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Research Article

Distribution patterns of invasive alien species in Alabama, USA

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Abstract

Invasive alien species (IAS) cause environmental and economical problems. How to effectively manage all IAS at a large area is a challenge. Hypotheses about IAS (such as the "human activity" hypothesis, the "biotic acceptance" and the "biotic resistance") have been proposed from numerous studies. Here the state of Alabama in USA, widely occupied by IAS, is used as a case study for characterizing the emergent patterns of IAS. The results indicate that most IAS are located in metropolitan areas and in the Black Belt area which is a historical intensive land use area. There are positive relationships between the richness of IAS and the change of human population, the species richness and the number of endangered species, as well as the total road length and farmland area across Alabama. This study partially supports the above three hypotheses and provides a general pattern of local IAS. Based on possible processes related with IAS, some implications for strategically managing local IAS are discussed.

Key words: farmland; human population; invasive alien species; urban area; road length

Introduction

Invasive alien species (IAS) have been major ecological, recognized to cause environmental and economical problems, such as threaten native biodiversity (Wilcove et al. 1998; Clavero and García-Berthou 2005), disrupt entire ecosystems by altering community structure, nutrient cycling rates, or disturbance regimes (Vitousek et al. 1987, 1997; D'Antonio and Vitousek 1992; Mack et al. 2000; Byrnes et al. 2007), and also cost millions of dollars to eradicate and manage (Pimentel et al. 2005). Numerous theoretical and experimental studies have been dedicated to identifying the varied factors and processes which may contribute to the success of IAS in habitats where they have been introduced or are spreading (Reichard and Hamilton 1997; Lonsdale 1999; Mack et al. 2000). Patterns of IES distribution are thus relevant in forecasting future species distribution, evaluating overall impact of invasion, and assisting management agencies to adopt effective conservation policies (Williamson 1996; Levine and D'Antonio 2003; Pyšek and Richardson 2006).

The alien species invasions are considered as a component of man-made global change (Williamson 1996; Vitousek et al. 1997). So far, three major hypotheses have been proposed to explain the establishment of IAS (Leprieur et al. 2008). The first is the "human activity" hypothesis. It suggests that disturbing natural landscapes could increase propagule pressure (i.e., the number of individuals released and the frequency of introductions in a given area) and human activities facilitate the establishment of IAS (Chown et al. 1998; McKinney 2001; Taylor and Irwin 2004; Meyerson and Mooney 2007). Second is the "biotic acceptance" hypothesis, which indicates that the establishment of IAS would be greatest in areas rich in native species with optimal environmental conditions for growth, such as energy availability and habitat heterogeneity (Oberdorff et al. 1995; Guéguan et al. 1998; Stohlgren et al. 2006; Fridley et al. 2007). Third, the "biotic resistance" hypothesis predicts that species-poor communities will host more IAS than species-rich communities due to high competition in high biodiversity communities which act as a barrier the establishment of invasive species (Levine 2000; Kennedy et al. 2002; Stohlgren et al. 2008). Thus, a negative relationship is expected between native and invasive alien species richness. Testing the relative importance of these hypotheses regarding IAS has been conducted from different perspectives. A recent study of fish invasion in the world's major rivers indicates that human activity indicators account for most of the global variation in richness of IAS, not the "biotic "biotic acceptance" and the hypothesis (Leprieur 2008). Based on a variety of observational, experimental and theoretical studies, the invasion paradox was found. This refers to the negative relationships between the number of native species and the number of IAS at fine scales (often at a resolution of 10 m² or less), but also the positive correlation between native and invasive alien species at broad-scale studies (Fridley et al. 2007). Although the generalized principles that govern the probability of invasion success across different scales remain elusive, most studies only emphasize a limited number of species or one type of species (such as fishes or plants). This knowledge may not be adequate for our understanding of invasive species as a whole. Thus, more tests including overall invasive species at different scales are needed, such as mesoscale (county level). The management and restoration of local habitats native-dominated depends understanding the possible different interactions between invaders and residents from varied scales at different regions of earth.

In the USA, the state of Alabama is well known for its wilderness areas and biodiversity (Lydeard and Mayden 1995; Barone 2005; Polyakov et al. 2008; Johnston and Maceina 2009). Several factors interrelate to produce this diversity including a mild and humid climate. drainage remarkable surface and physiographic subdivisions (Mount 1975). Some of the primary patterns of species distribution in this area have been studied, such as fish (Chen 2006), herpetofauna (Chen and Wang 2007), and biodiversity and roadless area (Chen and Roberts 2008). Many introduced alien species have been an essential part of the American economy, such as cotton, peanut, winter cereal grains, ring neck pheasant and honeybee. Now, some introduced species have become invasive (e.g., Kudzu and bamboo). IAS including plants and animals are common and widely distributed in Alabama, but little has been established about their overall patterns and ecological processes.

