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Plant hybridization: the role of human disturbance and biological invasion

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ABSTRACT

Aim Anderson & Stebbins (1954, *Evolution*, **8**, 378–388) posited that human activities promote species hybridizations by creating opportunities for hybridization and new habitats for hybrids to persist through disturbances (i.e. the 'disturbance hypothesis'). While the first part of this hypothesis appears to be well supported, the second part has not been corroborated with empirical evidence, probably because of the lack of appropriate data. In this study, I (1) document the richness and distribution of hybrid plants in the United States; (2) examine the relationships between hybrids of different origins and between hybrid plants and native or exotic plants; and (3) examine possible mechanisms for these relationships and test the disturbance hypothesis.

Location The United States.

Methods The richness and distribution of plant hybrids was examined at the county level according to origin, that is, formed between native–native species ($N \times N$), native–exotic species ($N \times E$) and exotic–exotic species ($E \times E$), using data from the Biota of North America Program.

Results The three hybrid types ($N \times N$, $N \times E$ and $E \times E$) were positively related to each other and showed stronger positive relationship with exotic richness than with native richness. They also exhibited similar spatial patterns, with richness hotspots concentrated in the north-east United States and Great Lakes region. However, the richness of hybrids of exotic origin ($E \times E$ and $N \times E$) was not related to county area, as often observed for native species; instead, it showed strong positive relationships with human population density. Thus, the overall patterns of hybrid richness and distribution support the 'disturbance hypothesis'.

Main conclusions The results are generally consistent with the disturbance hypothesis. The relationship between the number of hybrids of exotic origin and overall exotic richness provided stronger evidence for human-induced than for naturally caused hybridization, although other possible explanations may also exist.

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Biological invasions, conservation, distribution, exotics, genetic novelty, richness.

INTRODUCTION

Both intra- and inter-taxon hybridizations can occur, leading to vastly different consequences including novel traits, new species, increased invasiveness and extinction (Rhymer & Simberloff, 1996; Rieseberg, 1997; Whitney & Gabler, 2008; Ellstrand, 2009; Schierenbeck & Ellstrand, 2009; Hegarty, 2012). While there are many forms, hybridizations between co-occurring, closely related species have long fascinated ecologists and evolutionary biologists (Rieseberg, 1997). More recently, the impacts of hybridization, especially those related to biological invasions, have attracted attention (Vilà *et al.*, 2000; Blair & Hufbauer, 2010; Lu *et al.*, 2010). While it has long been recognized that human activities have increased the likelihood of hybridization of previously isolated species or populations (e.g. Kahilainen *et al.*, 2011),

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how these newly formed hybrids persist in certain habitats is less clear (Abbott, 1992). More than half a century ago, Anderson & Stebbins (1954) predicted that human disturbance would create novel and suitable habitats for newly formed hybrids, allowing them to both establish and persist (Ellstrand & Schierenbeck, 2000; Vilà *et al.*, 2000; Huston, 2004; Hasselman *et al.*, 2014; see also Soltis & Soltis, 2009). Yet despite the recent and drastic increase in hybrid species (Schierenbeck & Ellstrand, 2009), direct and detailed evidence connecting hybrid success to anthropogenic disturbance and actions (i.e. the 'disturbance hypothesis') is still lacking (but see Mack, 1981; Hoban *et al.*, 2012; Thompson *et al.*, 2012).

Introductions of exotic species into previously unoccupied areas may lead to rapid evolution and commonly result in two types of hybridization which in turn affect invasion success (Richardson & Pyšek, 2006). First, multiple introductions from different or remotely related exotic populations of the same species from either the species' native or invaded ranges into one location can form intra-specific hybrids (Molofsky *et al.*, 1999; Novak & Mack, 2001; Dlugosch & Parker, 2008). This is evidenced by the role of the adaptive evolution of polyploidy formed through hybridization in facilitating invasions (see review by Richardson & Pyšek, 2006). Second, introducing exotic species into geographic locations where their close relatives (i.e. sister species) exist often leads to inter-specific hybrids. Both types of hybrids could potentially form highly invasive populations as hybridization can lead to increased genetic variation or even to the generation of novel genotypes. Some well-known hybrids in the United States that have become invasive include *Myriophyllum spicatum* × *sibiricum* (native–exotic species or $N \times E$), *Spartina foliosa* × *alterniflora* (native–native species or $N \times N$) and *Tamarix chinensis* × *ramosissima* (exotic–exotic species or $E \times E$; Gaskin & Kazmer, 2009). Additional examples are given in Appendix S1 in Supporting Information (see also Cox, 2004).

