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The formation of species pools: historical habitat abundance affects current local diversity

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ABSTRACT

Aim Explanations of biogeographic diversity patterns have emphasized the role of large-scale processes that determine species pools, whereas explanations of local patterns have not. We address the hypothesis that local diversity patterns are also primarily dependent on the size of the available species pools, which are expected to be large when the particular habitat type has been evolutionary more abundant, or in unproductive habitats due to shorter generation time and hence higher diversification rates.

Location The Canary Islands.

Methods We determined the geographic distribution and habitat requirements of all native vascular plant species in the Canary Islands. Species pools for each habitat type on particular islands were further split into two categories according to origin: either originating due to local diversification or due to natural immigration. The dependence of historical diversification and diversification rate on habitat type, area, age, altitude and distance to the mainland was tested with general linear mixed models weighed according to the Akaike information criterion.

Results The largest portion of the local variation in plant species diversity was attributed to the historic (pre-human) habitat area, although island age was also important. The diversification rate was higher in unproductive habitats of coastal scrub and summit vegetation.

Main conclusion Our study supports the species pool hypothesis, demonstrating that natural local patterns of species diversity in different habitats mirror the abundance of those particular habitats in evolutionary history. It also supports the community-level birth rate hypothesis, claiming that stressful conditions result in higher diversification rates. We conclude that much of the observed local variation in plant diversity can be attributed to the differing sizes of species pools evolved under particular habitat conditions, and that historic parameters are far more important determinants of local diversity than suggested by ecological theory.

Keywords

Canary islands, diversification, endemics, large-scale processes, plant species diversity, species pools.

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INTRODUCTION

Species diversity shows contrasting values both among biogeographic regions and locally within biogeographic regions (Huston, 1994; Ricklefs, 2004). Explanations of diversity variation at a biogeographic scale have relied on large-scale processes (Mittelbach *et al.*, 2007; de Aguiar *et al.*, 2009; Wang *et al.*, 2009).

For instance, the most thoroughly studied pattern in biogeography – the latitudinal diversity gradient – has been attributed to the ‘time and area hypothesis’, which maintains that tropical climates, being older and historically larger, have experienced more opportunity for diversification (Terborgh, 1973; Rosenzweig, 1995; Chown & Gaston, 2000; Fine & Ree, 2006). Although the potential role of large-scale processes in generating local

diversity patterns has been emphasized for a considerable time as well (Ricklefs, 1987; Cornell & Lawton, 1992; Zobel, 1992), this question has only recently garnered more theoretical interest (Ricklefs, 2006; Ricklefs, 2007; Harrison & Cornell, 2008; Ricklefs, 2008; Zobel & Pärtel, 2008). In particular, the role of historical factors in generating local patterns of species richness, e.g. change of diversity along edaphic and climatic gradients within a region, has been largely ignored.

The 'species pool hypothesis' in ecology is an analogous concept to the 'time and space hypothesis', aiming to address local diversity patterns through large-scale historical factors. This hypothesis suggests that more species are expected to occur in conditions that have been more abundant (in space or time) throughout evolutionary history (Hodgson, 1987; Taylor *et al.*, 1990; Schamp *et al.*, 2002). The predictions made by the species pool hypothesis are specific to a habitat type and do not consider diversity at the landscape level, where different habitat types co-occur.

The species pool hypothesis has received indirect support from large-scale studies. For example, the different local diversity–productivity relationships in the temperate zone and tropics (Pärtel *et al.*, 2007), as well as the locally different responses of plant communities to nitrogen fertilization at low or high regional temperatures (Clark *et al.*, 2007) can be attributed to the divergent evolutionary history of species pools present in different areas. For instance, productive habitats in tropical regions have been more prevalent throughout evolutionary history (Beerling, 1999; Wiens & Donoghue, 2004), while highly productive sites in the temperate zone are less common or are fairly young (Hodgson, 1987). Thus, one can expect that diversification in the tropics has been greater in abundant productive habitats, and in temperate regions in abundant unproductive habitats, and the locally different diversity in productive and unproductive habitats can be attributed to the different evolutionary history of respective species pools. Being the first to establish a direct link between evolutionary history and diversity, Harrison & Grace (2007) showed that the biogeographic affiliation of plant species is related to their distribution along productivity gradients, and local diversity patterns might reflect the different evolutionary histories of species pools in particular habitat types. However, there are no studies relating the number of species currently present in a habitat type with the historical commonness of the habitat.

