island Countries (n=23)				
Invasive species = latitude precipitation temperature population GDP	0.625	132.3	8.3	0.0004
Invasive species = latitude precipitation temperature population	0.521	137.2	7.0	0.0014

being driven by trade because trade represents a well-documented route for species exchange (Griffiths et al. 1991; May & Marsden 1992; Fritts and Rodda 1998) and is highly correlated with GDP (r=0.9736, P<0.0001). To test this idea, I conducted three further analyses, the results being shown in Figure 1 b-d. First the number of invasive species increases with the number of free trade agreements held by a country, independent of all other factors (b=0.24, F=27.13, P<0.0001, r^2=0.17, Figure 1B). The free flow of goods among nations is therefore likely accompanied by a similar free flow of exotic species. Second, I expect that smaller organisms such as insects and plants would more readily evade detection during transport, and so be transported more frequently than larger terrestrial and freshwater aquatic animals. Figure 1C lends support to this idea: the slope of the regression for small, inconspicuous species groups (plants and insects) is steeper than the slope for both large terrestrial and aquatic animals, a result confirmed by a significant species group x GDP interaction (F=19.7, $DF_{species\ group\ x\ GDP}$=2, DF_{error}=393, P<0.0001).. Third, countries that trade more should not only contain larger numbers of non-native species but also supply more of their own species to other countries, suggesting that there should be a positive relationship between GDP and the number of species native to a country that are invasive elsewhere. Figure 2D shows that this is indeed the case. Taken together, these results strongly implicate trade as the proximate factor underlying the invasive species-GDP relationship. The free flow of goods among nations is likely to be accompanied by a similarly free flow of exotic species.

Potential sources of bias

I cannot formally exclude the possibility that my results are biased by the fact that countries with higher GDP report more species to the GISD because they invest more in natural history research. Different measures of natural history research were collected, including number of researchers, number of students enrolled in tertiary education, volume of publications on the flora and fauna of a country; but each of these indices was highly correlated with GDP. Thus I was unable to account statistically for variance in natural history knowledge. However, if such a bias exists, I would expect proportional increases with GDP in the number of invasive species across broad groups and no significant interaction between species groups and GDP in an analysis of covariance. My species group-based analysis (Figure 1d) suggests this is not the case.

Conclusions

My leading result is that economic factors, specifically GDP, account for more of the variance on average in invasive species diversity across countries of the world than more traditional ecological factors. This result is, perhaps, not surprising given that the link between human activities and the introduction, intentional or not, of invasive species, has been well-documented (Mack & Lonsdale 2001, Vila & Pujadas 2001, Lodge & Shrader-Frechette 2002, Taylor and Irwin 2004, Keller and Lodge 2007). Classic examples include the introduction of the Caspian Sea zebra mussel (*Dreissena polymorpha*) through ship's ballast into the Great Lakes in the 1980's (Griffiths et al. 1991; May & Marsden 1992) and the brown tree snake (*Boiga irregularis*) introduced to Guam after World War II through military shipping crates (Fritts & Rodda 1998). Nevertheless, the magnitude of the importance of economic activities relative to other explanations for patterns of invasive species diversity has only previously been documented at much smaller spatial scales (Taylor & Irwin 2004; Vilas & Pujadas 2001). My global analysis clearly indicates a strong correlation between economic activities and the number of invasive species found in countries around the world.

Moreover, international trade is strongly implicated as the driving force underlying this relationship. The logical connection between trade and invasive species is apparent: increasing trade among countries provides more opportunities for potentially invasive species to 'hitchhike' along with goods being traded. One of the few clear generalizations to emerge from studies of causes of invasions is that the probability of a species becoming invasive increases with propagule pressure (Lockwood et al. 2005). The positive relationship I observed between the number of invasive species and the number of free trade agreements held by a country, the variance in slopes between smaller 'hitchhiker' taxa and larger terrestrial or aquatic animals and the positive relationship between the number of species native to a country but invasive elsewhere and GDP suggests that propagule pressure may be the dominant ecological mechanisms governing the success of invasions. If in our analysis GDP did not remain in the final minimal model, I would have concluded that establishment effects, like niche availability (environmental heterogeneity) or level of anthropogenic disturbance, would be more important than transport effects. Since this is not the case, my results imply that the control or prevention of exotic species invasions will become increasingly difficult as economic and political barriers to international trade disappear and goods and people move more freely around the globe. A focus on economic hot spots around the world will be more successful at preventing the spread of invasive species than focusing on ecological hot spots. Policies aimed at containing putatively invasive species at destination, such as quarantine, are likely to fail in the face of persistent rain of exotics being introduced through anthropogenic sources. Instead, policies geared towards preventing the transport of species at source will be much more effective at preventing the dispersal of invasive species around the world.

Acknowledgements

I thank D. Currie and A. Ricciardi for comments and A. Algar for help with the spatial autocorrelation analysis. RK was supported by Natural Science and Engineering Research Council (NSERC) Discovery Grant, GS by an Ontario Graduate Scholarship.

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Appendix

Table 1: Matrix of correlation between all variables collected showing the correlation coefficient (r), probability value (P) and sample size (N).