Hybridization has long been regarded as a major mechanism for speciation and/or endemism (Stebbins, 1959, 1985; Rieseberg, 1997; Soltis & Soltis, 2009). In addition to the proven cases where hybridization can promote the invasiveness of a species or genotype (Ellstrand & Schierenbeck, 2000; Moody & Les, 2007; Ridley & Ellstrand, 2009; Hovick *et al.*, 2012), hybridization may also have other unidentified ecological and evolutionary consequences. For example, Whitham (1989) showed how plant hybrids have important effects across trophic levels (e.g. on pests). In a recent study, Adams *et al.* (2011) found that overstorey tree hybrids (cottonwoods) could promote understorey species richness by forming unique assemblages.

Not only do human activities and associated biological invasions increase exotic species diversity, but they may also produce hybrids that would not otherwise be formed (Hasselman *et al.*, 2014). With ongoing expansion of human population via both growth and migration, it could be expected that hybridization events will continue to increase over time. Nonetheless, despite the diversity and distribution of exotic plant species across the United States being studied extensively (e.g. Rejmánek, 2003; Stohlgren *et al.*, 2005; Qian & Guo, 2010), the patterns in richness and distribution, mechanisms and consequences of plant hybridization related to biological invasion are not well understood.

The majority of previous studies on hybridization have focused on individual hybrids, often in comparison with their parent species within particular taxonomic groups (e.g. Gaskin & Schaal, 2002) or on biosystematics (Vilà *et al.*, 2000), but not on the overall richness or distribution of hybrids within a particular region or habitat type. Here, instead of exploring the causes for the success of individual hybrid invaders, I examine for the first time the richness and distribution of hybrid plants at the county level across the contiguous United States. Specifically, I examine: (1) the geographic presence of three types of hybrid plants ($N \times N$, $N \times E$ and $E \times E$) and relationships between them, (2) the relationships between hybrid plants and natives/exotic species richness and (3) the possible mechanisms of hybridization that relate to human population, especially for hybrids of exotic origin. Although hybridization can occur both within and between species (i.e. intra- and inter-specific hybrids, respectively), for the purpose of this study, I only focus on inter-specific hybrids and emphasize hybridizations involving exotic species. The expected results will provide baseline information for biological invasion, hybridization and especially biodiversity conservation in the future.

METHODS

For this study, I used data on the absence/presence of plant hybrids collected as part of an extensive survey of plant richness at the county level ($N = 3107$ counties) throughout the contiguous United States. For detailed description and reference sources, see http://www.bonap.org/ regarding the Biota of North America Program (Kartesz, in press; see also Rejmánek, 2000). The native or exotic status of a species was defined relative to the boundary of each surveyed county, not to those of the entire United States or each state (Guo & Ricklefs, 2010; Guo *et al.*, 2012), that is, we considered a finer resolution of native and exotic than is typically employed. Hybrids were divided into one of three groups (types) based on their origin: both parents were native ($N \times N$), one parent was native and the other exotic ($N \times E$), or both parents were exotic ($E \times E$). For this investigation, I did not include hybrids formed from domestically introduced species, although data were collected on these hybrids and each was categorized as $N \times N$ hybrids for the purposes of future investigation.

To identify possible causes of plant hybridization, I examined the relationships of hybrid richness with selected county-level variables, such as climate (maximum, minimum and annual mean temperature, precipitation and potential evapotranspiration – PET), county area, location (latitude, longitude), mean elevation, human population density, years in the Union and the presence/absence of the most recent glaciation (i.e. Wisconsin). These analyses were conducted for both the total number of hybrids and the total number of hybrids belonging to each hybrid type. Human population density was used as the indicator of intensity and magnitude of human disturbances.

County area and population data were compiled from http://www.census.gov/2010census; climate and elevation data were compiled from Coulson & Joyce (2010) and www.ncdc.noaa.gov/; and glaciation data (presence/absence) were based on estimates derived by Ray & Adams (2001), Kearney (2005) and Kartesz (in press). Additional data and information related to the richness and distribution of hybrid plants were compiled from http://plants.usda.gov/, Stein *et al.* (2000) and the U.S. Exotic Plant Database that the USDA Forest Service has been compiling since 2006 (for details, see Guo *et al.*, 2009).

