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Genetic variation increases during biological invasion by a Cuban lizard

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A genetic paradox[1,2] **exists in invasion biology: how do introduced populations, whose genetic variation has probably been depleted by population bottlenecks, persist and adapt to new conditions? Lessons from conservation genetics show that reduced genetic variation due to genetic drift and founder effects limits the ability of a population to adapt, and small population size increases the risk of extinction**[1,3,4]**. Nonetheless, many introduced species experiencing these same conditions during initial introductions persist, expand their ranges, evolve rapidly and become invasive. To address this issue, we studied the brown anole, a worldwide invasive lizard. Genetic analyses indicate that at least eight introductions have occurred in Florida from across this lizard's native range, blending genetic variation from different geographic source populations and producing populations that contain substantially more, not less, genetic variation than native populations. Moreover, recently introduced brown anole populations around the world originate from Florida, and some have maintained these elevated levels of genetic variation. Here we show that one key to invasion success may be the occurrence of multiple introductions that transform among-population variation in native ranges to within-population variation in introduced areas. Furthermore, these genetically variable populations may be particularly potent sources for introductions elsewhere. The growing problem of invasive species introductions brings considerable economic and biological costs**[5,6]**. If these costs are to be mitigated, a greater understanding of the causes, progression and consequences of biological invasions is needed**[7]**.**

Ecological approaches have identified many factors that are important for invasion success and have made quantitative predictions of establishment and spread of invaders[8]. Genetic approaches, however, have received less attention, even though the loss of genetic variation associated with bottlenecks during introductions may compromise the ability of populations to adapt to new environments[9], thus limiting their long-term viability. As a result, biological invasions may be evolutionary dead ends[10]. Introduced species are nonetheless pervasive and in some cases evolve rapidly[11], suggesting an ability of some invasive species to circumvent loss of genetic variation associated with bottlenecks during introductions.

An ideal opportunity to study the genetics of an invading species is provided by the brown anole, *Anolis sagrei*, a small, diurnal lizard introduced worldwide from its native range in the Caribbean. *A. sagrei* is highly invasive; it reaches high population densities, shows exponential range expansion and is competitively superior to and a predator of native lizards[12–14] (Supplementary Fig. S1). Introductions to Jamaica (possibly natural) and southern Florida were first reported in the mid- to late-1800's (ref. 15). The *A. sagrei* invasion of Florida is well documented; it first appeared in the late nineteenth century in the Florida Keys (Supplementary Table S1). For at least half a century its range did not expand appreciably, but beginning in the 1940's, and accelerating in the 1970's, *A. sagrei* spread northward throughout most of Florida (Supplementary Fig. S1). This expansion probably resulted from a combination of northward movement by the early introductions in southern Florida and additional introductions into peninsular Florida[16,17]. More recent introductions have established populations in Hawaii, Grand Cayman, Taiwan, Grenada and other parts of the United States. By examining the geographic distributions of genetic variants in populations today, we infer the history of these introductions and evaluate their consequences for population-genetic variation.

To identify the precise geographic source of colonists, it is essential that the native range be thoroughly sampled. We collected over 600 samples of *A. sagrei* from 71 native and 59 introduced populations to assay levels of genetic variation and to identify the source populations for introductions (Supplementary Table S2). Genetic variation in the native range of *A. sagrei* is highly structured geographically with most genetic variation being among, rather than within, populations (Fig. 1 and Table 1). This genetic structure in the native range allows us to assign haplotypes from introduced populations to geographic localities in the native range with high confidence and to determine the minimum number of introductions. Over 99% of individuals sampled from introduced populations have haplotypes identical or closely related to ones found in Cuba (Fig. 1 and Supplementary Fig. S2). Two kinds of evidence suggest that multiple introductions have occurred into Florida. First, haplotypes from eight different clades are present in Florida, none of which occur together in the native range, indicating eight geographically distinct source populations (Fig. 1). Phylogenetic reconstruction similarly suggests a minimum of eight introductions into Florida. Second, haplotypes whose distributions are distantly separated in Cuba occur together in Florida. Two-thirds of the introduced populations sampled in Florida have haplotypes originating from more than one distinct native population (Fig. 2), but there is no evidence for mixing of haplotypes from different regions within Cuba (Fig. 1 and Table 1). As a result of these multiple introductions from different parts of Cuba, most Florida populations of *A. sagrei* have substantially more genetic variation than native populations. This is evident both in the higher genetic variation within, rather than among, introduced populations (Table 1) as well as their higher mean within-population sequence divergence (Wilcoxon rank sum test: $z = 3.98$; $P < 0.0001$; see Supplementary Fig. S3). Furthermore, more recently established populations have higher genetic variation than older introduced populations owing to the mixture of haplotypes from multiple sources (Figs 2 and 3).