	Area	Population	Latitude	Temperature	Precipitation	Disturbance	Heterogeneity	GDP	Free Trade Agreements	Trade	Tourism	Research and Development Personnel	Tertiary Students	Publication
Area r P N		0.6719 <.0001 135	-0.1628 0.0592 135	0.0104 0.9049 135	-0.1680 0.0514 135	-0.0611 0.4814 135	0.4508 <.0001 135	0.4034 <.0001 135	-0.1908 0.0266 135	0.3330 0.0001 135	0.2071 0.0232 120	0.3637 0.0017 72	0.5373 <.0001 111	0.5157 <.0001 135
Population	0.6719 <.0001 135		0.0664 0.4440 135	-0.0768 0.3759 135	-0.0923 0.2870 135	0.2236 0.0091 135	0.3627 <.0001 135	0.6614 <.0001 135	0.0440 0.6122 135	0.5677 <.0001 135	0.4801 <.0001 120	0.7065 <.0001 72	0.8124 <.0001 111	0.6242 <.0001 135
Latitude	-0.1628 0.0592 135	0.0664 0.4440 135		0.6619 <.0001 135	-0.2080 0.0155 135	-0.0768 0.3757 135	-0.0581 0.5033 135	0.3620 <.0001 135	0.4848 <.0001 135	0.4247 <.0001 135	0.3738 <.0001 120	0.4582 <.0001 72	0.3315 0.0004 111	0.0662 0.4457 135
Temperature	0.0104 0.9049 135	-0.0768 0.3759 135	0.6619 <.0001 135		0.1731 0.0447 135	-0.0841 0.3322 135	-0.1864 0.0304 135	-0.3879 <.0001 135	-0.4671 <.0001 135	-0.4386 <.0001 135	-0.4308 <.0001 120	-0.4546 <.0001 72	-0.3600 0.0001 111	-0.1725 0.0454 135
Precipitation	-0.1680 0.0514 135	-0.0923 0.2870 135	-0.2080 0.0155 135	0.1731 0.0447 135		-0.0907 0.2957 135	-0.0325 0.7087 135	-0.1503 0.0819 135	-0.0315 0.7172 135	-0.1621 0.0603 135	-0.1427 0.1201 120	-0.1797 0.1309 72	-0.8667 0.3657 111	-0.0350 0.6871 135
Disturbance	-0.0611 0.4814 135	0.2236 0.0091 135	-0.0768 0.3757 135	-0.0841 0.3322 135	-0.0907 0.2957 135		0.0585 0.5007 135	0.0317 0.7152 135	0.0658 0.4484 135	0.0229 0.7920 135	0.1585 0.0838 120	-0.0157 0.8958 72	0.1641 0.0853 111	-0.0057 0.9474 135
Heterogeneity	0.4508 <.0001 135	0.3627 <.0001 135	-0.0581 0.5033 135	-0.1864 0.0304 135	-0.0325 0.7087 135	0.0585 0.5007 135		0.2018 0.0189 135	-0.1352 0.1179 135	0.1231 0.1549 135	0.1224 0.1829 120	0.2184 0.0653 72	0.3033 0.0012 111	0.2402 0.0050 135
GDP	0.4034 <.0001 135	0.6614 <.0001 135	0.3620 <.0001 135	-0.3879 <.0001 135	-0.1503 0.0819 135	0.0317 0.7152 135	0.2018 0.0189 135		0.4798 <.0001 135	0.9736 <.0001 135	0.8674 <.0001 120	0.8524 <.0001 72	0.8478 <.0001 111	0.8121 <.0001 135
Free Trade Agreements	-0.1908 0.0266 135	0.0440 0.6122 135	0.4848 <.0001 135	-0.4671 <.0001 135	-0.0315 0.7172 135	0.0658 0.4484 135	-0.1352 0.1179 135	0.4798 <.0001 135		0.5214 <.0001 135	0.5850 <.0001 120	0.3358 0.0039 72	0.2339 0.0135 111	0.3938 <.0001 135
Trade	0.3330 0.0001 135	0.5677 <.0001 135	0.4247 <.0001 135	-0.4386 <.0001 135	-0.1621 0.0603 135	0.0229 0.7920 135	0.1231 0.1549 135	0.9736 <.0001 135	0.5214 <.0001 135		0.8759 <.0001 120	0.8418 <.0001 72	0.8062 <.0001 111	0.7575 <.0001 135
Tourism	0.2071 0.0232 120	0.4801 <.0001 120	0.3738 <.0001 120	-0.4308 <.0001 120	-0.1427 0.1201 120	0.1585 0.0838 120	0.1224 0.1829 120	0.8674 <.0001 120	0.5850 <.0001 120	0.8759 <.0001 120		0.7742 <.0001 66	0.7288 <.0001 103	0.7169 <.0001 120
Research and Development Personnel	0.3637 0.0017 72	0.7065 <.0001 72	0.4582 <.0001 72	-0.4546 <.0001 72	-0.1797 0.1309 72	-0.0157 0.8958 72	0.2184 0.0653 72	0.8524 <.0001 72	0.3358 0.0039 72	0.8418 <.0001 72	0.7742 <.0001 66		0.8569 <.0001 65	0.5979 <.0001 72
Tertiary Students	0.5373 <.0001 111	0.8124 <.0001 111	0.3315 0.0004 111	-0.3600 0.0001 111	-0.8667 0.3657 111	0.1641 0.0853 111	0.3033 0.0012 111	0.8478 <.0001 111	0.2339 0.0135 111	0.8062 <.0001 111	0.7288 <.0001 103	0.8569 <.0001 65		0.6535 <.0001 111
Publications	0.5157 <.0001 135	0.6242 <.0001 135	0.0662 0.4457 135	-0.1725 0.0454 135	-0.0350 0.6871 135	-0.0057 0.9474 135	0.2402 0.0050 135	0.8121 <.0001 135	0.3938 <.0001 135	0.7575 <.0001 135	0.7169 <.0001 120	0.5979 <.0001 72	0.6535 <.0001 111	

Chapter 2

Is diversity limited by the extent of the market?