I used analysis of variance (ANOVA) and *t*-tests to compare richness among different types of hybrids (i.e. $N \times N$, $N \times E$ and $E \times E$) across all counties and regression analyses for identifying the relationships between the three hybrid groups, again across all counties. As some variables could be strongly correlated as a result of spatial relationships (Liebhold *et al.*, 2013), to identify the major contributing factors for hybrid plant richness and possible confounding effects, I conducted spatial autoregression analyses (SAR) and ordinary least squares (OLSs) after a data reduction procedure using principal component analysis (PCA; Rangel *et al.*, 2006). These spatial analyses and PCA were performed using spatial analysis in macroecology (SAM; Rangel *et al.*, 2006), which is freely available at www.ecoevol.ufg.br/sam. For comparative purposes, I also performed multiple regression analyses based on the same variables examined in SAR/OLS using SAS 9.3 (SAS Institute Inc. 2011).

To quantify how the spatial variation in hybrid richness can be attributed to the independent effects of individual sets of variables of special interests, I first classified the selected variables into three classes, that is, (1) 'space factors' including area, latitude and longitude; (2) 'human factors' including years in the Union, population density and exotic richness (but not in panel-a); and (3) 'environmental factors' including mean annual precipitation, mean annual temperature, potential evapotranspiration (PET), elevation and glaciation. I then conducted partial regression analyses using SAM, which can take into account spatially structured environmental variation and intrinsic spatially contagious processes (Rangel *et al.*, 2006).

RESULTS

In the contiguous United States, a total of 1126 named hybrids were detected (6.23 ± 6.78 per county; mean ± SE). Of which, 941 were formed by two native parent species ($N \times N$; 5.03 ± 5.35 per county), 138 by two exotic parent species ($E \times E$; 2.26 ± 1.85 per county) and 47 by one native and one exotic parent species ($N \times E$; 1.51 ± 0.95 per county). The hybrids formed due to species introductions ($N \times E$ and $E \times E$) accounted for a large proportion (16.43%) of the overall hybrid plants in the United States. The hybrid richness at the county level was significantly different among the three types ($F = 1140$, d.f. = 2, $P < 0.0001$). Also, at the county level, the number of $E \times E$ hybrids was significantly higher than that of $N \times E$ hybrids ($t = 18.18$, d.f. = 551, $P < 0.0001$; Fig. S1 in Supporting Information). Overall, in addition to the 47 hybrids formed by native × exotic pairs, 6% of native plants were hybrids, while 3.3% of exotics were hybrids.

There was strong spatial variation in hybrid richness at the county level across the continental United States that varied little among the three hybrid types (Fig. 1). More than half the counties (1824 of 3107) had only two to six hybrids, while 57 counties had 30 or greater hybrids (Fig. 1). There were three hotspots identified that contained a greater proportion of hybrids across the contiguous United States: the north-east corner (New England), the Great Lakes region and the coast of California (Fig. 1).

As expected, based on the overall similarity among the spatial patterns for all three hybrid types ($N \times N$, $N \times E$ and $E \times E$), strong positive relationships for richness were observed (Fig. 2). In addition, the numbers of total hybrids and native hybrids ($N \times N$) were both positively correlated with the area of the county; whereas the number of hybrids of exotic origin was not ($N \times E$ or $E \times E$; Table 1, Table S1 in Supporting Information).

PCA results showed that the first two principal components (out of 13) together explained 61% of the total variation in the data (PCA1 = 39%, PCA2 = 22%). The PCA also revealed strong positive correlations (collinearity) between several county-level social-physical variables, such as (1) population density and years in the Union and (2) minimum, maximum and annual mean temperatures (in all cases, $r > 0.90$; Fig. S2). Note that because (1) population density would better reflect the true intensity and frequency of human disturbances than population size (which is positively related to area) and (2) mean annual temperature is a commonly used climatic variable, population size and minimum/maximum temperatures were excluded in subsequent SAR/OLS, partial and multiple regression analyses to remove or minimize the confounding effects; see detected collinearity in PCA results (Fig. S2).