Some of these IAS were introduced into Alabama accidentally or brought as ornamentals or livestock forage (e.g., Kudzu for soil erosion). Invasive plants, including trees, shrubs, vines, grasses, ferns and forbs, invade under and along forest canopies and occupy small forest openings. This in turn erodes forest productivity, hinders forest use and management activities, and degrades wildlife habitat (Miller 2004; Litton et al. 2006; Mascaro et al. 2008). Although there is still no completed species list and detailed distribution map for each invasive species, there have been recent efforts in this regard. These data permit us to study the general emergent patterns of overall IAS in Alabama even with possible species missing, as the distribution of some IAS may not change the overall patterns of IAS. The detailed objectives are phrased as the following questions. (i) What are the general patterns of overall invasive species at county level? (ii) What is the relationship between IES and human activity? (iii) What is the relationship (positive or negative) between invasive species richness and biodiversity at county level? and (iv) Will invasive species lead to the endangerment of indigenous species? Since this study covers the entire state of Alabama, it provides a case study for regionally invasive species, tests current hypotheses and provides implications devising local management strategies.

Material and methods

Study area and relevant background information

In the USA, the state of Alabama is roughly between 30° - 35° N and 84°45′-88°30′W. It includes 67 counties and is located between the southern foothills of the Appalachian Mountain Range and the Gulf of Mexico. Alabama has a warm, humid, subtropical climate with summers that are hot and humid at an average high temperature around 33°C and winters that are typified by a series of cold fronts. The driest times of the year are in late summer and fall. Regional rainfall varies from 150 cm to 162 cm in the north part and 180 cm to 195 cm along the coast (Carter and Carter 1984). The county level is selected here because most data are only available at this level.

In Alabama there are five recognized physiographic zones which include the Highland Rim, the Cumberland Plateau, the Alabama Valley and Ridge, the Piedmont Upland, and the East Gulf Coastal Plain (Fenneman 1938). Forests cover about 70% of the state based on data from Alabama Forestry Commission (http://www.forestry.state.al.us/forest facts.aspx).

Alabama is ranked as the third largest commercial forest industry state in the nation. Alabama's forests mainly consist of four types: pine, pine-hardwood mixture, bottomland hardwood and upland hardwood. South Alabama is abundant in pure stands of pine. From South to North, the type changes to mixed pine-hardwood conditions and then to more complex hardwood forests near Tennessee boundary.

The state of Alabama has a population of nearly 4.5 million and most populations concentrate around major cities. According to the U.S. Bureau of Economic Analysis, the top five leading employers in Alabama were services (27%), retail trade (17%), government (16%), manufacturing (15%), and construction (7%) (http://www.glencoe.com/sec/socialstudies/alabama_o nline). The U.S. Department of Commerce reported that in 2009 Alabama's per personal income was \$33,096 compared to \$39,138 for the U.S.

Dataset of invasive alien species

The IAS in this study include fishes, aquatic mollusks, amphibians, reptiles and plants. Table 1 shows the specific species. The detailed distribution of aquatic species (including invasive alien ones) for all 67 counties was obtained from Mettee et al. (1996), Boschung and Mayden (2004) and Mirarchi (2004). The classification of native or exotic fish species of North America was based on Jeschke and Strayer (2005).

The distribution of reptiles and amphibians was obtained from Mount (1975). This study also includes 357 plants species and their distribution across counties of Alabama (http://www.alabama-plants.com).

The distribution of invasive plant species in Alabama counties was acquired from the database of Forest Inventory Analysis at USDA Service Southern Research Station Forest (http://srsfia2.fs.fed.us). Information on dangered species (including plants, mammals, amphibians, reptiles, birds, invertebrates, and fishes) for each county was obtained from Alabama Department of Conservation and Natural Resources (http://www.outdooralabama.com). This is based on the US Fish and Wildlife Service's list of state and federal endangered and

Table 1. List of included invasive alien species in this study. The number in () is total included species in this study.

Species groups and included species number	Common and latin names
Fish (5)	Bighead carp (Hypophthalmichthys nobilis), Flathead catfish (Pylodictus loivaris), Silver carp (Hypophthalmichthys molitrix), Common carp (Cyprinus carpio), Grass carp (Ctenopharyngodon idella)
Reptiles and amphibians (2)	Bullfrog (Rana catesbeiana), Cane toad (Bufo marinus)
Aquatic mollusks (3)	Zebra mussel (Dreissena polymorpha), Asian clam (Corbicula fluminea), New Zealand mud snail (Potamopyrgus antipodarum)
Plants (33)	Tree of heaven (Ailanthus altissima), Mimosa or Silk Tree (Albizzia benth), Royal Paulownia or princesstree (Paulownia tomentosa), Chinaberry (Melia azedarach), Popcorn tree or tallowtree (Triadica sebifera), Russian olive (Elaeagnus angustifolia), Silverthorn (Elaeagnus pungens), Autumn olive (Elaeagnus umbellata), Winged euonymus or burning bush (Euonymus alatus), Chinese/European privet (Ligustrum sinense), Japanese/glossy privet (Ligustrum japonicum), Bush honeysuckle (Lonicera tararica), Nandina or heavenly or sacred bamboo (Nandina domestica), Exotic roses (Rosa multiflora or R. bracteata or R. laevigata), Oriental/Asian bittersweet (Celastrus orbiculata), Exotic climbing yams or Air yam or Chinese yam (Dioscorea oppositifolia), Wintercreeper (Euonymus fortunei), English ivy (Hedera helix), Japanese honeysuckle (Lonicera japonica), Kudzu (Pueraria montana), Periwinkle (Vinca minor), Chinese/Japanese wisteria (Wisteria sinensis), Giant reed (Arundo donax), Tall fescue (Schedonorus phoenix), Cogongrass (japgrass) (Imperata cylindrica), Nepalese browntop (Microstegium vimineum), Chinese silvergrass (Miscanthus sinensis), Exotic bamboos (Phyllostachys aurea), Japanese climbing fern (Lygodium japonicum), Garlic mustard (Alliaria petiolata), Shrubby lespedeza (Lespedeza bicolor), Chinese lespedeza (Lespedeza cuneata), Tropical soda apple (Solanum viarum)