Abstract

The relationship between productivity and diversity is widely studied in the ecological literature but the evolutionary response of populations to changes in productivity is not. Here I evaluate the idea that selection in environments that vary in productivity will impact the degree of ecological specialization among individuals, and thus the quantity of diversity maintained in the community. To test this prediction I selected the soil bacterium *Pseudomonas fluorescens* in heterogeneous environments composed of two carbon substrates at varying levels of productivity and compared fitness measures to those selected in homogeneous environments of corresponding single carbon substrates. My results show that although the degree of specialization increases with productivity there was no comparable increase in diversity. As well, the mixture lines (heterogeneous environments) appeared to adapt specifically to the mixture environment itself suggesting the evolution of a plastic phenotype. Overall, productivity played a role in governing the outcome of evolution in both homogeneous and heterogeneous environment but this outcome was varied.

Introduction

Ecologists have often noted that productivity – the rate of production of organic matter –plays a central role in governing species diversity in natural communities (Waide et al. 1999, Mittelbach et al. 2001). The prevailing view has been that at the scale of a collection of communities distributed across a landscape, species diversity tends to peak at intermediate rates of production or increase monotonically (Abrams 1995, Gillman & Wright 2006, Waide et al. 1999) although recent reviews have cast a lot of doubt on the generality of this pattern (Mittelbach et al. 2001). A comparable effort towards understanding the evolutionary response of populations to changes in productivity has been lacking, and constitutes the subject of this paper.

The starting place for any discussion on the effects of productivity on the evolutionary fate of diversity begins, as Bell (1997) pointed out, with Adam Smith. In the third chapter of the Wealth of Nations, Smith outlines the argument that the division of labour in a competitive economy is limited by the extent of the market. Thus, in the small isolated villages of 18th century Scotland "every farmer must be butcher, baker and brewer for his own family" (Smith 1776, pt. I, ch. 3, par.2). In larger cities, where the market for products of individual trades is also larger, labour specialization on individual tasks is possible. In ecology, whether diversity is limited by the extent of the market can also be studied if diversity is interpreted as species diversity and the market as productivity of the environment. For environments with a low productivity, even if environmental heterogeneity is high, there is not enough resources present in each portion of the environment to support different resource specialized populations. In this case, generalization would occur and organisms should adapt to using all portions of the environment to use the low resources as best as possible. At higher productivities, enough resources occur in each portion of the environment to sustain an entire population thus allowing for specialization to occur. In this case, specialist can emerge that are adapted to individual resource niches. Variance in total productivity across a landscape should therefore lead to the evolution of different kinds of communities. In unproductive environments where a preferred resource is quickly exhausted, I expect selection to favour the evolution of a broadly-adapted generalist capable of using the other available resources. As productivity increases, the strength of competition for using different resources in the heterogeneous environment declines and selection will lead to the evolution of more specialized types. Thus the degree of ecological specialization that evolves should depend on the total productivity of the environment.

This argument may be extended to account for the more widely-studied phenomenon of the response of diversity to productivity. Unproductive communities, if dominated by a single generalist type, will be incapable of supporting diversity to any significant extent. This prediction is in line with observations from the ecological literature that many unproductive communities tend to be species-poor (Naeem et al. 1996, Tilman 1999). Communities that are more productive, on the other hand, favour the evolution of specialist types and so may be capable of supporting more diversity, depending on the strength of divergent selection for resource specialization and the relative productivity of the different resources (Jasmin & Kassen 2007). When divergent selection is strong and each resource supports a roughly equal number of individuals diversity can be maintained; if one resource is much more productive than another, then the type adapted to the most productive resource will come to dominate the community and diversity will be low (Kassen et al. 2000, Jasmin & Kassen 2007). Whether or not diversity increases with rates of production thus depends on how the *relative* production of individuals specialized on different resources changes as the *total* productivity of the community increases (see for example Kassen et al 2000).

Selection in environments that vary in productivity is thus expected to impact the degree of ecological specialization among individuals, and so the diversity of the community. To test this idea, I selected the soil bacterium, *Pseudomonas fluorescens*, in a fine-grained resource driven heterogeneous environments comprised of a mixture of two carbon sources at three levels of total productivity and in the comparable single-substrate homogeneous environments. I then measured the fitness of evolved genotypes from each selection line on each component substrate as well as in the mixture in order to estimate the degree of resource specialization and the quantity of diversity that evolved. The direction I am concerned with in this work is how productivity can influence diversity, not the reverse, although attention has been given to the reverse (Tilman et al. 1996).

Materials and Methods

Model Organism

The founding material was a single clone of the soil bacterium *Pseudomonas fluorescens* SBW25::*lacZ* (constructed by X.-X. Zhang, University of Auckland). Colonies with *lacZ* are blue on agar plates supplemented with 40 mg/L of 5-bromo-4-chloro-3-indolyl-beta-D-galactopyranoside (X-Gal) and can be easily discriminated from the pale yellow colonies produced by the isogenic (save for the *lacZ* gene) SBW25 used in previous experiments (Kassen 2000, Jasmin & Kassen 2007). Selection lines were periodically checked for contamination by monitoring the loss of the *lacZ* marker, with no lines displaying evidence of contamination for the entire experiment. The ancestral clone was stored at -80°C in 50% glycerol *(w/v)* during the experiment in case contamination necessitated restarting of any line and for use as the ancestral genotype in later fitness competitions.

Selection Experiment

The experiment consisted of three replicate lines selected in factorial combinations of three selection environments (two homogeneous environments consisting of a single carbon source, either mannose or mannitol and a heterogeneous environment comprised of a mixture of both substrates) at three productivity levels. Productivity was manipulated by adjusting the amount of carbon substrate in the medium. The growth medium consisted of minimal salts (NH_4Cl 1 g/L, KH_2PO_4 3 g/L, NaCl 0.5 g/L, Na_2HPO_4 6.8 g/L) supplemented with $CaCl_2$ (15 mg/L), $MgSO_4$ (0.5 g/L) and the appropriate carbon substrate (mannose: low 0.0382 g/L, medium 0.1529, high 0.6115 g/L, mannitol: low 0.0386 g/L, medium 0.1546 g/L, high 0.6183 g/L). Note that the mixture contained twice the total carbon as either single substrate line at a given productivity level due to wanting to maintain the same amount of mannose or mannitol in the homogeneous and heterogeneous lines. Cultures were maintained in 24 well plates (Greiner Bio-One Cellstar®) at 28°C and shaken continuously at 150 rpm in an orbital shaker. Propagation involved transferring 5 μL aliquots of a dense culture into 2 mls of fresh medium daily for 50 days (approximately 450 generations). All populations were stored at -80°C in 50% glycerol *(w/v)*.