In recent years, *A. sagrei* has been introduced to Hawaii, Grand Cayman, Taiwan and Grenada (Supplementary Table S1), but the

source for these introductions is not documented. As in Florida, these introductions may have occurred one or more times directly from Cuba. Alternatively, owing to the widespread establishment of *A. sagrei* (Supplementary Fig. S1), its high population densities[13] and heightened levels of genetic variation in Florida (Fig. 2), secondary introductions from Florida are possible. Several lines of evidence suggest that Florida populations have been the source for more recent introductions elsewhere. First, recently introduced populations sampled outside Florida contain only haplotypes identical or nearly identical to those sampled in Florida (Supplementary Fig. S2). Second, populations in Hawaii and Taiwan

have combinations of distantly related haplotypes that co-occur in Florida but not in the native range (Fig. 2). Remarkably, some of these secondarily introduced populations have maintained the elevated levels of genetic variation found in Florida populations. These secondary introductions might easily be misinterpreted as resulting from multiple introductions themselves except that the same haplotype combinations exist within Florida populations, and Florida introductions occurred much earlier than those in Hawaii and Taiwan (Fig. 2 and Supplementary Table S1).

By combining genetic variation from multiple source populations, the biological invasion of *A. sagrei* illustrates not only how introduced populations can avoid the reduction in genetic diversity thought to be typical of most introductions, thus solving a paradox in invasive-species genetics[1], but also how genetic variation within introduced populations can actually increase during an invasion (Fig. 3). Although precedents exist for multiple introductions and increased genetic variation in introduced populations[18,19], the detailed knowledge of the history of *A. sagrei* introductions and its impact on genetic variability is unparalleled. Populations from initial introductions in the Florida Keys, which today contain haplotypes primarily from western and west-central Cuba, generally have genetic variation similar to or even slightly lower than native Cuban populations (Fig. 2 and Supplementary Fig. S3), probably a result of population bottlenecks during introduction. Conversely, populations from central and northern Florida, which have highly elevated levels of genetic variation, are dominated by haplotypes from central and eastern Cuba, suggesting that additional introductions from Cuba preceded the northward spread of earlier introductions in southern Florida. This pattern is confirmed by the significant geographic genetic structure found in Florida despite high levels of within-population genetic variation (Table 1). Regardless of the chronology or location of each introduction,
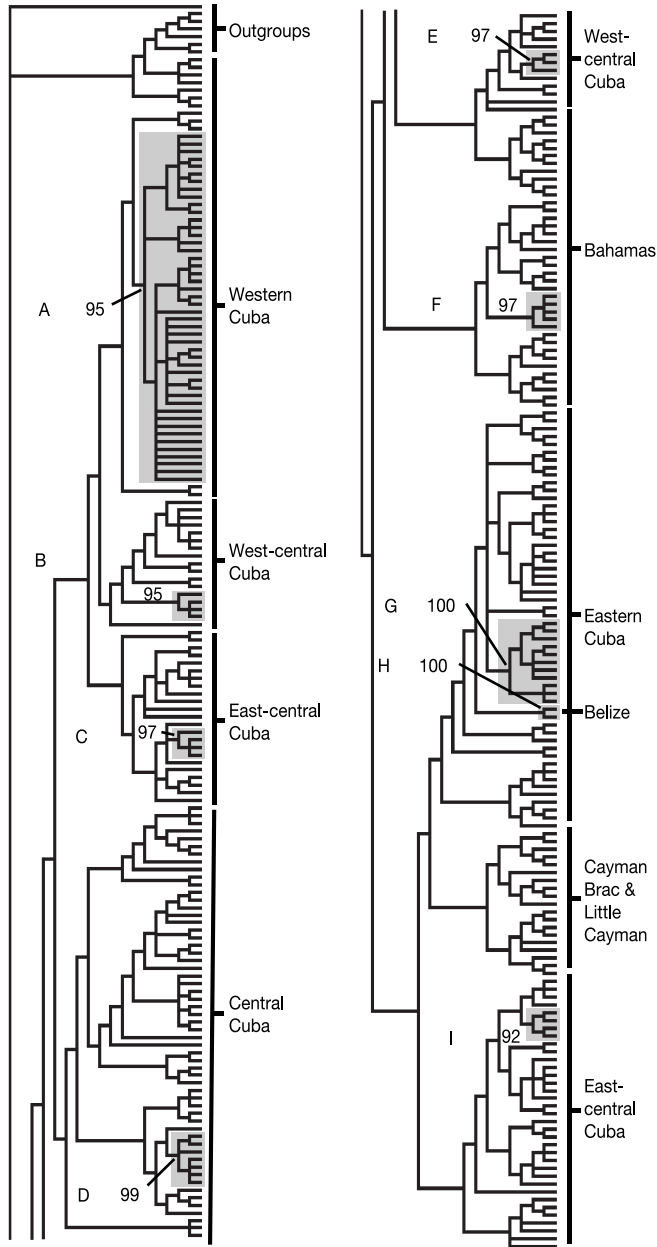
Figure 1 Phylogenetic tree of *A. sagrei*. The tree is from a bayesian analysis of all unique mtDNA haplotypes sampled from the introduced and native ranges of *A. sagrei* (Supplementary Table S2). The tree is split with the top half to the left. Background shading and letters (A–I) indicate nine well-supported clades that are geographically distinct in the native range but contain all haplotypes sampled from introduced populations (see Supplementary Fig. S2). Bayesian posterior probabilities are shown above the branches leading to these nine clades. Geographic regions in the native range are shown to the right.