Spatial autocorrelation analyses showed that the richness for total hybrids and for each hybrid type was spatially autocorrelated, but the distances at which this spatial autocorrelation occurred varied among these categorizations (e.g. Fig. S3). However, in examining the effects of social and physical factors on hybrid richness, AICc values indicated that OLS produced better-fitted models than SAR for total hybrids and $N \times N$ hybrids, but the reverse was true for $N \times E$ and $E \times E$ hybrids (Table 1). Overall, SAR/OLS and multiple regression analyses yielded remarkably similar results with a few exceptions (Table 1 and Table S1). Human population density and the presence of the latest (Wisconsin) glaciation

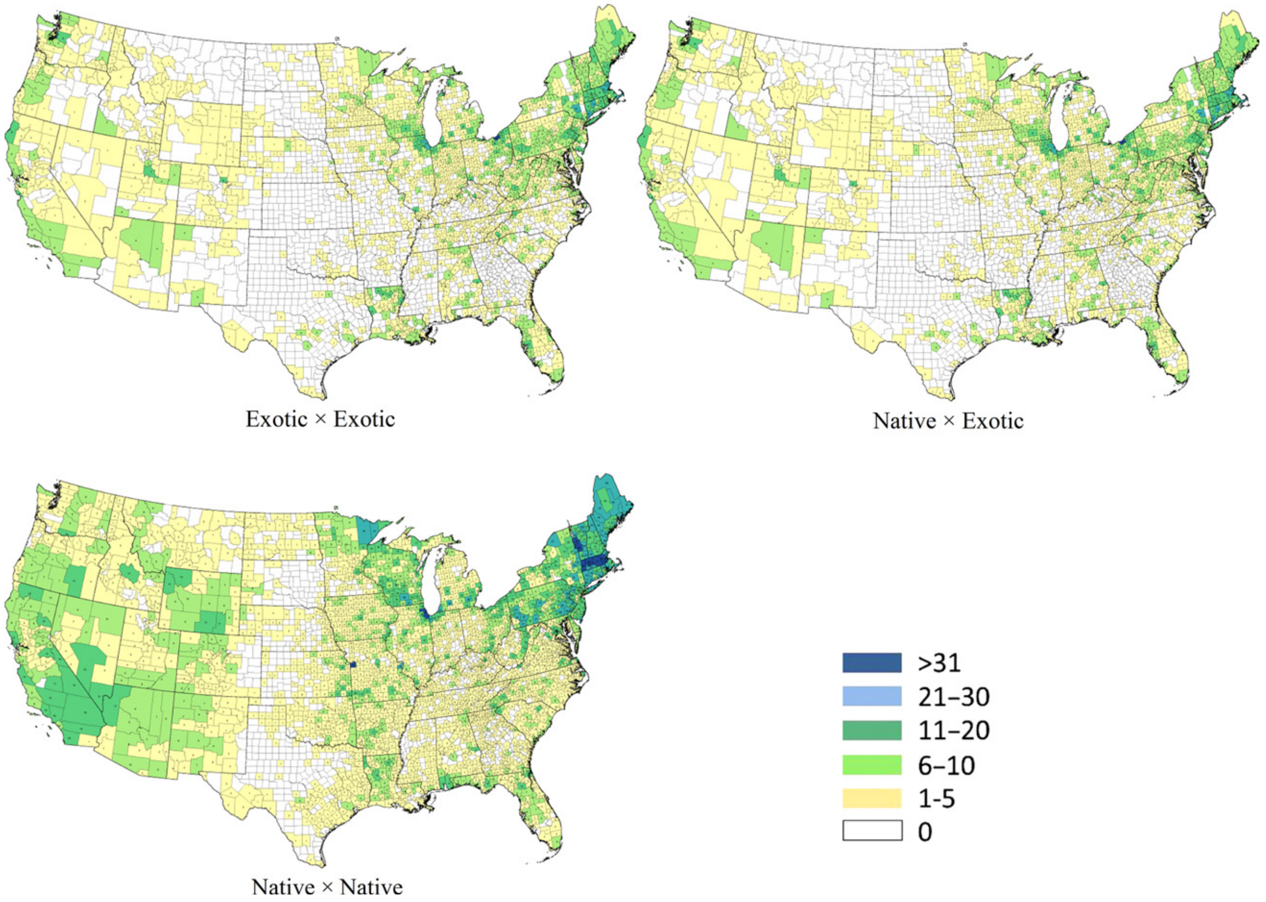

Figure 1 The richness and distribution of inter-specific hybrid plants of various origins, that is, native–native ($N \times N$), native–exotic ($N \times E$) and exotic–exotic ($E \times E$), recorded from each county in the contiguous United States. The north-east United States (New England), Great Lakes region and Californian coast have the highest concentration of inter-specific hybrid plants.

were both positively related to the richness of all hybrid categories (Table 1, Fig. 3a). Similar to population density, historical factors such as years in the Union were also strongly related to hybrid richness (Fig. 3b). In addition, the number of all hybrid plants and the number of hybrids of native origin ($N \times N$) were positively related to precipitation, native richness and exotic richness, but negatively related to mean annual temperature and total (native plus exotic) species richness. The richness of hybrids with both native and exotic origin ($N \times E$) was also positively related to temperature, elevation and total species richness. The hybrids of exotic origin ($E \times E$) were positively related to precipitation, elevation, total species richness and exotic richness (Table 1, Table S1; Fig. 4).