Competitive Fitness Assays

I conducted two sets of fitness assays. The first involved estimating the fitness of the entire population from each treatment at the end of the experiment. This was done through competition of each selected line against the ancestral strain with the opposing genetic marker across all environments (mannose, mannitol and mixture) at the same productivity at which they were selected (low, medium or high). In the second I isolated eight colonies from each selection line and assayed their fitness in the two component single-substrate environments. The general procedure was the same in both cases. Competitions were performed by first culturing the selected population or isolated genotypes and the ancestral genotype separately for a single growth cycle in Luria Bertani medium (tryptone: 10.0 g/L, yeast extract: 5.0 g/L, NaCl: 5.0 g/L) followed by mixing the two cultures in a 1:1 ratio (by cell number) to initiate the competition. The mixed population was cultured for three growth cycles in the medium of competition. After the first (initial) and third (final) round of growth, relative frequencies of the two types were estimated by plating onto minimal salts agar plates ((NH_4Cl 1 g/L, KH_2PO_4 3 g/L, NaCl 0.5 g/L, Na_2HPO_4 6.8 g/L, Agar 15 g/L) supplemented with X-gal (5-bromo-4-chloro-3-indolyl-beta-D-galactopyranoside 40 mg/L) . The selection coefficient, s, was calculated using the frequency of the evolved population relative to the ancestral population (f_E) and the number of doublings (N):

$$s = \frac{\ln(f_E)_{final} - \ln(f_E)_{initial}}{N} \qquad \text{Eq. 1}$$

All competitions were replicated twice for the isolated genotype competitions, and four times for the whole line competitions.

Analysis

The estimates of fitness from the whole line assay were used to assess the significance of the response to selection using analysis of variance (ANOVA). All factors were fixed and the variance among replicate selection lines served as the error variance.

Estimates of fitness on each of the single-carbon substrates for the eight colonies isolated from each selection line were used to calculate the breadth of adaptation and the quantity of diversity in each selection line. Breadth of adaptation was measured as the average environmental variance expressed by all eight genotypes isolated from a given selection line. Diversity was estimated as the genotype-by-environment interaction variance (GxE) among the eight genotypes using Robertson's equation (1959; same method used in Kassen & Bell 2000);

$$\sigma^2_{GE} = \tfrac{1}{2}(\sigma_{G1} - \sigma_{G2})^2 + \sigma_{G1}\sigma_{G2}(1 - \rho_{G1G2}) \qquad \text{Eq. 2}$$

where σ_{G1} and σ_{G2} are the genetic standard deviations of fitness in mannose and mannitol, respectively for a given set of genotypes, and ρ_{G1G2} is the Pearson product-moment correlation coefficient of fitness among genotypes on both substrates. GxE thus expresses the extent to which genotypes vary in their response to environmental variation.

Growth Curves

To understand in more detail how selection impacted the dynamics of population growth over the course of a single growth cycle, I assayed the growth of the evolved populations in