Table 1 **Analysis of molecular variance results**

| Region* (area†)	Source of variation‡	d.f.	% of variation	*P*-value
Native range				
Cuba (100,000 km²)				
	Among	56	79.91	<0.0001
	Within	198	20.09	
	Total	254		
Bahamas (10,000 km²)				
	Among	8	93.22	<0.0001
	Within	34	6.78	
	Total	42		
Cayman Brac (35 km²)				
	Among	1	57.35	0.0059
	Within	8	42.65	
	Total	9		
Little Cayman (25 km²)				
	Among	1	62.57	0.0020
	Within	9	37.43	
	Total	10		
Introduced range				
Florida (70,000 km²)				
	Among	39	24.67	<0.0001
	Within	159	75.33	
	Total	198		
Jamaica (10,000 km²)				
	Among	7	87.67	<0.0001
	Within	27	12.33	
	Total	34		
Hawaii (300 km²)				
	Among	3	16.98	0.1056
	Within	9	83.02	
	Total	12		
Grand Cayman (200 km²)				
	Among	5	17.98	0.0430
	Within	23	82.02	
	Total	28		

*Taiwan and Grenada are not included in these analyses because only one population was sampled in each country.
† The estimated area occupied by *A. sagrei* in each region.
‡ Among populations, within populations or total.

intermingling of genetic variation from distinct introductions produced elevated levels of genetic variation within introduced populations (Figs 2 and 3, and Supplementary Fig. S3).

The lag time between initial Florida introductions in the 1880's and widespread establishment of *A. sagrei* that began in the 1940's is a common feature of biological invasions[2,9,20] (Supplementary Fig. S1). Such delays between the initial establishment of colonists and subsequent expansion are often explained as either an ecological phenomenon, the lag phase in the exponential population growth curve, or an evolutionary phenomenon, the time needed for adaptation to new environments[2]. The genetic data for *A. sagrei* suggest an alternative explanation: Florida populations established during the expansion phase of the invasion contain primarily haplotypes from later introductions, suggesting that separate introductions, not spread of initially introduced populations, explain the range expansion. Unfortunately, the role of multiple introductions in explaining lag times in other biological invasions may be difficult to assess. Detection of multiple introductions may prove difficult except in cases, such as this one, in which geographic sampling of the native range is thorough, genetic variation in native populations is geographically structured and introductions are clearly from multiple areas.