threatened species in Alabama. Although some information may be added in the future, this data is sufficient to indicate the general patterns of invasive species in Alabama.

The GIS data of state and county boundaries were obtained from the Alabama State Water Program. The human population, housing unit, average income and farm land area at each county during the corresponding time period was obtained from Alabama Quick Facts at the US Census Bureau (http://quickfacts.cencus.gov/qfd/index). Historical roads (including freeway, highway and country way) and metropolitan areas were taken from maps provided by the University of Alabama (http://alabamamaps.us.edu, accessed Nov. 30, 2011).

All these data from 67 counties were integrated and organized using GIS. It is recognized that this dataset may not represent new IAS) and may not represent the current exact distribution of species in this area due to land use change. Further, there is limited information about invasive alien birds and insects. A time gap may exist between the road information and the different species distribution data. Even so, this dataset may best represent the current overall invasive species and diversity across Alabama counties. This integrated dataset may provide an understanding about the general patterns of IAS and its social, economic and environmental relationships at a county level in Alabama.

Data categorizing and statistical analysis

Data categorizing and reorganization — i.e., pooling data in ranked categories or using the average values, is a popular tool in ecological research, especially when the original patterns are not clear. It can make the general trend clear for certain classes (or scales) and also limit the noise and confounding factors (i.e., species richness and area size) although the class number is somewhat arbitrary. By using this method, autocorrelation between variables, such as between human population and road length (or total species richness), may be avoided (Chen and Wang 2007; Chen and Roberts 2008; Liebhold et al. 2006). In this study, data categorizing (or categorizing after transform) was used when the direct relationship was not obvious. The number of constructed category classes follows the most commonly applied rule from Scott (1979). In this study, based on the number of IAS in each county, five types were classified. Finally, a least-squares linear (or nonlinear) correlation was used to analyze these relationships, such as the relationship between alien species and native species as well as the total road length and farmland area across Alabama counties.

Results

General patterns of invasive exotic species

including fishes, aquatic amphibians, reptiles and plants exist in every county of Alabama (Figure 1a) and each county has more than one invasive species. Tuscaloosa County has the most invasive species and is a hotspot of IAS. If the richness of total IAS is classified into 5 types with type 1 reflecting the fewest number of species and type 5 representing the greatest, counties with types 3 to 5 are mainly located at metropolitan areas with airports and are located in the Black Belt area (Figure 1b). Although there are different functional groups, the general distribution of aquatic IAS is similar to that of IAS of plants (Figure 1c and 1d). It is necessary to study the emergent patterns of functional groups rather than just study one set of species.

Relationships between richness of invasive alien species and socio-economic condition

The relationship between the richness of total invasive species and human population in each county is not obvious. However, the relationship between the richness of total invasive species and the change (increase or decrease) of human population during the past 16 years (from 1990 to 2006) is positive (Figure 2a). The relationship between the increase of housing unit or the increase of average income (per capita) and the number of invasive species is weakly positive but not statistically significant. There are positive relationships between the change in human population and the increase of housing unit (Figure 2b) and the increase of average income (per capita) (Figure 2c). If the human population change (increase or decrease) in the past 126 years (from 1880 to 2006), using the earliest available census data, is considered, there is still a strong positive linear relationship between the change in human population and the total number of invasive species (Figure 2d).

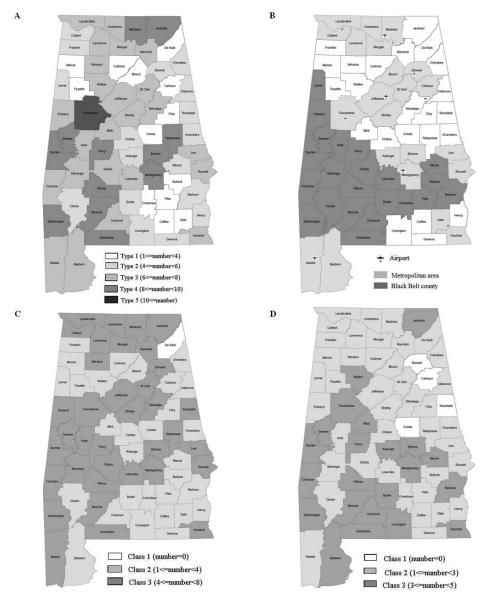


Figure 1. Spatial patterns of invasive alien species in Alabama. (A) distribution of invasive species; (B) metropolitan areas and the Black Belt in Alabama; (C) distribution of aquatic invasive species; and (D) distribution of invasive alien plants.