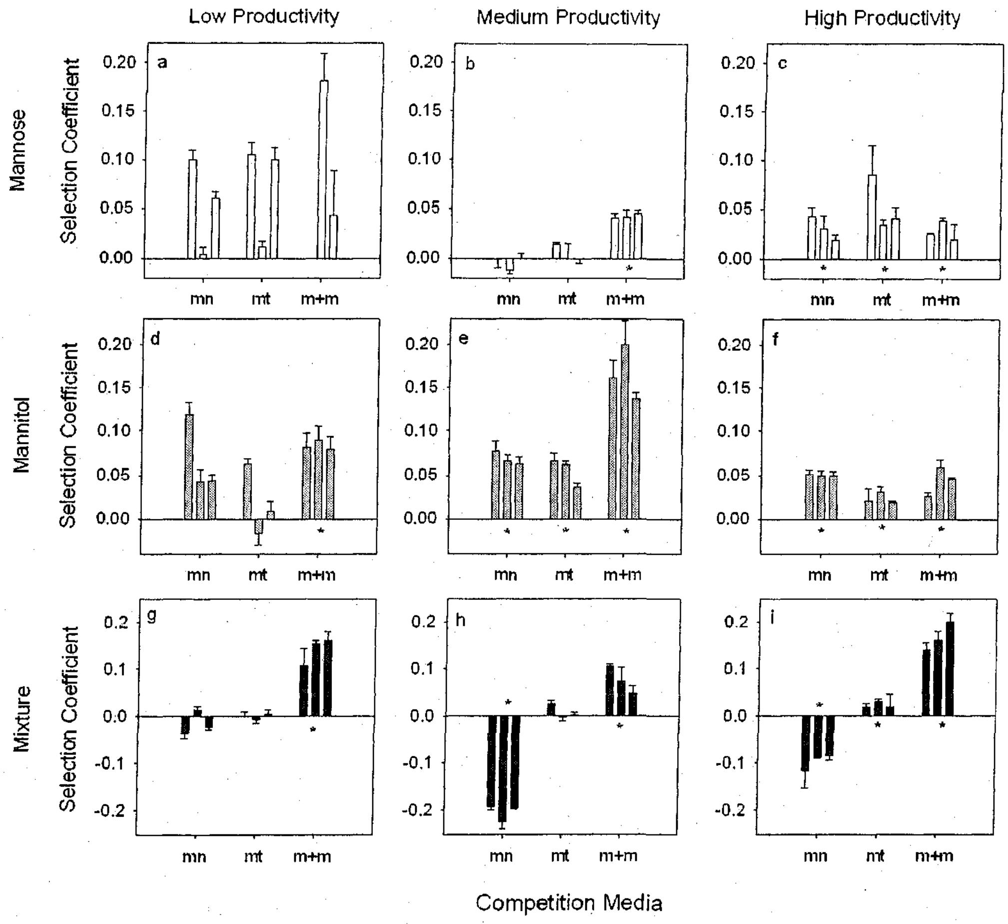

Figure 1: Results of whole line competitive fitness assays for all selection lines after selection in a) mannose low productivity, b) mannose medium productivity, c) mannose high productivity, d) mannitol low productivity, e) mannitol medium productivity, f) mannitol high productivity, g) mixture low productivity, h) mixture medium productivity and, i) mixture high productivity. Competitions occurred in mannose (mn), mannitol (mt) and the mixture (m+m). Using lines as replicate fitness estimates, significant treatments are noted with an asterisk (after Bonferonni correction $\alpha<0.02$).

their environment of selection and the ancestor over the course of a typical 24-hour growth period. Population density was measured by optical density at 660 nm every 40 minutes with an EL_X-800 Bio-Tek Instruments Inc. spectrophotometer . All populations were first grown overnight in Luria Bertani and then acclimated for three days in the appropriate test environment.

Results

Direct responses to selection

The response to selection across all replicate lines in all selection environments is shown in figure 1. The direct response to selection, adaptation to the specific environment of selection, produced a positive response in most, but not all, lines, and the extent of adaptation depended on productivity (see Table 1). The average direct response to selection across all three replicate lines was significantly greater than zero in all cases except for low and medium productivities in mannose and the low productivity mannitol environment (see Fig. 1 a,b,d). Note that at least some lines did respond to selection in each of these three treatments except for those in the medium productivity mannose environment (see appendix Table 1).

Correlated responses to selection

Selection in mannose and mannitol alone invariably led to positive correlated responses in the alternative substrate and in mixtures (Fig. 1 a-f). Remarkably, the correlated response on mannose and mannitol due to selection in mixtures varied depending

Table 1: Analysis of Variance of the direct response to selection for those lines selected in homogeneous environments.

Source	df	MS	*F*	*P*
Selection Environment	1	0.00011	0.15	0.706
Productivity	2	0.00022	0.30	0.743
Selection Environment x Productivity	2	0.00359	4.88	0.028
Error	12	0.00074		

Table 2: Analysis of Variance among heterogeneous populations for fitness in both competition environments (mannose and mannitol) at all three productivity levels.

Source	df	MS	*F*	*P*
Competition Environment	2	0.1209	257.96	<0.0001
Productivity	2	0.0179	38.16	<0.0001
Assay Media x Productivity	4	0.0082	17.52	<0.0001
Error	18	0.0005		

on productivity level (Table 2). At low productivity, adaptation to the mixture produced no response on either mannose or mannitol (Fig. 1g), whereas lines selected at medium productivity exhibited a cost of adaptation in mannose and no response in mannitol (Fig. 1h). *Similarly, lines at high productivity showed a cost of adaptation in mannose but now a* positive correlated response in mannitol (Fig. 1i).

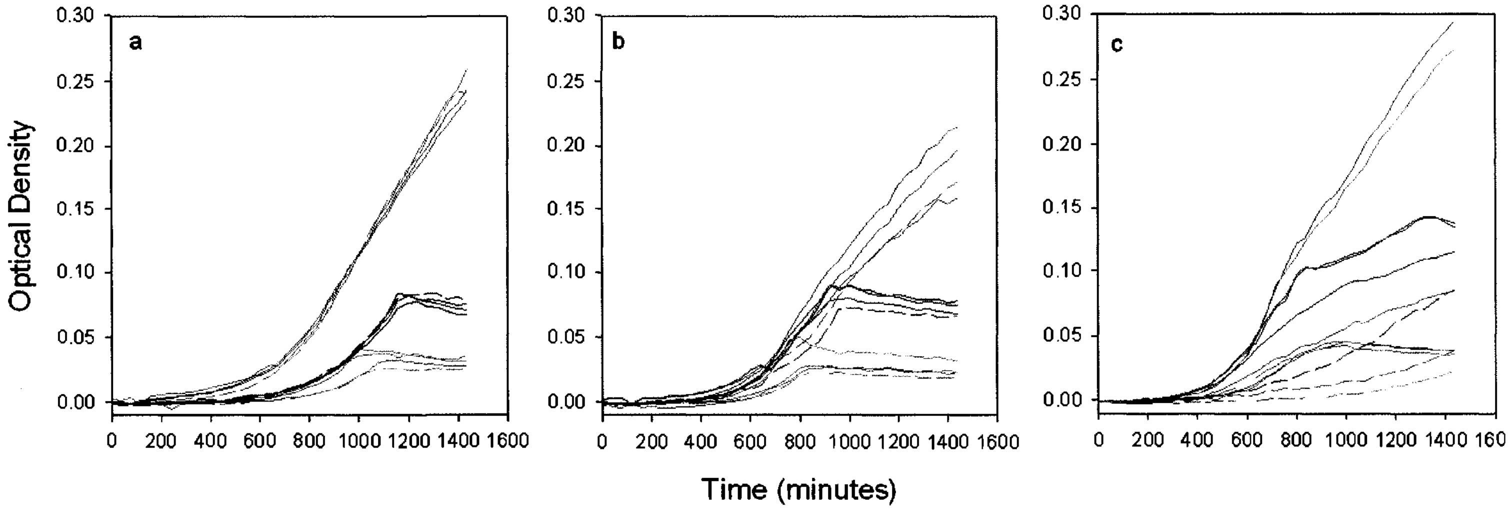

Figure 2: Growth curves over one 24 hour growth cycle for all populations selected in a) mannose, b) mannitol and c) mixture environments at low (green), medium (blue) and high (red) productivities. Ancestor presented as dashed lines and evolved populations as solid.