Another explanation for the latitudinal diversity gradient in biogeography – 'the diversification rate hypothesis' – holds that tropical regions diversify faster due to higher rates of speciation, caused by increased opportunities for the evolution of reproductive isolation, faster molecular evolution or other mechanisms, or by lower extinction rates (Mittelbach *et al.*, 2007). When explaining the local between-habitat variability of diversity, an analogous concept was introduced by Grime (1979), who associated the high richness of semi-arid communities with higher rates of turnover in plant populations and accompanying rapid speciation. Bruun & Ejrnæs (2006) elaborated this idea and developed the hypothesis of 'community-level birth rate', which claims that the rate at which new individuals recruit and reach reproductive

maturity is highest in relatively unproductive habitats, resulting in higher speciation rates due to the shorter generation time under such conditions. However, one has to bear in mind that the explanations by both Grime (1979) and Bruun & Ejrnæs (2006) address situations in which the maximum diversity is observed in relatively unproductive environments, although such a pattern is not a ubiquitous phenomenon (Mittelbach *et al.*, 2001; Gillman & Wright, 2006; Laanisto *et al.*, 2008).

The paucity of studies supporting the species pool hypothesis and the community-level birth rate hypothesis is related to the lack of suitable model areas with communities from which there is sufficient background information on the origin of species. In particular, one would require areas containing locally radiated endemic species, because the diversity pattern of local endemics makes it possible to evaluate the role of evolutionary history in generating local diversity. Also, the presence of clearly distinguishable habitat types strongly facilitates an understanding of diversity patterns. Oceanic islands, where the flora and fauna is the result of species accumulation through time by chance dispersal from mainland sources or neighbouring islands, and *in situ* speciation and extinction, constitute a suitable locale for analysis of diversity patterns (Emerson & Kolm, 2005; Losos & Ricklefs, 2009), in contrast to mainland biogeographic areas which might have had historically different degrees of connectivity. In particular, the floristic history of the Canary Islands is well documented (Francisco-Ortega *et al.*, 1996), and detailed information on the distribution of habitat types has recently been made available (del Arco Aguilar, 2006). In addition, these islands also allow study of the diversity patterns of ancient immigrants.

In this communication we report on the legitimacy of the species pool hypothesis (analogous to the time and area hypothesis in biogeography) and community birth rate hypothesis (analogous to the diversification rate hypothesis in biogeography) in explaining current local diversity patterns, using the Canary Islands as a model system. We defined species pools for five main habitat types (subdesert coastal scrub; thermophilous forest; laurel forest; pine forest; and summit scrub; Juan *et al.*, 2000) on seven islands according to ecological requirements and distribution of species. We hypothesized that historical diversification (speciation minus extinction of single island endemics) is positively related both to habitat area and age; and that the diversification rate – the log-ratio of single island endemics compared with native species – differs among habitat types, being highest in relatively unproductive habitats. We also hypothesized that immigration (arrival of native non-endemic species minus local extinction) is positively related to the area and age of the habitat type, and negatively to the distance to the mainland.

MATERIALS AND METHODS

Study area

The Canarian Archipelago consists of seven major islands, with a total area of 7447 km², located in the North Atlantic Ocean off the coast of north-west Africa. The islands belong to the sub-

tropical Macaronesian biogeographic region. The archipelago originates from hotspot magmatism ranging in age from about 20 Ma for the eastern islands (Lanzarote and Fuerteventura) to < 2 Ma for the westernmost islands of La Palma and El Hierro (Juan *et al.*, 2000). Fuerteventura and Lanzarote were a single island during the Pleistocene and separation of these islands was as recent as 10,000 years ago (Whittaker *et al.*, 2008). Therefore we considered Fuerteventura and Lanzarote as a single island called Mahan.

The flora of the Canary Islands consists of 2036 vascular plant species from 515 genera and 171 families: 408 species are native non-endemic species (ancient immigrants, considered native or probably native) (Izquierdo *et al.*, 2004); 524 are endemic to the Canary Islands (endemics at the subspecies level are not considered); 1104 species are classified as introduced and probably introduced or have an uncertain status and thus were excluded from this study.