The colonization of *A. sagrei* in Jamaica provides a second example of this phenomenon. As in Florida, populations established by an initial, possibly natural, introduction in the mid-nineteenth century or earlier did not expand rapidly for more than a century[15], followed by rapid expansion across the island. Genetic data confirm that this rapid expansion resulted from a second introduction from Cuba. Unlike the case in Florida, however, this second introduction came from a single source population; thus, elevated levels of genetic variation occur only in one population in which the two introductions seem to make contact (Fig. 2).

Multiple introductions have clearly enhanced the ability of *A. sagrei* to occupy non-native areas by accelerating its geographic expansion over that possible by simple diffusion alone. Separating the demographic effects of multiple introductions themselves from the effect of increased within-population genetic variation is not easy[2]. Some successful invasions occur despite substantial reductions in genetic variation[21], so genetic variability is not always necessary, at least in the short term[10]. However, if enhanced genetic variation increases the rate of adaptive evolution, then introduced populations might be expected to show phenotypic divergence from native-range populations. Available data for *A. sagrei* are limited but consistent with this conjecture: Florida populations are more
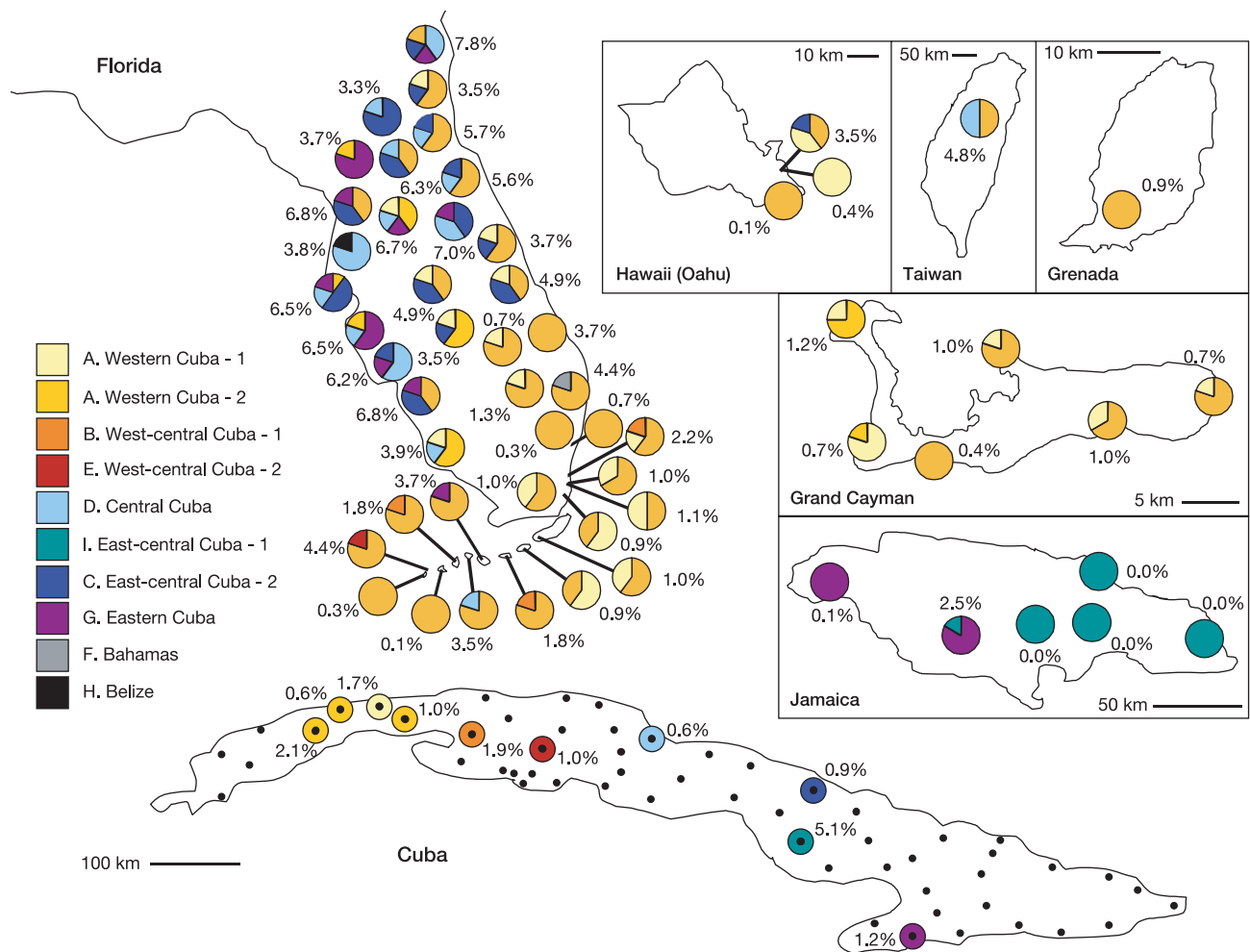