Growth curves

The dynamics of growth over a single growth period for the ancestor and the evolved lines in their respective selection environments are shown in figure 2. As expected, the main effect of productivity is to increase final population densities in all environments. Lines selected in the homogeneous environments varied in the particular components of growth responding to selection – time lag (λ), intrinsic rate of growth (r_{max}), carrying capacity (K) – with some lines showing evidence of increase in just one component of fitness (mannitol line 3 at high productivity) and others all three (mannitol line 1 at low productivity, see Appendix table 2). More interesting is the pronounced responses to selection in the mixtures. All lines show clear evidence of substantial increases in growth parameters relative to the ancestor (see Fig. 2c). Notably, the two distinct peaks in Figure 2 c provide evidence for the emergence of diauxic growth (use of substrates in sequential order) in lines selected at medium productivity, but not at either low or high productivities.

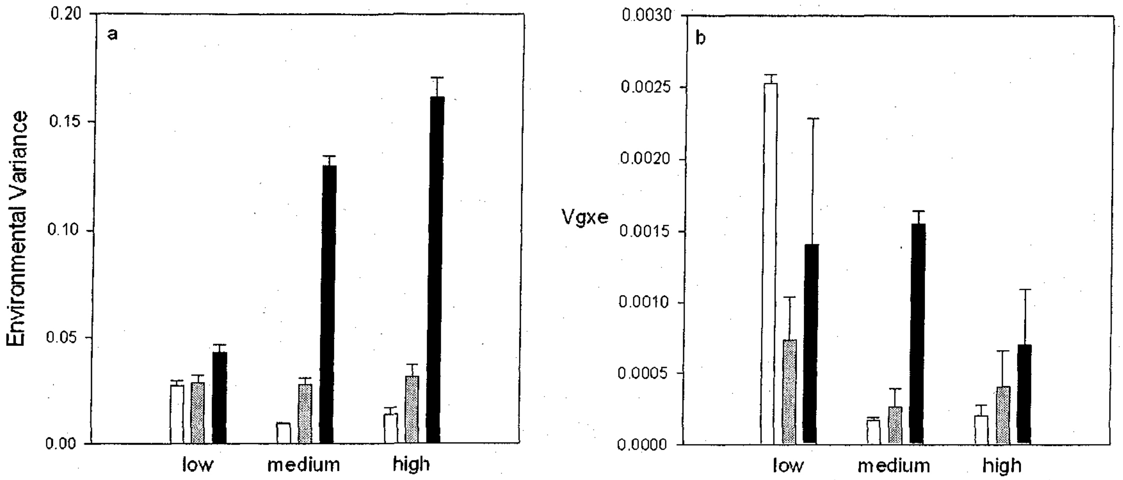

Figure 3: a) Average environmental variance in fitness across mannose and mannitol among genotypes for all replicate selection lines. b) Genotype-by-environment interaction variance in fitness among genotypes averaged over all three replicate selection lines. Results for lines selected in mannose (open bar), mannitol (grey bar) and mixture (solid bar) environments at low, medium and high productivities.

The evolution of niche breadth

The average environmental variance in fitness across both substrates for all genotypes from each of the selection lines is shown in figure 3a. The environmental variance of lines selected in a single substrate was low, indicating the evolution of more generalized types across all levels of productivity. Inspection of figure 1 suggests that the evolution of generalists in these lines was caused by positive correlated responses to selection in each homogeneous environment. The environmental variance increased as productivity in the mixture lines increased, as expected. Interestingly the source of this increase in environmental variance appears to stem largely from adaptation to the mixture itself, which comes at a cost of adaptation to mannose but not mannitol (Fig 1g-i).

Table 3: Analysis of Variance among all populations for genotype-by-environment interactions calculated according to equation 2.

Source	df	MS	*F*	*P*
Selection Media	2	3.2×10^{-6}	8.49	0.003
Productivity	2	1.3×10^{-6}	3.53	0.051
Selection Media x Productivity	4	1.6×10^{-6}	4.22	0.014
Error	18	0.4×10^{-6}		

Diversity

The response of diversity, measured as the genotype-by-environment interaction variance in fitness among genotypes averaged over all three replicate selection lines, is shown in figure 3b. Analysis of variance indicates that there is a significant effect of selection environment, productivity and their interaction. However my results provide little support for the idea that diversity increases with productivity: on average, diversity was highest at low productivities, although there was a tendency for the mixture environments to maintain more diversity than the homogeneous environments at medium and high productivities.

Discussion

The experiment was designed to investigate the effect of variance in productivity on the evolutionary response of populations occupying heterogeneous environments but my results were unexpected. The dominant effect of productivity was to change total population density but had little effect on either the degree of ecological specialization or the quantity of diversity that evolved. My main result, by contrast, was the emergence of populations specifically adapted to life in a mixture. This adaptation came about without increases in fitness on the component substrates of the environment, suggesting that I have observed the selection of genes involved in switching between substrates or, in other words, genes for plasticity (Via et al. 1995). This result is particularly surprising in light of the fact that selection in homogeneous environments of either substrate led not only to adaptation to those substrates but also positive correlated responses on the alternative substrate.

The physiological mechanisms underlying these responses remain unclear, in part because little is known about the physiology of carbohydrate metabolism in *P. fluorescens* (Callier et al. 1996, Stulke & Hillen, 1999). In *P. aeruginosa,* a closely related species, both sugars enter the cell through different transport systems and undergo a series of different enzymatic steps before being converted into either fructose-6-phosphate or glucose-6-phosphate that enter the same Etner-Dudoroff pathway for conversion into energetically suitable products (Wolff et al. 1991). My observation of positive correlated responses to selection in the single-substrate environments suggests that adaptation has occurred via mutations in this common portion of the metabolic pathway. The mutations responsible for adaptation in the mixtures must therefore occur elsewhere or I would not have observed the lack of adaptation in the mixture environments to the single substrate components.