Relationships between invasive species richness and biodiversity, exotic and endangered species at county level

There is a significantly positive relationship between the total number of IAS and the total species richness across all counties of Alabama (Figure 3a). The relationship between the total number of IAS and the number of invasive aquatic species is also positive (Figure 3b). The relationship between the number of alien species and the number of IAS at each county level is not obvious, but after data categorizing there is a nonlinear relationship (Figure 3c). With an increase in alien species, the number of IAS also increases. However, when the number of alien species reaches a certain level (such as around 25 here), the number of IAS starts to decrease. There is a positive linear relationship between the number of IAS and the average endangered species across counties (Figure 3d).

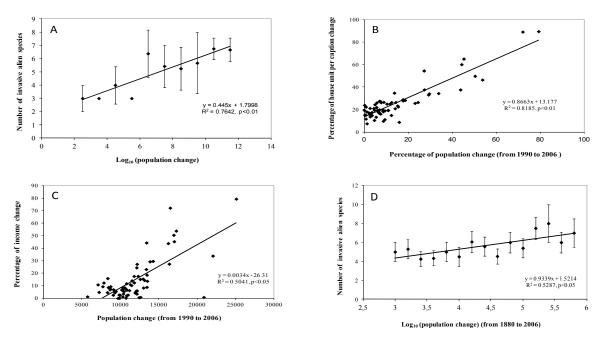


Figure 2. Correlations between socio-economical factors and invasive species. (a) The relationship between the richness of total invasive species and change of human population from 1990 across Alabama Counties; (b) the relationship between change human population and change of housing unit across Alabama Counties; (c) the relationship between change of human population and change of average income (per capita) across Alabama Counties; and (d) the relationship between change of human population from 1880 and the number of invasive species across Alabama Counties.

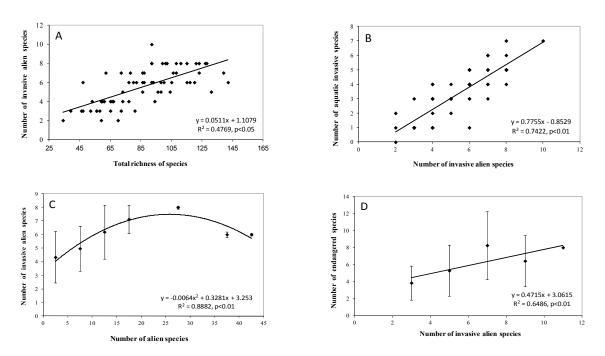


Figure 3. The relationships between the number of invasive alien species and other species across Alabama Counties. (a) total species richness vs total species richness; (b) total number of invasive alien species vs number of invasive aquatic species; (c) number of alien species vs number of invasive alien species; and (d) number of invasive alien species vs number of endangered species.

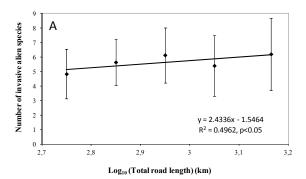
Roads, farmland and invasive species

After data categorizing for the total road length of all counties, there is a positive relationship between the total road length and the invasive species richness across all counties in Alabama (Figure 4a). For farmland across counties, there is an increase of IAS with the increase of farmland (Figure 4b).

Discussion

General patterns of invasive alien species in Alahama

All counties in the state of Alabama have IAS, which include fishes, aquatic mollusks, amphibians, reptiles and plants. The distribution of severely invaded counties (here in types 3, 4 and 5) is mainly in the metropolitan areas and in the Black Belt area. This may partially support the first hypothesis that "human activity" is a principal driver for IAS, because in Alabama there is no limit for human distribution by altitude or climate; in metropolitan areas there is more population movement (immigration and emigration), more commercial interactions, and more transportation including airports. Previous studies have indicated that airports play an important role for biological invasion (Liebhold 2006; McCullough et al. Economically rich areas are more likely to have land use change or habitat disturbances which facilitate the dispersal and establishment of IAS through urbanization, wetland modification and reservoir construction for water supply (Williamson 1996; Havel et al. 2005; Light and Marchetti 2007). Commercial opportunities, such as horticulture, gardening and aquaculture, also increase the dispersal of IAS (Levine and D'Antonio 2003; Taylor and Irwin 2004; Chen Furthermore, imported 2006). products associated with economic development may also likelihood of unintentional increase the introductions through importing processes (Levine and D'Antonio 2003). Thus, there are greater chances for deliberate and accidental introduction of IAS in these metropolitan areas. The new finding in this study is that the Black Belt area, which is not in itself a metropolitan area, has been severely permeated by IAS. This might be related to its land use history prior to the American Civil War when these counties were worked by African American slaves in plantations on rich black topsoil over a chalk



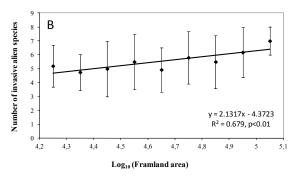


Figure 4. The relationships between the number of invasive alien species and the total road length (a) and farmland area (b) across Alabama Counties.

layer and when the region attained its highest density of population (Barone 2005). The general distribution pattern of IAS across all Alabama counties qualitatively supports the "human activity" hypothesis.