There are five distinct zonal terrestrial habitats in the Canary Islands (Juan *et al.*, 2000): subdesert coastal scrub (found on all seven islands); thermophilous forest (seven islands); laurel forest (five islands); pine forest (four islands); and summit scrub (two islands). These habitats cover a wide range of productivity, from 0.12 kg m⁻² year⁻¹ for the subdesert coastal scrub to c. 1 kg m⁻² year⁻¹ for both the laurel and the windward pine forests (Fernández-Palacios, 1999). Thus, the productivity is unimodally related to altitude on the islands.

Coastal scrub

Situated between 0 and 400 m a.s.l., this type covered half the archipelago area (4172 km²) prior to human settlement. Its species pool consists of 484 native species, 234 of which are endemics. It is an arid to semi-arid vegetation zone, with low precipitation (0–250 mm year⁻¹) and high average temperature (> 20 °C); and as coastal habitat, there is abundant sunshine, wind and salinity. Therefore, many plant species are succulent, grow in patches and overall productivity is relatively low (net primary productivity (NPP) = 0.12 kg m⁻² year⁻¹) (Fernández-Palacios, 1999).

Thermophilous forest

The total original area of this habitat is 969 km². Thermophilous forest can vary between semi-arid and humid with annual precipitation of 300–700 mm and an average temperature of 15–19 °C, depending on exposure and elevation (habitat belts 200–600 m a.s.l.). The native species pool of thermophilous forest contains 349 species, of which 219 are endemics. This ecosystem is assumed to have a lower NPP than laurel forest, but empirical data are lacking.

Laurel forest

These forests with a total original area of 951 km² and total native species pool of 319 species (149 endemics) are located between 600 and 1200 m a.s.l. on the north and east sides of

higher islands, where they are strongly affected by wet trade winds resulting in high precipitation (c. 1000 mm year⁻¹) and relatively low temperatures (annual average 13–18 °C). This habitat type has the highest productivity (Fernández-Palacios, 1999), with a NPP of c. 1 kg m⁻² year⁻¹.

Pine forest

This habitat is situated at 700–2300 m a.s.l., where a dry Mediterranean climate predominates – precipitation is very variable depending on the slope, ranging from 400 mm year⁻¹ (leeward slopes) to 1500 mm year⁻¹ (windward slopes) and average annual temperature is 10–15 °C. Pine forests originally covered 1077 km², and in contrast to the diverse laurel forest they are dominated by one tree species – an endemic Canary Island pine (*Pinus canariensis*). Yet the understorey is fairly species rich – the total native species pool consists of 224 species, of which 123 are endemics. Productivity is highly variable depending on the slope where the pine forest is located, with NPP ranging from c. 0.4 (leeward slopes) to 1 kg m⁻² year⁻¹ (windward slopes) (Fernández-Palacios, 1999).

Summit scrub

This is a high-mountain cushion-like scrub at 2000–3000 m a.s.l. Such altitudes are present only on Tenerife and La Palma, where this habitat type occupies 259 km². Annual temperature is low (5–10 °C) and frost is frequent. The diurnal temperature range is large. Most precipitation (c. 500 mm) falls as snow. This habitat contains a total native species pool of 89 species, 52 of which are endemics.

Details of data and statistics

We compiled species pools (omitting subspecies) for each habitat type on particular islands by assigning all native species to at least one habitat type. Species pools were further split into two categories according to origin: either originating due to local diversification (single island endemics, mostly neo-endemics) or due to natural immigration (native non-endemic species, also occurring on other islands and regions). Historical diversification was defined as speciation minus extinction of single-island endemics and measured as the currently known number of single-island endemics. We did not include the so-called multi-island endemics (Canary endemics present on more than one island) in this study because the exact location of their speciation is unknown. In each habitat, multi-island endemics outnumber single-island endemics many-fold. There is a theoretical possibility that some single-island endemic species originate from another island where they became extinct. This scenario, however, is probably uncommon and does not contradict the main results. For statistical analysis species numbers were log-transformed.