Figure 2 Source of genetic variation in introduced *A. sagrei* populations. The map shows the distribution of genetic variation in introduced populations in Florida, Hawaii, Taiwan, Grenada, Grand Cayman and Jamaica, and the source of this genetic variation from native Cuban populations. Blacks dots indicate native Cuban populations sampled. Colours encircling some black dots denote Cuban populations containing haplotypes to which introduced-population haplotypes are most closely related. Pie charts representing each introduced population indicate the frequency of haplotypes from different Cuban sources (populations for which only one individual was sampled are not shown). Percentages next to each pie chart give the mean pairwise mtDNA sequence divergence within that population (overall means are 3.5% for Florida and 1.7% for Cuba). Letters (A–I) in the key correspond to clades in Fig. 1 and haplotype networks in Supplementary Fig. S2.
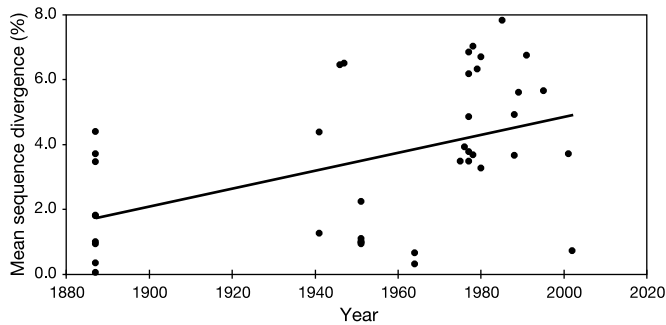
Figure 3 Genetic variation increases during the biological invasion. The *A. sagrei* invasion of Florida shows a positive relationship between genetic diversity within a population (as measured by mean pairwise percent sequence divergence) and the date that each population was established ($Y = 0.028X - 50.652$; $P = 0.002$; $R^2 = 0.220$). Nearly all introduced Florida populations established after 1975 have an average within-population sequence divergence higher than the mean for Florida populations (overall Florida mean is 3.5%).