Results from partial regression analyses showed that human (or demographic) factors accounted for the largest amount (about 64%) of the total spatial variation in hybrid richness across the 3107 counties in the contiguous United States, followed by space–environment interaction, environmental factors alone and space. The combination of human and space factors together accounted for 67% of spatial variation in hybrid richness (in a separate analysis when the selected variables were recombined; not shown).

DISCUSSION

The proportion of hybrid plants in the United States (6% among native species and 3.3% of exotics) is within the ranges found on other large land masses (i.e. 2–25% among world-wide floras; Rieseberg, 1997; Mallet, 2007). However, hybrid plants are clearly an increasingly pervasive element of local and regional floras world-wide (Blair & Hufbauer, 2010). The geographic hotspots for each of the different types of hybrid plants very much overlapped (Fig. 1), with concentrations being highest for all in the north-east (especially New England), the Great Lakes region and along the Californian coast. These patterns are very similar to the spatial patterns of overall exotic richness (Rejmánek, 2003).

Unlike the patterns and drivers for native species, the inconsistent effects of temperature on total hybrid richness and those of different origins further highlight the importance of primary sources of species introduction and human disturbance (Guo *et al.*, 2012). In contrast, many states, especially those in the south-eastern United States and some other border states that have high exotic plant richness, do not necessarily have more hybrids. This is true of both hybrids formed from exotic plants (one or both parents are

Table 1 Results of the spatial autoregression analysis (SAR) and ordinary least square (OLS) and showing the relationships of hybrids with selected physical and social variables in the 3107 counties across the conterminous United States, as well as the relative contribution of space or spatial autocorrelation (bold-faced *t*-values highlight the significant relationships in SAR at $P < 0.05$). All variables were log-transformed prior to analysis. Because tmin, tmax and annual mean temperature are strongly and positively related to each other ($r > 0.95$), only annual mean temperature is used here to remove or minimize the confounding effects (Fig. S2)

	All hybrids		$N \times N$		$N \times E$		$E \times E$	
Source	R^2	AICc	R^2	AICc	R^2	AICc	R^2	AICc
Predictor	0.792	35.11	0.739	331.27	0.494	−3093.80	0.505	−1510.40
Predictor and space	0.623	71.80	0.733	390.04	0.536	−3275.56	0.514	−1562.69

Variable	OLS*	SAR*	*t*	OLS	SAR	*t*	OLS	SAR	*t*	OLS	SAR	*t*
Constant	−0.714	−1.099	**−3.32**	−1.249	−1.397	**−4.034**	0.424	0.233	1.174	−0.458	−0.578	**−2.218**
Area (km^2)	0.102	0.05	**2.239**	0.111	0.067	**2.859**	0.055	0.008	*0.622*	0.027	0.007	*0.377*
Population density	0.152	0.142	**14.304**	0.149	0.141	**13.581**	0.049	0.044	**7.369**	0.083	0.074	**9.46**
Precipitation (cm)	0.166	0.288	**6.237**	0.152	0.241	**4.989**	−0.039	0.053	1.92	0.071	0.116	**3.183**
Temperature (°C)	−0.289	−0.318	**−3.518**	−0.499	−0.51	**−5.383**	0.123	0.141	**2.599**	0.07	0.056	0.782
PET (cm)	−0.284	−0.099	*−0.598*†	0.168	0.247	1.421	−0.433	−0.367	**−3.687**	−0.214	−0.136	*−1.04*
Elevation (m)	−0.024	0.012	0.869	−0.025	0.006	0.448	−0.006	0.016	***1.969***	0.011	0.026	***2.452***
Glaciation (1/0)	0.588	0.527	**9.903**	0.62	0.554	**9.95**	0.209	0.15	**4.708**	0.528	0.47	**11.219**
No. all species	−2.192	−2.128	**−7.18**	−2.693	−2.636	**−8.496**	0.792	0.703	**3.963**	0.598	0.554	**2.374**
No. natives	2.275	2.215	**8.407**	2.814	2.764	**10.025**	−0.769	−0.682	**−4.322**	−0.65	−0.618	**−2.979**
No. exotics	0.56	0.551	**10.727**	0.467	0.446	**8.288**	0.037	0.051	1.658	0.315	0.336	**8.292**

*OLS or SAR coefficients.