Diversification rates were obtained by calculating a log-ratio of single-island endemics compared with native species. The proportion of endemic species to native species was used by

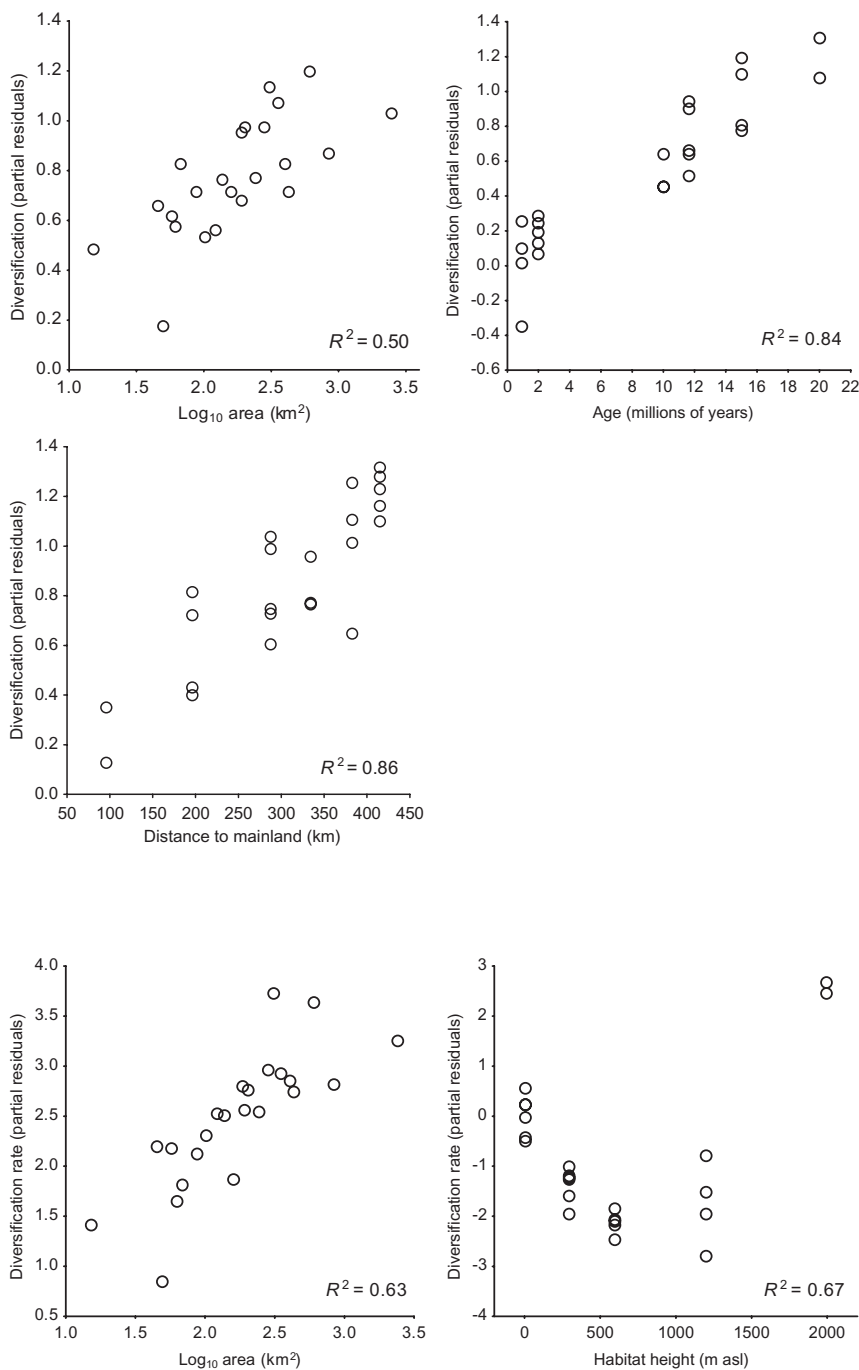


Figure 1 Relationships (partial residuals) between historical diversification (speciation minus extinction, measured as the currently known number of single-island endemics) and log habitat area, island age and distance to the mainland, given that independent variables listed on other subgraphs are also in the model. Each data point represents a particular habitat type on one island (in each graph $n = 23$; R^2 is given to quantify the linear relationships on the graph).