variable morphologically than Cuban populations[22], thus potentially providing variation that could lead to rapid evolution by natural selection. Furthermore, introduced *A. sagrei* in Florida have diverged morphologically from Cuban populations in a variety of characters[22], including increased body size[23]. Future work is required to examine the underlying genetic basis for the morphological variation observed as well as to investigate its adaptive significance. The role of ecological factors (for example, escape from predators or competitors) also needs to be examined. Studies comparing introduced and native populations as well as introduced populations with varying amounts of genetic variation are needed to disentangle the relative importance and interaction of ecological and genetic factors in determining the spread and adaptive change of this species.

Two disturbing consequences emerge regarding invasive species management and control. First, owing to multiple introductions, invasive populations can become more rather than less genetically variable during an invasion (Figs 2 and 3). Thus, the ability of invasive populations to adapt to new environments will not be constrained for genetic reasons and may be enhanced[24,25]. Second, introduced populations that are widespread and genetically diverse become a source for secondary introductions that maintain elevated genetic variation. Such secondary introductions are likely when the introduced area has higher levels of commercial trade and transport that would aid the spread of a particular species to a greater extent than in the native area; this situation is probably true for Florida versus Cuba. Moreover, if a lack of genetic variation decreases the chances of establishment during an introduction[3,20,26], both multiple introductions and secondary introductions from highly variable introduced populations may greatly favour the establishment and persistence of new introductions. As a result, invasive-species management, such as biological control, may need to account for genetically diverse biological invasions resulting from multiple introductions[27]. □

Methods

Data

We conducted phylogenetic and population-genetic analyses of mitochondrial DNA (mtDNA) sequences from individuals collected in introduced and native populations of *A. sagrei* (Supplementary Table S2). Sampling ranged from one to ten individuals per population with five individuals sampled for most populations. We sequenced an approximately 1,200-base-pair region of mtDNA including the genes encoding ND2, tRNA^{Trp} and tRNA^{Ala}. We extracted genomic DNA using Viogene extraction kits, amplified gene products using standard PCR methods and purified PCR products using Viogene Gel-M purification kits. Sequencing reactions were run with Big-Dye Terminator Ready-Reaction kits (PerkinElmer) on a Basestation automated sequencer (MJ Research). Sequences were obtained with primers H5730, L4882c and L4437[28], and aligned manually

using secondary-structural models[28]. All sequences are deposited in GenBank (Supplementary Table S3).

Phylogenetic and population-genetic analyses

The bayesian phylogenetic analysis included 313 unique *A. sagrei* sequences and eight outgroup sequences from *Anolis homolechis*, *Anolis bremeri* and *Anolis quadriocellifer*[29]. Likelihood-ratio tests selected the GTR + I + Γ model for the bayesian analysis[30], which was run for 1,000,000 generations sampling trees every 9,000 generations[29]. We discarded the trees during the 'burn-in period' (the initial 10% of trees) and made a 50% majority-rule consensus tree from the remaining set of bayesian trees. We repeated this analysis twice to avoid searching within local optima. This tree was used to identify well-supported clades showing geographic endemism in the native range and containing haplotypes sampled from the introduced range nested within them (Fig. 1). Additionally, we used parsimony to reconstruct the number of separate introductions on each of 102 trees in the bayesian tree set. Once we had identified clades containing introduced haplotypes, we used statistical parsimony to connect introduced and native-range haplotypes within these clades into haplotype networks using a 95% confidence criterion (Supplementary Fig. S2). The combination of phylogenetic, parsimony reconstruction and population-genetic approaches allowed us to identify populations within the native range from which haplotypes sampled in introduced populations originate.

Statistical analyses

We tested for significant geographic structure among populations in both the introduced and native ranges using analysis of molecular variance (AMOVA), and for a difference in the average within-population genetic variability between introduced Florida and native Cuban populations using a Wilcoxon rank sum test. Lastly, using approximate dates of introduction or establishment for Florida populations obtained from the literature (see the Florida Fish and Wildlife Conservation Commission's website at http://wld.fwc.state.fl.us/critters/exotics/SpeciesNumberResults.asp?SPPNO = 25), we tested for a relationship between year and genetic diversity within a population (Fig. 3). Also, we tested for an exponential pattern of range expansion within Florida using the same dates of introduction or establishment (Supplementary Fig. S1).

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Ecosystem stability and compensatory effects in the Inner Mongolia grassland

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Numerous studies have suggested that biodiversity reduces variability in ecosystem productivity through compensatory effects[1–6]; that is, a species increases in its abundance in response to the reduction of another in a fluctuating environment[1,7]. But this view has been challenged on several grounds[8–10]. Because most studies have been based on artificially constructed grasslands with short duration, long-term studies of natural ecosystems are needed. On the basis of a 24-year study of the Inner Mongolia grassland, here we present three key findings. First, that January–July precipitation is the primary climatic factor causing fluctuations in community biomass production; second, that ecosystem stability (conversely related to variability in community biomass production) increases progressively along the hierarchy of organizational levels (that is, from species to functional group to whole community); and finally, that the community-level stability seems to arise from compensatory interactions among major components at both species and functional group levels. From a hierarchical perspective, our results corroborate some previous findings of compensatory effects[1,4,7,11]. Undisturbed mature steppe ecosystems seem to culminate with high biodiversity, productivity and ecosystem stability concurrently. Because these relationships are correlational, further studies are necessary to verify the causation among these factors. Our study provides new insights for better management and restoration of the rapidly degrading Inner Mongolia grassland.