†Values in italic indicate different results from multiple regression analyses, which showed the relationships of same sign (direction) but different significance (see Table S1).

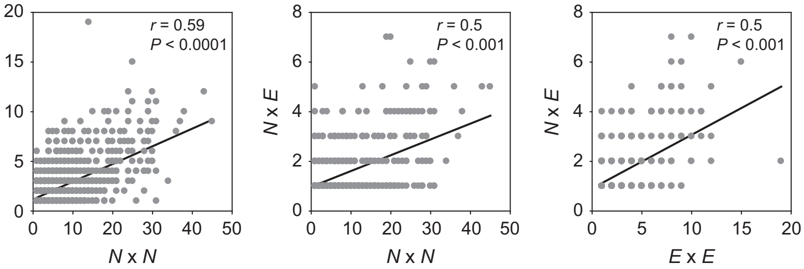

Figure 2 Positive relationships between the three types of inter-specific hybrid plants with different parent types (i.e. native–native or $N \times N$, native–exotic or $N \times E$ and exotic–exotic or $E \times E$) at the county level across the contiguous United States (in all cases, $P < 0.001$).

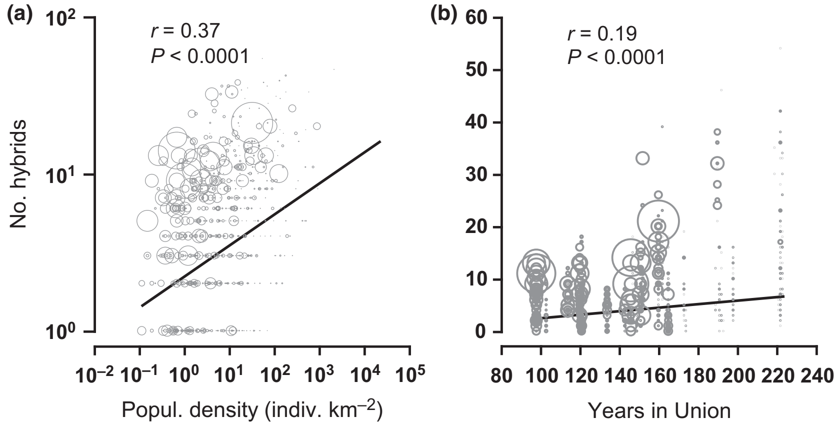

Figure 3 Positive relationships (a) between human population density (no. people/km^2) and hybrid plant richness (of all origins) and (b) between years in the Union and hybrid richness (of all origins) at the county level across the contiguous United States. Circle size = relative county area.

exotic) and those formed by natives. Thus, the results in this study indicate that human disturbances can be a catalyst that stimulates the formation and persistence of hybrid plants, thus offering clear evidence supporting Anderson & Stebbins' (1954) disturbance hypothesis (Stebbins, 1959; Ellstrand & Schierenbeck, 2000; Hasselman *et al.*, 2014).

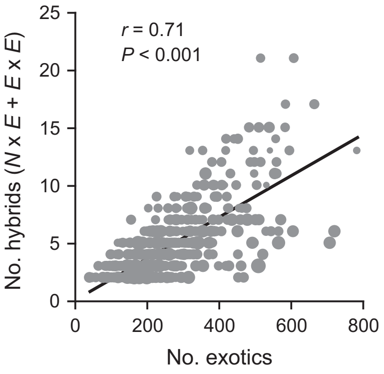

Figure 4 Positive relationships between the number of interspecific hybrid plants of exotic origin (i.e. one or both parents are exotics, $N \times E$ or $E \times E$) and exotic plant richness (foreign + domestic) at the county level across the contiguous United States.