Figure 2 Relationship (partial residuals) between diversification rate (a log-ratio of single-island endemics compared with non-endemic native species) and log habitat area, and different habitats across elevation from lowest to highest: summit scrub, thermophilous forest, laurel forest, pine forest and summit scrub, given that independent variables listed on other subgraphs are also in the model. Each data point represents a particular habitat type on one island (in each graph $n = 23$; R^2 is given to quantify the relationships on the graph: linear relationship for area, quadratic relationship for height).

Emerson & Kolm (2005), and possible pitfalls of using this characteristic have been discussed elsewhere (Cadena *et al.*, 2005; Emerson & Kolm, 2007; Pereira *et al.*, 2007; Whittaker *et al.*, 2007). Chen & He (2009) showed in their theoretical model that the proportion of endemics is linearly related to the speciation rate. We also compared this index with speciation rates in different habitats (Paradis & Gavrillets, 2005) from robust phylogenies of endemic species (see Appendix S1 in Supporting Information) and both indices were strongly related. Because we have no information on extinctions, we use the proportion of island endemics as the most suitable proxy to describe variation in speciation rate, being aware of limitations of this character-

istic. Here we use only log-ratios since these are obtained from the same type of data as other parameters.

Diversity of ancient immigrants was measured as the currently known number of non-endemic native species. The total species pool was calculated as a sum of historical diversification and diversity of ancient immigrants.

We calculated habitat areas using GIS-based maps of the potential distribution areas of natural vegetation types (del Arco Aguilar, 2006), assigning the mapped phytosociological units to the five major habitats distinguished in this study, and with consideration that current vegetation patterns are strongly modified by human impact. Habitat age was defined, in a sim-

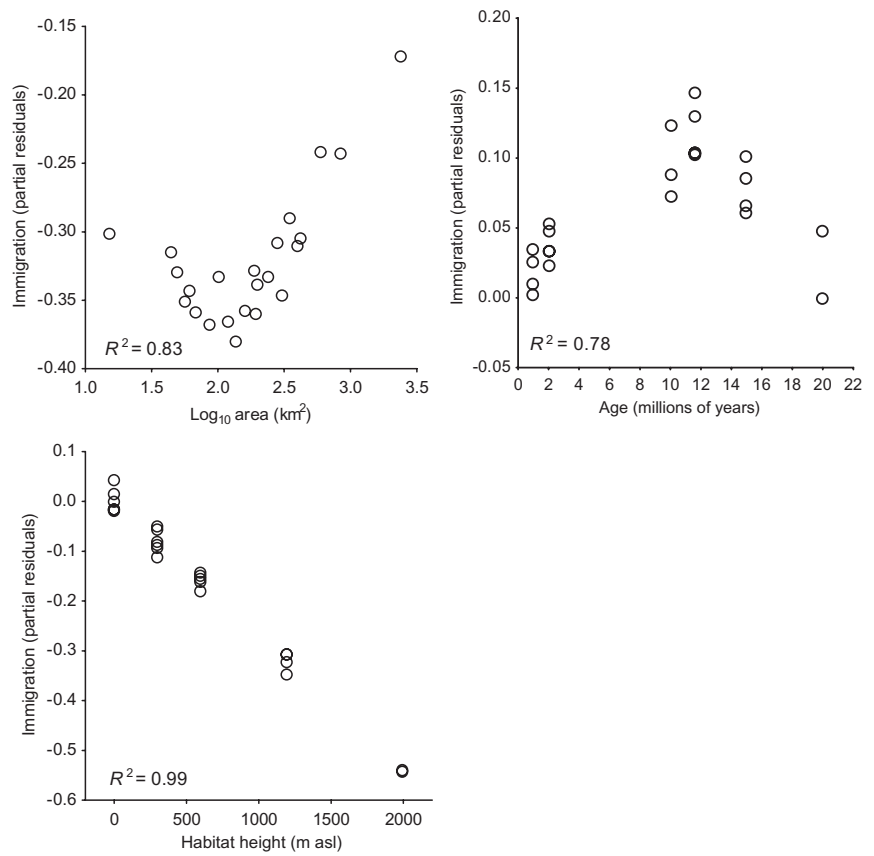


Figure 3 Relationships (partial residuals) between diversity of ancient immigrants (the currently known number of non-endemic native species) and log habitat area, island age and habitat elevation, given that independent variables listed on other subgraphs are also in the model. Each data point represents a particular habitat type on one island (in each graph $n = 23$; R^2 is given to quantify the relationships on the graph: linear relationship for height, quadratic relationships for area and age).