Relationships between richness of invasive alien species and socio-economic condition

The strong correlation between changes in human population (amount of increase or decrease) from 1990 to 2006 and richness of IAS suggests that human population change may be a main driver for IAS, since the correlations between change of housing unit (amount of increase or decrease), change of income per capita (amount of increase or decrease) and the richness of IAS are not significant. Moreover, both change of housing unit and change of income per capita are significantly correlated with human population change. Therefore, it is possible to use human population change as an indicator for IAS. Leprieur et al. (2008) use a human activity indicator which includes GDP, percentage of urban area and population to characterize fish invasions in the world's major river systems. The results of our study provide

strong correlations between change of human population and housing unit and average income per capita. It is easy to understand that with the increase of human population, there is an increase of housing units. With the increase of income per capita, then, more people come to work in the area. Furthermore, it is not clear how long it would take for population change to contribute to IAS in this area, because historical population (European colonies and African American) might affect the question of current IAS. During the 18th century, human immigrants arrived in North America from Europe and brought weeds with them (Dewey 1896). In this study, the change of human population over the past 126 years (from 1880 to 2006) also suggested a strong correlation with the number of IAS. Therefore, human population change may be used to provide an indicator for IAS across Alabama counties.

Relationships between invasive species richness and biodiversity, alien and endangered species at county level

In this study, there is a positive correlation between the total invasive species and the total species richness across all counties of Alabama. This supports the "biotic acceptance" hypothesis which means that what is good for other species is also good for IAS (Stohlgren et al. 2006). The relationship between biodiversity and invasive species is scale dependent but in complex ways and most empirical studies at landscape and broad scale levels in temperate zones show this positive relationship, such as at continental or island level (Planty-Tabacchi et al. 1996; Sax 2002; Stohlgren et al. 2003; Seabloom et al. 2006; Fridley et al. 2007). Herben et al. (2004) suggested a positive relationship for study areas greater than 30 m² based on the review over 50 published observations. Other researchers show instances of negative relationships for freshwater fishes at the watershed level and some marine invertebrates at landscape scales (Brown 1995; Stachowicz et al. 2002). On a global scale, tropical communities (both marine and terrestrial), which are the most diverse communities on earth, appear to support relatively few alien species (Rejmánek 1996; Sax 2001). To date, there are limited reports from tropical areas. Another problem for this positive relationship between biodiversity and IAS at a large scale is related to interactions of human activity and disturbances (Fridley et al. 2007; Leprieur et al.

2008). Several studies indicate that there is a positive relationship between human population and species richness on large scales (Luck 2007; Pautasso 2007; Pautasso and McKinney 2007). Because human population in a specific area changes over time even though the total number may be stable, the change of human population in any one area may be much adequate for describing human impacts. In this study, there is significant positive relationship between human population change and the number of IAS. Strong covariates represent human-caused habitat disturbance and propagule pressure in the data from Stohlgren et al. (2003) which indicates a positive relationship for the 50 U.S. states (Rejmánek 1996; Taylor and Irwin 2004). In this study it is impossible to control the effects of human activities and disturbances at the county level. In fact, in the real world all other factors, such as income and human activities, are rarely constant values. Current broad-scale research cannot demonstrate causation and all the results are the combined responses of native and invasive alien species (Fridley et al. 2007). Due to data categorization and scale change in this study the confounding factors were avoided (or minimized) in identified patterns.

Only a limited number of alien species become invasive. In this study it appears that there is a saturation point for the richness of IAS as the number of alien species continues to increase (around 25). This may be partially related to the "biotic resistance" attributable to high competition which impedes the establishment and spread of IAS. Nevertheless, the increase of IAS with increasing species number looks likely to be in conflict with the "biotic resistance" hypothesis. The results of this study further indicate a positive relationship between the number of IAS and the average endangered species across Alabama. A positive correlation exists between the number of exotic species and imperiled species of California (Seabloom et al. 2006). The correlative nature of the data may not mean that IAS have directly caused more species to become endangered, but it is clear that endangered species are exposed to a large number of IAS. A meta-analysis of 63 published experimental studies concluded that native species provide biotic resistance to biological invasion, but the widespread replacement of native with IAS eliminates this ecological service and facilitates biological invasion (Parker et al. 2006). However, as suggested above, the increase in human activities may also

cause the increased extinction of native species and the invasion of alien species. Seabloom et al. (2006) found that in California the direct correlation between habitat conversion and imperiled species is much weaker than the direct correlation between alien and imperiled species. Although this study partially supports both "Biotic resistance" and "Biotic acceptance" hypotheses at some scales, it is still a subject of debate whether direct competition from IAS at large scales is a significant threat to native species (Davis 2003).