The overlap between the southern limits of the last glacial ice sheets (25 000–15 000 BP; Ray & Adams, 2001; Kearney, 2005) and the distribution of native hybrids ($N \times N$) also seems to support the disturbance hypothesis (Table 1; Koch *et al.,* 2003). In this case, these disturbances were natural and caused by short-distance advances and retreats of the glacier's front due to climatic oscillations, leading to strong disruptions of both aboveground vegetation and soil. The locations where the last glacial ice sheet extended southwards across the northern half of New Jersey, across central Pennsylvania, westward to southern Ohio, eastern Michigan, northern Indiana and then through central Illinois and westward are precisely where the preponderance of $N \times N$ hybrids occurs. It is also possible that the resulting hybridization may have later been further enhanced by human activities (Schierenbeck & Ellstrand, 2009).

The mechanisms related to glaciation events cannot be used to explain the richness and distribution of newly formed hybrids of exotic origin. The richness and distribution of these hybrids are mostly related to species introduction (e.g. horticultural hybrids) and human disturbance. In California, especially along the coastline where the glaciation effect is lacking, intense human activities coupled with high richness of both native and exotic species may be responsible for the large number of hybrids (Schwartz *et al.*, 2006; Kraft *et al.*, 2010). The three regions (north-east, Great Lakes and coastal California) with high hybrid richness also have the highest population density, largest travel and trading ports and longest history of European settlement associated with the most intense developments (Withers *et al.*, 1998; Rejmánek, 2003; Gavier-Pizarro *et al.*, 2010; Liebhold *et al.*, 2013).

If human disturbance increases hybridization, the proportion of hybrids would have indeed increased dramatically over the past five hundred years. Given the history of human colonization and activities in the north-eastern United States (Gavier-Pizarro *et al.*, 2010), one may expect increases in hybrid richness to occur over the next few hundred years in other regions where vast human immigration is taking place (e.g. south-eastern and south-western United States). The exact manner by which human disturbance enhances hybrid persistence, however, has been less clear and is often more debated (e.g. Abbott, 1992; Vilà *et al.*, 2000) than is the well-recognized effect of species introductions.

However, hybrid formation likely has multiple causes, and human disturbance alone is unlikely to explain the patterns in hybrid richness that I found as hybrid formation also needs source (parent) species and suitable habitats. For example, the Great Plains region despite having strong human impacts (agriculture) usually has fewer hybrids because of low overall species richness (as 'parent species') and vast habitat loss (Guo, 2000). In many cases, the breakdown of various kinds of pre-mating reproductive barriers might also be responsible for hybrid formation. In addition, variation among counties in field sampling intensity could influence estimates of hybrid richness. This potential bias, however, is limited in this study as data on hybrid richness were collected as part of balanced sampling efforts across all counties aimed at collecting information on all major aspects of plant communities, such as native and species richness. However, like all studies involving species identification and richness estimation, this sampling effect should always be accounted for, or at least considered, when interpreting results.

For three reasons, the interpretation of partial regression results using class variables (Fig. 5) needs caution. First, plant species richness, especially exotic richness, is closely linked to 'demographic' and 'space factor' variables, such as human population density, area and longitude (Rejmánek, 2003; Guo *et al.*, 2012). Second, variables can also be classified into multiple and different numbers of classes, and different conclusions may be reached by doing so. Third (and most importantly), the number of variables included in each class could change the results (e.g. it is likely that the class with more variables could explain more variation). Due to these complications of interpretation, field experiments that focus on a local flora (e.g. Mayr, 1992) might be an efficient way to further test the disturbance hypothesis.

Human disturbances may not only cause extinction of native species, but may also create novel niches for new hybrids that their parent taxa could not fill. With climate change, pure species may become maladapted, and hybrids could potentially fill in and to some level maintain ecological integrity of habitats. However, although exotic species introductions, with or without hybridization, would temporarily increase local or especially regional species diversity, the long-term ecological and evolutionary consequences of these introductions remain elusive. The long-term, positive effects of hybridization could include speciation through hybridization, which promotes diversity (e.g. Adams *et al.*, 2011). On the other hand, the long-term, negative impacts of hybridization could be far reaching, as hybridization could disrupt local adaptation, leading to genomic extinction (Rhymer & Simberloff, 1996).

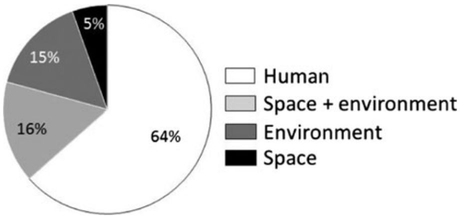

Figure 5 Results from partial regression analyses: human factors accounted for the largest amount (64%) of the total spatial variation in hybrid richness across the 3107 counties in the contiguous United States, followed by space–environment interaction, environmental factors alone and space. Here, 'space' variables include area, latitude and longitude; 'human' variables include years in the Union and population density; 'environment' variables include mean annual precipitation, mean annual temperature, potential evapotranspiration (PET), elevation and glaciation.