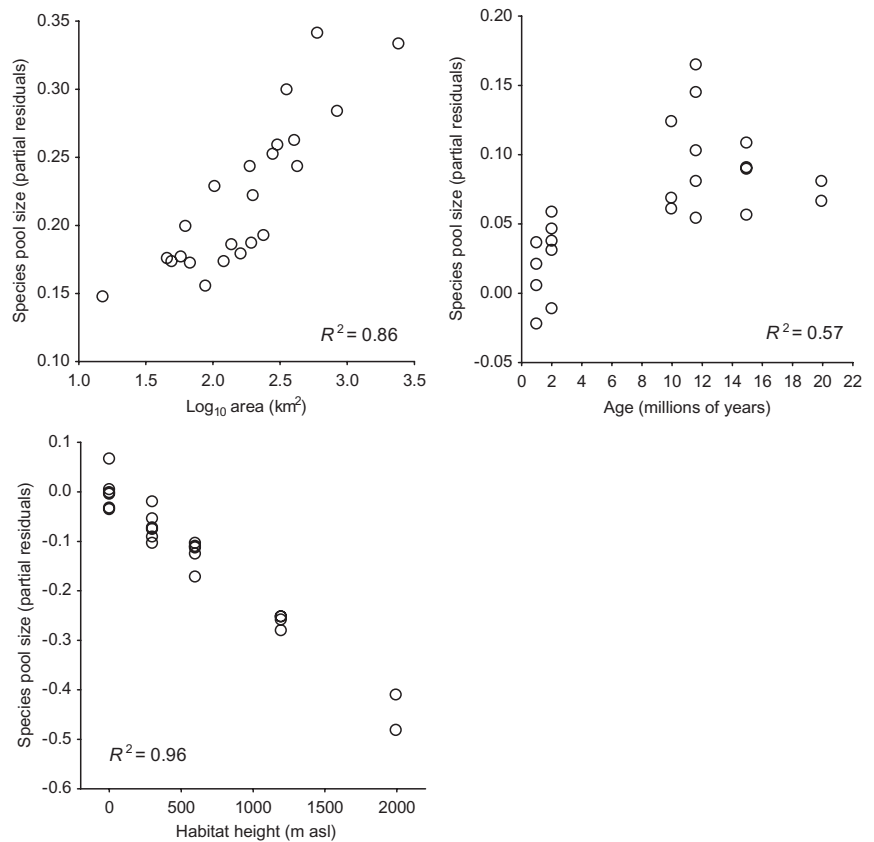


Figure 4 Relationships (partial residuals) between total native species pool size (a sum of numbers of endemic and non-endemic native species), and log habitat area, island age and habitat elevation, given that independent variables listed on other subgraphs are also in the model. Each data point represents a particular habitat type on one island (in each graph $n = 23$; R^2 is given to quantify the relationships on the graph: linear relationships for area and height, quadratic relationship for age).

plified manner, as island subaerial age (Juan *et al.*, 2000), since sufficient detailed information is lacking on the geological history of each island. Lower altitude limits of particular habitat zones were included to describe environmental and productivity gradients. Distance to the mainland was measured from a digital map as a shortest distance between coastlines.

Historical diversification, diversification rate, diversity of ancient immigrants and the total species pool size were used as dependent variables. Habitat area (log-transformed for normality), age, altitude and distance to the mainland were used as fixed factors in general linear mixed models (GLMMs; SAS 'proc mixed' procedure; Littell *et al.*, 1996). Island and habitat type were included as random factors, because specific local factors might have caused variation in species pool sizes for different habitats and islands. In the model addressing diversification rate, habitat type was included as a fixed factor.