Bacteria commonly use mixtures of substrates sequentially, metabolizing the most productive substrate first and then switching their cellular machinery to the other substrate once the first is exhausted, a process termed catabolite repression (Stulke & Hillen 1999, Bruckner & Titgemeyer 2002). This mechanism may explain my results in the heterogeneous environment. Diauxic growth, the hallmark of catabolite repression (Harder et al. 1982) is clearly observed at the medium productivity but not at both high and low (Figure 2c). It is conceivable, however, that mannose and mannitol are mutually repressive, each acting to reduce the catabolism of the other (Harder & Dijkhuizen 1983, Eglie et al. 1993). Adaptation to the mixture would then involve the emergence of mutations capable of overcoming this physiological constraint. The fact that so little is known about the physiology of carbon use in *P. flourescens* makes evaluation of these explanations challenging.

Surprisingly I found no direct response to selection in mannose at medium productivity in any lines. Previous work (Jasmin and Kassen, in review) has shown that the supply of beneficial mutations at this concentration of mannose is extremely low relative to most other carbon substrates, including mannitol (Kassen and Bataillon 2006). If so, then the lack of response to selection in this treatment may be due to a limited supply of beneficial mutations. This may also explain the variable response to selection among replicate lines at low productivity in mannose as well, although the fact that two mannitol lines at low productivity failed to respond to selection suggests that the supply of novel mutations may further be compromised by the lower population sizes (see growth curves in Figure 2) under the lowest productivity levels (Fisher, 1930).

Hall & Colegrave (2007) recently published a similar study to that presented above. In their experiment, populations of *P. fluorescens* were selected in 4mL glass vials in a mixture of 8 carbon substrates at 6 different resource supply rates. They found that diversity peaked at intermediate productivities, a pattern expected from ecological studies (Waide et al. 1999). There are several possible explanations for the discrepancy between my study and that performed by Hall & Colegrave (2007). The first is related to the extent of ecological opportunity provided. In the study by Hall & Colegrave (2007) more substrates were available in their mixture environment possibly allowing for more opportunities of niche specialization, and therefore supporting higher levels of diversity than can be supported in my two carbon substrate mixture. As well, they performed their competition assays in 96-well plates despite performing selection in 4mL glass vials. In previous experiments it has been shown that transferring cultures adapted to growth in 24-well plates into 96-well plates for competition causes the adapted strain to be outcompeted by the ancestor (personal communication S. Schoustra, July 2007). It is possible that this occurred when Hall & Colegrave transferred their lines selected and adapted to the 4 mL glass vial into 96-well plates for competitive fitness assays. The testing environment could differ greatly from the selection environment resulting in unrepresentative values for long term selection in the glass vials. The lack of a peak in diversity at intermediate values of productivity in my experiment may be explained by the larger range of resource concentrations studied by Hall & Colegrave. The 6 different concentrations chosen spanned a larger spectrum of productivities with their intermediate level corresponding to my high productivity. Finally, the identity of the carbon substrates chosen for the Hall & Colegrave (2007) experiment are different than those chosen in my experiment, leading to different physiological mechanisms for the uptake of carbon substrates and therefore different ways in which selection can act on these populations.

In conclusion, I did not provide support that diversity is limited by the extent of the market, although the degree of specialization did increase with productivity (Figure 3). It is conceivable that my results may be somewhat idiosyncratic reflecting the specific carbon substrates chosen. Despite this, my study is first to demonstrate the emergence of populations adapted to a mixture environment without increasing fitness on the components of the environment or decreasing fitness on these components. The generality of this result deserves further study, especially since it suggests that I have observed the selection of genes for plasticity.

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Appendix

Appendix Table 1: Student t-tests for all selection coefficients for all selected lines at all three productivities and competed in all environments, $H_0=0$ and df=2.

Selection Environment	Productivity	Competition Environment	Line	*T*	*P*
Mannose	low	mannose	1	9.945	0.0011
			2	0.723	0.2610
			3	10.057	0.0010
		mannitol	1	8.125	0.0019
			2	2.076	0.0647
			3	7.898	0.0021
		mixture	1		
			2	6.455	0.0038
			3	0.941	0.2081
	medium	mannose	1	0.099	0.4634
			2	3.807	0.0159
			3	0.026	0.4905
		mannitol	1	6.462	0.0038
			2	0.029	0.4892
			3	0.058	0.4788
		mixture	1	8.633	0.0016
			2	6.484	0.0037
			3	12.332	0.0006
	high	mannose	1	4.633	0.0095
			2	2.637	0.0389
			3	3.205	0.0246
		mannitol	1	2.760	0.0351
			2	6.654	0.0035
			3	3.792	0.0161
		mixture	1	33.503	<0.0001
			2	13.336	0.0005
			3	1.383	0.1304
Mannitol	low	mannose	1	8.473	0.0017
			2	3.071	0.0273
			3	3.198	0.0247
		mannitol	1	10.089	0.0010
			2	1.225	0.1539
			3	0.771	0.2483
		mixture	1	3.847	0.0155
			2	5.253	0.0067
			3	5.202	0.0069
	medium	mannose	1	6.732	0.0033
			2	9.192	0.0014
			3	7.705	0.0023