The role of compensatory interactions between species[6,7] has been a key issue in the debate concerning the diversity–stability relationship of an ecosystem. In particular, because different species respond to environmental fluctuations differently, the reduction in biomass of a certain species is more likely to be recompensed by the increased biomass of other species in a species-rich rather than species-poor community[1,4,6]. Such compensatory effects have been reported for both plant and animal communities[1,7,11–14]. However, others have argued that plant diversity has no consistent effect, or even a negative effect, on biomass production and ecosystem stability[10,15,16]. Undoubtedly, ecosystem stability depends not only on community composition but also on disturbance, nutrient supply and climatic conditions[3,4,9,13,15,17], and long-term studies of natural ecosystems are needed for better understanding of compensatory effects and thus the diversity–stability relationship.

Here we present the results of a long-term (1980–2003) study of two natural steppe communities in the Inner Mongolia grassland. The first (site A) is a rhizome-grass-dominated community, and the second (site B) is a bunchgrass-dominated community (see Methods). We classified species into the following five plant functional groups (PFGs) primarily on the basis of life forms: perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB). PFGs also differ in plant stature, rooting depth, root-to-shoot ratio, water use efficiency, nutrient use efficiency and C:N:P stoichiometry[18–21] (Supplementary Information). Our study addresses the following three questions: first, what are the most important climatic drivers for the aboveground biomass production of steppe communities? Second, how does biomass production respond to precipitation fluctuations at different levels of organization (that is, at the species, plant functional group and community level)? And third, are there detectable compensatory effects reducing the variability in biomass production and thus increasing ecosystem stability?

To address the first question, we used multiple regressions to examine how the aboveground community biomass (B_{comm}) was related to several climatic variables: precipitation (annual, January–July, January–August and May–August); cumulative temperature (°C), that is, the accumulated excess when temperature exceeded 0 °C (January–July and January–August), 5 °C (annual) and 10 °C
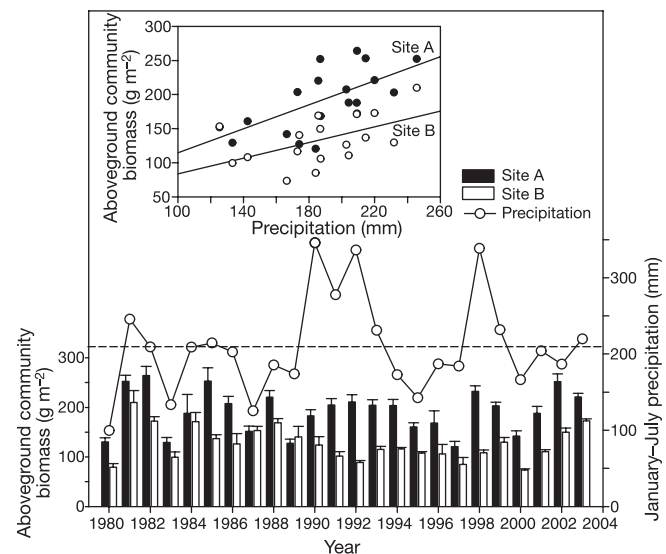
Figure 1 The relationship between January–July precipitation and total community aboveground biomass (B_{comm}) for the *Leymus chinensis* (site A) and *Stipa grandis* (site B) steppe ecosystems of the Inner Mongolia grassland, using data from 1980 to 2003. Bottom panel: B_{comm} was positively correlated to January–July precipitation in site A ($r^2 = 0.25$, $P = 0.01$), but not in site B ($r^2 = 0.003$, $P = 0.81$; $n = 24$). Error bars represent s.e.m., and the horizontal dashed line is the mean January–July precipitation from 1980 to 2003. Top panel: a significant positive correlation was found between B_{comm} and January–July precipitation in both sites after removing the four extraordinarily wet years (1990, 1991, 1992 and 1998). For site A (black dots) $r^2 = 0.49$, $P < 0.001$, $n = 19$; for site B (open circles) $r^2 = 0.35$, $P < 0.01$, $n = 19$.