All possible candidate models (all combinations of variables, continuous variables both linear and linear + quadratic terms) were weighted according to corrected Akaike information criterion (AICc) (Burnham & Anderson, 2002). All models with Akaike information criteria compared are presented in Table S1. We selected the best model from all candidates. For comparison, we provide general linear model statistics for the best models, which were always significant at $P < 0.05$ (Table S2). Potential effects of spatial autocorrelation were tested from the residual Moran's I and were not significant in any models presented.

To illustrate relationships with the most informative variables, we used partial residual graphs from the best model to show the effects of single factors given other independent variables also in the model (Larsen & McCleary, 1972). The relationships on the graphs are quantified by R^2 but detailed statistics are found in Table S2.

RESULTS

The flora of the Canary Islands consists of 2036 vascular plant species of which 524 are endemic to the Canary Islands, 408 are native non-endemic species and 1104 species are introduced. We compiled species pools for each habitat type on particular islands by assigning all native species – notably single-island endemics and native non-endemic species – to at least one habitat type. General linear models were used to determine the relationships between diversity, historical area and habitat age, altitude and distance to the mainland and all possible candidate models were weighted according to AICc (Table S1). We selected the best model from all candidates listed in Table S1 (the best model for each case is presented in Table S2) and used partial residual plots from the best model to show the relationship between a given independent variable and the response variable, given that other independent variables are also in the model.

Historical diversification, measured as the currently known number of single-island endemics, was linearly positively dependent on habitat area, island age and distance to the mainland (Fig. 1). According to model statistics (F and P -values, Table S2), area was the most important factor, followed by island age and distance to the mainland. The diversification rate – a

log-ratio of single-island endemics compared with non-endemic native species – was linearly positively dependent on habitat area (Fig. 2). There is a U-shaped relationship between diversification rate and altitude – the diversification rate is highest in unproductive habitat types, e.g. coastal scrub or summit, whereas productive habitats, e.g. laurel and pine forest, exhibit lower rates. Diversity of ancient immigrants, estimated as the currently known number of non-endemic native species, was nonlinearly positively dependent on habitat area, unimodally with island age and negatively linearly on elevation (Fig. 3). Habitat elevation and age are more important than habitat area in this case (Table S2). The second best model contained all the parameters of the first model, but the relationship with elevation is nonlinear. The total species pool size – the sum of the numbers of endemic and non-endemic native species – was linearly positively dependent on habitat area, nonlinearly positively on habitat age, and negatively linearly on elevation (Fig. 4). Elevation was the strongest explanatory variable in this model, followed by area and age (Table S2). The second best model contains all the parameters of the first model, but exhibits a nonlinearly positive relationship to habitat area. Consequently, the possible evolutionary mechanisms underlying local diversity patterns mentioned above remain important when the overall local diversity, including plant species of different historical origin, is addressed.

DISCUSSION

Many studies have reported positive relationships between habitat area and species diversity (Lomolino, 2000; Bellwood & Hughes, 2001; Triantis *et al.*, 2008), but because of confounding effects of evolutionary history, dispersal limitation and local ecological factors like heterogeneity of the area, these relationships sometimes tell us little about the mechanism generating the local diversity pattern. Our study is the first to report a positive relationship between the historical area of a habitat and the number of local endemics. In particular, the pattern of historic diversification on the Canary Islands affirms the species pool hypothesis (Taylor *et al.*, 1990) – the current number of endemic species characteristic of a particular habitat type in an island is positively related to the historic area of this habitat type.

Although the relationship described above does not allow us to draw conclusions about the particular processes underlying this pattern, different authors have shown that possible mechanisms can be manifold. For instance, habitats with a larger area are presumably physiographically and ecologically more heterogeneous and therefore provide more opportunity for local isolation and speciation (Rosenzweig, 1995; Lomolino, 2000; Losos & Schluter, 2000; Fine & Ree, 2006; Losos & Ricklefs, 2009). Larger population size associated with larger areas might also depress extinction rates and hence increase historical diversification (Chown & Gaston, 2000; Ricklefs, 2007).

Island age was positively related to historical diversification as well, indicating that longer periods available for evolution can result in greater local diversification. This relationship is enhanced by the fact that the Canary Islands have experienced a

relatively stable climate compared to mainland temperate and Mediterranean Europe, at least since the Pleistocene (Edmunds, 2001), although drier and wetter periods occurred on islands closer to the continent (Ortiz *et al.*, 2006). Whereas habitat areas have varied to a certain degree on each island during geological genesis, the actual potential habitat areas reflect the overall historical abundance of the habitat.