Roads, farmland and invasive species

Roads and farmland are important results of human activities. Roads facilitate urbanization. land use change and also dispersal of IAS (Forman et al. 2002). In this study, there is a positive relationship between the total road length and invasive species richness across Alabama counties. This strongly indicates that roads could help to spread IAS. Road side areas are known to harbor disproportionately more invasive plant species than surrounding habitats through changing micro environmental conditions (e.g., radiation, soil moisture, soil compaction and vegetation) (Trombulak and Frissell 2000; Watkins et al. 2003; Hansen and Clevenger 2005) and act as seed sources for some invasive plants (Tyser and Worley 1992; Hansen and Clevenger 2005). Some plant species with small seeds, high seed production or persistent long life in seed banks are most likely to be dispersed by vehicles (Schmidt 1989). These traits are general characteristics of invasive plants (Rejmánek and Richardson 1996). In California many undeveloped areas of high native diversity were invaded by alien species because some species have short generation times and can spread rapidly throughout a large undisturbed area (Seabloom et al. 2006).

With an increase in farm land, there are generally more IAS but fewer than in metropolitan areas. Historically the seed trade brought invasive seed species to farmlands (Muenscher 1949; Mack 1991; Rejmánek and Richardson 1996). Many exotic species, which are now considered as noxious, were available for purchase through seed catalogues in the 19th century. This practice was responsible for spreading at least 140 plant species in USA (Clements et al. 2004). Furthermore, farming practices that involve a greater number of people (or vehicles) provide a significant increase to the

possible numbers of invasive species and their coverage. Farmland management practices (e.g., irrigating and harvesting) may contribute to further spreading of these invasive species.

Implications for local invasive alien species management

Given the many possible complicated processes involved in the invasion of alien species in Alabama, there is no reason to expect one simple solution for all cases at different spatial and temporal scales. Successful management of the spreading of IAS depends on the insight from currently available results even though they may conflict at different scales. Due to the large scale invasion of alien species in all counties of Alabama, complete eradication of these IAS seems unpractical in terms of economic cost. Enhancing education and detection is a priority for strengthening voluntary self-regulation by the public and preventing further introduction and spreading. In the metropolitan areas and the Black Belt regions of Alabama, an intensive land use area, there are more IAS. It is unrealistic to suggest limiting population change (or human movement) or land use change except for public lands (i.e., national and state parks). The results of this study suggest that trade and transport of alien species (or agricultural products) should be prohibited without detailed risk and long term benefit assessments. Unintentional delivery of seeds and seedlings should be avoided during exchange horticulture trade (e.g., aquaculture) through strict state (county) border and trade inspection for invasive species. Governments at all levels should have clear regulations or laws for transporting or trading IAS. Decreasing the accumulation of invasive species and limiting their range are also important because accumulations of alien species facilitate one another's survival and accelerate the rate of successful invasion (Simberloff and Von Holle 1999). Maintaining the integrity of local biodiversity (including landscape) should also be important, such as proper roads construction (or use) and farmland practices, because native species (or landscape) may offer limited opportunity to IAS by providing biotic resistance to the spread of IAS. Furthermore, the knowledge that increasing the number of alien species may increase the risk of endangered species would be helpful for future local conservation strategies. More research is needed to develop an invasive species database, early

warning systems, monitoring strategies and to prevent or eliminate means of entry for invasive species. All this requires a coordinated effort between scientists, educators, policy-makers, and others in the community. Effective management requires proper inventories and monitoring practices at large spatial and temporal scales to provide detailed information about invasive species, native species, human population change and impacts of human activities.

Conclusions

IAS including fishes, aquatic mollusks, amphibians, reptiles and plants have occurred in all 67 counties in the state of Alabama, USA. Severely invaded counties are mainly in the metropolitan areas and the Black Belt area, which is historically an intensive land use area. There are more IAS in counties with greater population change, more commercial interactions (e.g., metropolitan areas) and increased transportation (e.g., airports and roads). This partially supports the hypothesis that "human activity" is a principal driver for IAS. Positive correlations between total invasive species and total species richness as well as the average endangered species across all counties of Alabama also partially support the "biotic acceptance" and "biotic resistance" hypotheses at the county level. Due to the wide distribution of IAS in all counties of Alabama, better education for the detection of IAS is urgently needed to strengthen voluntary self-regulation and to prevent further introduction and spread. Complete eradication of these IAS may be practical in small areas. There should be strict legal regulation of IAS at all government levels (e.g., state, county and town). Successful control of invasive species depends on detailed information about invasive species, native species, and local human activities. There is a need for accurate inventories, monitoring and integrative information analysis. The whole community has some part to play in prevention, detection and eradication of IAS in Alabama.