		mannitol	1	7.221	0.0027
			2	14.336	0.0004
			3	7.715	0.0023
		mixture	1	7.778	0.0022
			2	7.240	0.0027
			3	19.278	0.0001
	high	mannose	1	10.194	0.0010
			2	8.699	0.0016
			3	9.130	0.0014
		mannitol	1	1.489	0.1166
			2	5.111	0.0072
			3	8.686	0.0016
		mixture	1	5.740	0.0053
			2	7.194	0.0028
			3	21.474	0.0001
Mixture	low	mannose	1	3.173	0.0252
			2	1.993	0.0702
			3	33.527	0.0194
		mannitol	1	0.088	0.4676
			2	1.210	0.1565
			3	0.344	0.3768
		mixture	1	2.702	0.0368
			2	17.100	0.0002
			3	8.794	0.0015
	medium	mannose	1	24.074	<0.0001
			2	14.861	0.0003
			3	59.030	<0.0001
		mannitol	1	3.523	0.0194
			2	0.469	0.3354
			3	0.245	0.4110
		mixture	1	20.29	0.0001
			2	2.426	0.0467
			3	3.032	0.0281
	high	mannose	1	3.224	0.0242
			2	37.148	<0.0001
			3	9.337	0.0013
		mannitol	1	2.500	0.0439
			2	4.741	0.0089
			3	0.675	0.2739
		mixture	1	9.275	0.0013
			2	8.696	0.0016
			3	10.223	0.0010

Appendix Table 2: Parameter estimates of the intrinsic rate of growth (r), carrying capacity (K) and time lag (λ) modeled using the modified Gompertz equation presented in Zwietering et al. (1990) shown to sufficiently explain bacterial growth. The nonlinear equation was fitted to growth data presented in Figure 2 by nonlinear regression with a Marquardt algorithm in SAS Proc nlin. All models gave visually reasonable good fits of the data for lines selected in the homogeneous environments but not for lines selected in the mixture environments, which are therefore not presented.

Env.	Prod.	Line	r (SE)	K (SE)	λ (SE)
Mannitol	High	1	0.000284 (0.000004)	0.2679 (0.0055)	577.1 (4.7)
		2	0.000263 (0.000003)	0.2440 (0.0048)	603.7 (4.4)
		3	0.000201 (0.000003)	0.2054 (0.0055)	531.6 (6.2)
		Anc	0.000228 (0.000002)	0.2249 (0.0041)	606.7 (3.5)
	Med	1	0.000300 (0.000029)	0.0838 (0.0016)	581.1 (14.3)
		2	0.000326 (0.000035)	0.0822 (0.0015)	577.5 (14.5)
		3	0.000193 (0.000022)	0.0764 (0.0022)	485.6 (23.0)
		Anc	0.000195 (0.000019)	0.0712 (0.0017)	580.2 (17.8)
	Low	1	0.000275 (0.000061)	0.0381 (0.0009)	568.7 (16.7)
		2	0.000139 (0.000021)	0.0251 (0.0005)	585.3 (15.0)
		3	0.000135 (0.000014)	0.0257 (0.0004)	606.1 (10.4)
		Anc	0.000135 (0.000020)	0.0206 (0.0004)	628.3 (12.3)
Mannose	High	1	0.000300 (0.000002)	0.3322 (0.0106)	628.1 (4.0)
		2	0.000317 (0.000002)	0.4028 (0.0105)	645.4 (3.8)
		3	0.000351 (0.000007)	0.5141 (0.0370)	689.4 (12.0)
		Anc	0.000345 (0.000003)	0.3500 (0.0085)	667.9 (3.8)
	Med	1	0.000200 (0.000020)	0.0857 (0.0038)	762.6 (19.3)
		2	0.000187 (0.000018)	0.0825 (0.0035)	741.3 (19.3)
		3	0.000166 (0.000016)	0.0802 (0.0039)	729.3 (20.7)
		Anc	0.000185 (0.000014)	0.0918 (0.0040)	737.5 (17.1)
	Low	1	0.000111 (0.000013)	0.0307 (0.0009)	790.8 (16.5)
		2	0.000141 (0.000018)	0.0355 (0.0009)	715.7 (16.7)
		3	0.000150 (0.000021)	0.0374 (0.0010)	695.6 (17.9)
		Anc	0.000086 (0.000007)	0.0266 (0.0006)	755.4 (13.9)

Conclusion

Macroecology and miroecology were both used here to answer different questions in Chapter 1 and 2. In Chapter 1 I sought after predictors of the pattern of invasive species distribution around the world by describing a model that explained the most amount of variation as possible. In this model, GDP came out as the largest predictor of invasive species patterns. In Chapter 2, experimental manipulation was used to determine the effect of varying productivity in a heterogeneous environment on the outcome of selection, particularly with respect to diversity. From this experiment I showed that the environmental variance expressed by individuals increased with productivity, but this did not lead to a comparable increase in diversity at the population level. Instead, we observed specific adaptation to the heterogeneous environment corresponding to trade-offs in fitness for the individual components of the environment, suggesting selection of genes for plasticity.

Both macroecology and microecology can be used to inform each other. For example, in Chapter 1 I included environmental heterogeneity as a possible predictor of invasive species diversity due to the idea pronounced in microecology that heterogeneity plays a role in determining the final diversity of a community (see Kassen 2002 for review). Without macroecology, microecologists would not have patterns to study at the simpler level to determine a specific mechanism. In Chapter 2, I studied in a controlled environment what macroecologists have been studying for years, the question of how productivity shapes diversity, first posed in macroecology by Von Humboldt in 1908 (pointed out by Hawkins et al 2003).

I suggest that in the future a dual approach using both macroecology and microecology is employed to study patterns of species abundance and distributions. The patterns and hypotheses defined by macroecology can be tested through experimental manipulation by microecologists. If the patterns coincide, the mechanism identified during the experimental procedure becomes a possible explanation for the pattern at the broader scale. By experimentation we can shorten the list of mechanisms macroecologists have such a problem testing and hopefully determine the underlying reasons why there are so many species.

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