The area and time hypothesis, holding that tropical areas are historically larger and allow more opportunity for diversification, has found support with respect to latitudinal diversity gradients on a global scale (Chown & Gaston, 2000; Fine & Ree, 2006; Mittelbach *et al.*, 2007). The analogous species pool hypothesis, examining local variation of diversity (Taylor *et al.*, 1990), has not yet been supported by observational evidence. Our study is the first to show that historical area, as well as habitat age, is responsible for present-day local variation of species diversity.

We record higher diversification rates in habitats with lower productivity. Whereas a differential diversification rate can obviously partly account for latitudinal diversity gradients (Mittelbach *et al.*, 2007; Harrison & Cornell, 2008), our results give some indirect support to the analogous 'community birth rate hypothesis' (Bruun & Ejrnæs, 2006), claiming that speciation rates are higher and more species accumulate *in situ* in unproductive environments due to the shorter mean generation time. Our results should, however, be interpreted with caution in the context described above, because the diversification rate as used by us, although expected to be positively dependent on speciation rate (Chen & He, 2009), is certainly not an estimate of speciation rate *per se*. More precise information on true speciation rates, either taking into account the historical extinctions or relying on more thorough molecular phylogenies, is required to fully disentangle the possible evolutionary background of the variation described above.

The diversity of ancient immigrants varies similarly to historical diversification – more species are observed in habitat types with larger areas, although the relationship is not linear. Two mechanisms might account for this pattern. First, the species composition of immigrants reflects the structure of species pools in the source areas, which might be analogous to those in the Canary Islands and provide more potential immigrants for habitat conditions that are also common in the target area (Médail & Quézel, 1999). Also, the strong influence of elevation on ancient immigrants may reflect the abundance and distance of similar habitat types on the African continent as well (M. Steinbauer, pers. comm.). Second, larger areas might simply be more likely to experience random dispersal events (Whittaker & Fernández-Palacios, 2007). Unimodal relationships between the number of ancient immigrants and island age adhere to the general dynamic theory of oceanic island biogeography (Whittaker *et al.*, 2008), which claims that mid-aged islands have the greatest topographic complexity and possibly large vacant niche space.

Biogeographic patterns of species diversity are often explained in the context of evolutionary and historical processes, whereas explanation of the local variation of richness

has paid less attention to large-scale processes. The theory of species coexistence, concerning diversity maintenance in the same spatial region (Chesson, 2000), has been a central concept in community theory for decades but has not shown its power in explaining observed diversity patterns. The implication that local diversity is often not locally determined, and elucidation of local patterns in diversity requires concepts that include large-scale ecological and evolutionary processes expressed in a geographic setting (Ackerly, 2003; Wiens & Donoghue, 2004; Ricklefs, 2007; Ricklefs, 2008), is frequently accepted in theory, but with respect to empirical studies, the first steps in incorporating historical processes when explaining local patterns have been made only recently (Harrison & Grace, 2007). We argue that disentangling history-related, ecologically driven and human-induced variability in species diversity patterns is a challenging task. Oceanic archipelagos offer unique study systems in which part of the local diversity is determined locally through history-related processes like *in situ* diversification. The study of the flora of the Canary Islands supports the species pool hypothesis and demonstrates that natural patterns of species diversity mirror the abundance of those particular habitats in evolutionary history. It also supports to a certain extent the community-level birth rate hypothesis, claiming that stressful conditions result in higher diversification rates. We conclude that much of the observed local variation in plant diversity can be attributed to the differing sizes of species pools evolved under particular habitat conditions.

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SUPPORTING INFORMATION

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

Table S1 All candidate general linear mixed models (GLMMs) used for data analysis, ranked according to the corrected Akaike information criterion (AICc).

Table S2 General linear mixed models (GLMMs) for historical diversification, diversification rate, immigration and the size of the total species pool ranked according to the corrected Akaike information criterion (AICc).

Appendix S1 Speciation rate calculations.

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BIOSKETCH

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