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References

- Barone JA (2005) Historical presence and distribution of prairies in the Black Belt of Mississippi and Alabama. *Castanea* 70: 170–183
- Boschung HT, Mayden RL (2004) Fishes of Alabama. Smithsonian Books, WA, 960 pp
- Brown JH (1995) Macroecology. University of Chicago Press, Chicago, IL, 284 pp
- Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2: e295, http://dx.doi.org/10.1371/journal.pone.0000295
- Carter EA, Carter VGS (1984) Extreme weather history and climate atlas for Alabama. Strode Publishers, AL, 353 pp
- Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* 20: 110, http://dx.doi.org/10.1016/j.tree.2005.01.003
- Chen X (2006) Synthetic pattern of fishes diversity in Alabama, USA. Wildlife Biology in Practices 2: 38–46
- Chen X, Roberts KA (2008) Roadless areas and biodiversity: a case study in Alabama. *Biodiversity and Conservation* 17: 2013–2022, http://dx.doi.org/10.1007/s10531-008-9351-2
- Chen X, Wang Y (2007) Emergent spatial pattern of herpetofauna in Alabama, USA. *Acta Herpetologica* 2: 71–89
- Chown SL, Gremmen NJM, Gaston KJ (1998) Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist* 152: 562–575, http://dx.doi.org/10.1086/286190
- Clements DR, DiTommaso A, Jordan N, Booth BD, Cardina J, Doohan D, Mohler CL, Murphy SD, Swanton CJ (2004) Adaptability of plants invading North American cropland. *Agriculture, Ecosystems and Environment* 104: 379–398, http://dx.doi.org/10.1016/j.agee.2004.03.003
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87
- Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53: 481– 489, http://dx.doi.org/10.1641/0006-3568(2003)053[0481:BGD CFI]2.0.CO;2
- Dewey LH (1896) Migration of weeds. US Department of Agriculture Year book, pp 263–286
- Fenneman NM (1938) Physiography of eastern United States. McGraw-Hill, New York, NY, 714 pp
- Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France RL, Goldman CR, Heanue K, Jones J, Swanson F, Turrentine T, Winter TC (2002) Road Ecology: Science and Solution. Island Press, Washington D.C., 504 pp
- Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Holle BV (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88: 3–17, http://dx.doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2
- Guéguan JF, Lek S, Oberdorff T (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* 391: 382–384, http://dx.doi.org/10.1038/34899
- Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation* 125: 249–259, http://dx.doi.org/10.1016/j.biocon.2005.03.024
- Havel JE, Lee CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *BioScience* 55: 518–252, http://dx.doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2. 0.CO;2
- Herben T, Mandák B, Bímova K, Münzbergova Z (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology* 85: 3223– 3233, http://dx.doi.org/10.1890/03-0648

- Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. Proceedings of National Academy of Sciences USA 102: 7198–7202
- Johnston CE, Maceina MJ (2009) Fish assemblage shifts and species declines in Alabama USA streams. Ecology of Freshwater Fishes 18: 33–40, http://dx.doi.org/10.1111/j.16 00-0633.2008.00319.x
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–638, http://dx.doi.org/10.1038/ nature00776
- Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLOS Biology* 6: 0404–0410
- Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852–854, http://dx.doi.org/10.1126/science.288.5467.852
- Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. *Conservation Biology* 17: 322–326, http://dx.doi.org/10.1046/j.1523-1739.20 03.02038.x
- Liebhold AM, Work TT, McCullough DG, Cavey JF (2006) Airline baggage as a pathway for alien insect species invading the United States. American Entomology 52: 48–54
- Light T, Marchetti M (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology* 21: 434–446, http://dx.doi.org/10.1111/j.1523-1739.2006.00643.x
- Litton CM, Sandquist DR, Cordell S (2006) Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. Forest Ecology and Management 231: 105–113, http://dx.doi.org/10.1016/j.foreco.2006.05.008
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536, http://dx.doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA] 2.0.CO;2
- Luck GW (2007) A review of the relationships between human population density and biodiversity. *Biological Review* 82: 607–645, http://dx.doi.org/10.1111/j.1469-185X.2007.00028.x
- Lydeard C, Mayden RL (1995) A diverse and endangered aquatic ecosystem of the South-East United State. Conservation Biology 9: 800–805, http://dx.doi.org/10.1046/j.1523-1739.19 95.09040800.x
- Mack RN (1991) The commercial seed trade: an early disperser of weeds in the United States. *Economical Botany* 45: 257–273
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710
- Mascaro J, Becklund KK, Hughes RF, Schnitzer SA (2008) Limited native plant regeneration in novel, exotic-dominated forests on Hawaii. Forest Ecology and Management 256: 593–606, http://dx.doi.org/10.1016/j.foreco.2008.04.053
- McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biological Invasions 8: 611–630, http://dx.doi.org/10.1007/s10530-005-1798-4
- McKinney ML (2001) Effects of human population, area, and time on non-native plants and fish diversity in the United States. *Biological Conservation* 100: 243–252, http://dx.doi.org/10.1016/S0006-3207(01)00027-1
- Mettee MF, O'Neil PE, Pierson JM (1996) Fishes of Alabama and the Mobile Basin. Oxmoor House Inc., AL, 820 pp
- Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5: 199–208, http://dx.doi.org/10.1890/1540-9295 (2007)5[199:IASIAE]2.0.CO;2