Invasion by hybrids is a growing problem across the globe. Possible mechanisms explaining the success of hybrid invasions are many; these include the following: (1) the acquisition of new and more adaptive traits as well as the continued improvement of existing traits (Ellstrand & Schierenbeck, 2000; Hovick *et al.*, 2012), all of which could improve the ability of the hybrid to colonize, especially in human-created novel niches (e.g. earlier emergence, higher fecundity and increased seed number; Rejmánek & Richardson, 1996); (2) reduced competition due to hybrids either being more aggressive in highly disturbed areas or being able to use niches that differ from those of native species due to their possession of novel traits and phenologies; and (3) higher efficiency of energy use than native species (e.g. Wu *et al.*, 2013).

On the other hand, not all hybrids are invasive. For early detection of invasive hybrids, one should assume that a time-lag may exist before invasiveness or fitness becomes apparent (after an initial depauperate time or bottleneck in many colonizing or invading populations). Most hybrids resulting from biological invasions are newly formed; thus, their invasiveness (and short- versus long-term fitness) and conservation values need sufficient time to be assessed. Careful evaluation of all hybrids, especially the parents' taxonomic groups and nature of disturbance in new habitats where future human impacts would increase, is needed. The outcome of such evaluations may reveal the need for species- or hybrid-specific conservation efforts.

Some taxonomic or phylogenetic groups (e.g. families, genera) in a given flora have proportionally more hybrids than others (Table S3; see also Ellstrand *et al.*, 1996; Rieseberg & Wendel, 1993). Whitney *et al.* (2010) found that the possibility of hybrid formation within a specific taxon depends on the taxon's intrinsic properties (e.g. phylogeny, functional traits). However, plant families more prone to hybridization (Ellstrand *et al.*, 1996) do not necessarily contain correspondingly more invasive hybrids (Whitney *et al.*, 2009). Future work should pay special attention to: (1) the life history and genetic traits of various types of hybrids (Rejmánek & Richardson, 1996; Ricklefs *et al.*, 2008), (2) the specific locations where the hybrids are formed, (3) the drivers of hybridization that are common across both taxonomic groups (Whitney *et al.*, 2010) and geographic regions, including hybrid zones (Barton, 2001), and (4) the possible effects at multiple trophic levels (e.g. animals, pathogens, diseases; Whitham, 1989).

In short, studies on hybrids, especially those involving biological invasions and human disturbances, are on the rise (Hovick *et al.*, 2012). Next-generation sequencing (NGS) has great potential to effectively and accurately identify hybrids and their origins. Better-designed studies are clearly needed to examine how disturbance agents such as climate change and land use affect hybridization and determine whether hybridization will promote biotic (genetic) homogenization (Olden, 2006) or have other ecological and evolutionary consequences.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Box plots showing the numbers of interspecific hybrid plants of three origins, i.e., native-native ($N \times N$), native-exotic ($N \times E$), and exotic-exotic ($E \times E$), across 3,107 counties in the contiguous United States.

Figure S2 Results of principal component analysis (PCA) showing strong correlations among several variables (e.g., temperature measures, population size and density).

Figure S3 Spatial autocorrelation coefficient (Moran's I) of all hybrid plants, $N \times N$, $N \times E$, and $E \times E$ across the conterminous continental US states.

Table S1 Results from multiple regression analyses showing the relationships between hybrid richness and selected social-physical in the 3107 counties across the conterminous United States as well as the relative contribution of space or spatial autocorrelation (bold-faced *F*- and *t*-values highlight the significant relationships at $P < 0.05$).

Table S2 Additional results regarding the distribution of hybrids among plant families in the United States.

Appendix S1 Examples of plant hybrids with at least one exotic parent (i.e. formed between exotics [$E \times E$] and between native and exotics [$N \times E$]) in the contiguous United States.

BIOSKETCH

Qinfeng Guo has broad interests in community ecology and biogeography. He is currently working on biodiversity patterns at various scales that may affect the process and patterns of biotic invasions and ecosystem functions. He also studies how life history traits and genetics may influence species invasiveness and how history and habitat characteristics may affect invasibility.

Author contributions: Q.G. conceived the ideas, analysed the data and wrote the paper.

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