- Miller JH (2004) Nonnative invasive plants of southern forests: a field guide for identification and control. Revised. Gen. Tech. Rep. SRS-62. USDA Forest service, Southern Research Station, Asheville, NC, 93 pp
- Mirarchi RE (2004) Alabama Wildlife (vol. I, II, III, and IV). University of Alabama Press, Tuscaloosa, AL
- Mount RH (1975) The Reptiles and Amphibians of Alabama. Auburn Printing Co., Auburn, AL, 368 pp
- Muenscher CW (1949) Weeds. Macmillan, New York, NY, 577
- Oberdorff T, Guéguan JF, Hugueny B (1995) Global scale patterns of fish species richness in rivers. *Ecography* 18: 345–352,http://dx.doi.org/10.1111/j.1600-0587.1995.tb00137.x
- Pautasso M (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters* 10: 16–24, http://dx.doi.org/10.11 11/j.1461-0248.2006.00993.x
- Pautasso M, McKinney M (2007) The botanist effect revisited: plant species richness, county area, and human population size in the United States. *Conservation Biology* 21: 1333– 1340, http://dx.doi.org/10.1111/j.1523-1739.2007.00760.x
- Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311: 1459–1461, http://dx.doi.org/10.1126/science.1121407
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien invasive species in the United States. *Ecological Economics* 52: 273–288, http://dx.doi.org/10.1016/j.ecolecon.2004.10.002
- Planty-Tabacchi AM, Tabacchi E, Naiman RJ, Deferrari C, Decamps H (1996) Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10: 598–607, http://dx.doi.org/10.1046/j.1523-1739.1996.10020598.x
- Polyakov M, Majumdar I, Teeter L (2008) Spatial and temporal analysis of the anthropogenic effects on local diversity of forest trees. Forest Ecology and Management 255: 1379– 1387, http://dx.doi.org/10.1016/j.foreco.2007.10.052
- Pyšek P, Richardson DM (2006) The biogeography of naturalization in alien plants. *Journal of Biogeography* 33: 2040–2050, http://dx.doi.org/10.1111/j.1365-2699.2006.01578.x
- Reichard SH, Hamilton CW (1997) Predicting invasions of woody plants introduced into North America. Conservation Biology 11: 193–203, http://dx.doi.org/10.1046/j.1523-1739.19 97.95473.x
- Rejmánek M (1996) Species richness and resistance to invasions.
 In: Orians GH et al. (eds), Biodiversity and ecosystem processes in tropical forests. Springer-Verlag, Berlin, Germany, http://dx.doi.org/10.1007/978-3-642-79755-2
- Rejmánek M, Richardson DM (1996) What attributes make a species invasive? *Ecology* 77: 1655–1661, http://dx.doi.org/10.2307/2265768
- Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography* 28: 139–150, http://dx.doi.org/10.1046/j.1365-2699.2001.00536.x
- Sax DF (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8: 193–210, http://dx.doi.org/10.1046/j.1472-4642.2002.00147.x
- Schmidt W (1989) Plant dispersal by motor cars. *Vegetatio* 80: 147–152, http://dx.doi.org/10.1007/BF00048038
- Scott DW (1979) On optimal and data-based histograms. Biometrika 66: 605–610, http://dx.doi.org/10.1093/biomet/
- Seabloom EW, Williams JW, Slayback D, Stoms DM, Viers JH, Dobson A (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications* 16: 1338–1350, http://dx.doi.org/10.1890/1051-0761(2006)016 [1338:HIPIAI]2.0.CO;2

- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32, http://dx.doi.org/10.1023/A:101008632 9619
- Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83: 2575– 2590, http://dx.doi.org/10.1890/0012-9658(2002)083[2575:BIR AME]2.0.CO;2
- Stohlgren TJ, Barnett DT, Flather C, Fuller P, Peterjohn B, Kartesz J, Master LL (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions* 8: 427–447, http://dx.doi.org/10.1007/s10530-005-6422-0
- Stohlgren TJ, Barnett DT, Jarnevich CS, Flather C, Kartesz J (2008) The myth of plant species saturation. *Ecology Letters* 11: 313–322, http://dx.doi.org/10.1111/j.1461-0248.2008.01153.x
- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and Environment* 1: 11–14, http://dx.doi.org/10.18 90/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2
- Taylor BW, Irwin RE (2004) Linking economic activities to the distribution of exotic plants. *Proceedings of National Academy of Sciences USA* 101: 17725–17730, http://dx.doi.org/10.1073/pnas.0405176101
- Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30, http://dx.doi.org/10.1046/j.1523-1739.20 00.99084.x

- Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology* 6: 253–262, http://dx.doi.org/10.1046/j.1523-1739.1992.620253.x
- Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277: 494–499, http://dx.doi.org/10.1126/science.277.5325.494
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802–804, http://dx.doi.org/10.1126/science.238.4828.802
- Watkins RZ, Chen J, Pickens J, Brosofske KD (2003) Effects of forest roads on understory plants in a managed hardwood landscape. *Conservation Biology* 17: 411–419, http://dx.doi.org/10.1046/j.1523-1739.2003.01285.x
- Wilcove DS, Rothstein D, Bubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *BioScience* 48: 607–615, http://dx.doi.org/10.2307/1313420
- Williamson M (1996) Biological Invasions. Chapman and Hall, London, 256 pp