Frequency Dependence and Ecological Drift Shape Coexistence of Species with Similar Niches

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ABSTRACT: The coexistence of ecologically similar species might be counteracted by ecological drift and demographic stochasticity, both of which erode local diversity. With niche differentiation, species can be maintained through performance trade-offs between environments, but trade-offs are difficult to invoke for species with similar ecological niches. Such similar species might then go locally extinct due to stochastic ecological drift, but there is little empirical evidence for such processes. Previous studies have relied on biogeographical surveys and inferred process from pattern, while experimental field investigations of ecological drift are rare. Mechanisms preserving local species diversity, such as frequency dependence (e.g., rare-species advantages), can oppose local ecological drift, but the combined effects of ecological drift and such counteracting forces have seldom been investigated. Here, we investigate mechanisms between coexistence of ecologically similar but strongly sexually differentiated damselfly species (*Calopteryx virgo* and *Calopteryx splendens*). Combining field surveys, behavioral observations, experimental manipulations of species frequencies and densities, and simulation modeling, we demonstrate that species coexistence is shaped by the opposing forces of ecological drift and negative frequency dependence (rare-species advantage), generated by interference competition. Stochastic and deterministic processes therefore jointly shape coexistence. The role of negative frequency dependence in delaying the loss of ecologically similar species, such as those formed by sexual selection, should therefore be considered in community assembly, macroecology, macroevolution, and biogeography.

Keywords: ecological drift, frequency dependence, neutral theory, sexual selection, speciation, unified neutral theory of biodiversity.

Introduction

Understanding the causes of species coexistence and the dynamics of local and regional species assemblages are classic questions in ecology and evolutionary biology. Much previous research assumes that species must differ sufficiently in their ecological niches to be able to coexist (Peterson et al. 2011). Performance trade-offs between different environments can then explain species coexistence (Chesson 2000). However, classic niche-based models for species coexistence have been challenged by the unified neutral theory of biodiversity (Hubbell 2001; Rosindell et al. 2012). The neutral theory assumes that species are ecologically equivalent and suggests that species coexistence is counteracted by ecological drift that causes local species extinctions (Hubbell 2001; Rosindell et al. 2011, 2012).

The assumptions behind the neutral theory have been criticized (Ricklefs 2006, 2012). Empirical investigations of species abundances of coral reefs (Dornelas et al. 2006), continental birds (Ricklefs 2006), and regional rainforest tree communities (Wills et al. 2006) are inconsistent with neutral models. In these cases, ecological drift is too slow to explain community dynamics (Ricklefs 2006), and in other systems species are maintained longer than expected under pure neutrality (Wills et al. 2006). Defenders of the neutral theory have countered that it can be useful as an approximation of species-abundance patterns or a null model (Rosindell et al. 2012), similar to the neutral theory in population genetics (Orrock and Fletcher 2005; Hu et al. 2006). Moreover, species in some clades show weak ecological differentiation (Svensson 2012; Wellenreuther et al. 2012), yet they still co-occur (McPeek and Brown 2000; Siepielski et al. 2010). These and other findings have stimulated stochastic niche theory (Tilman 2004), the "nearly neutral" theory of biodiversity (He et al. 2012), and models aiming to reconcile niche and neutral perspectives (Adler et al. 2007). However, our understanding of how neutral and deterministic processes interact in nature is limited because few experimental investigations have yet been carried out (Adler et al. 2007; Harpole and Suding 2007). Most investigations are purely correlative and use species-abundance distributions alone to infer underlying processes (Hubbell 2001; McGill 2003; McGill et al. 2006). Theory and limited empirical data suggest that ecological drift can operate even if species are not entirely neutral (Orrock and Fletcher

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2005; Adler et al. 2007; Orrock and Watling 2010; Gilbert and Levine 2017).

One limitation of previous work is that researchers have focused on the dynamics of multispecies communities over long evolutionary time periods (e.g., millions of years) and large geographical scales, such as continents (Ricklefs 2006; Ricklefs and Renner 2012). The inferences from such large-scale correlative studies are limited, however, since ecological drift and interspecific interactions are highly localized processes that should operate at smaller spatial scales within larger metacommunities. As a complementary and alternative approach to such studies of species diversity over continent-wide scales (Ricklefs 2006; Ricklefs and Renner 2012), one could instead more directly study the dynamics of ecological drift on smaller geographic scales involving fewer interacting species, for instance, at high latitudes or high altitudes where species richness is typically low (Brown 2014; Ghosh-Harihar and Price 2014). Smaller-scale studies could be combined with direct experimental manipulations to obtain mechanistic data on species interactions. Mechanistic studies should provide more sensitive tests of ecological drift among interacting species. We emphasize that ecological drift can operate even if species are not completely ecologically equivalent and even if one does not totally embrace neutral theory. Just like genetic drift also operates on nonneutral alleles under selection in population genetics (albeit a weaker force than for neutral alleles), ecological drift can still operate on species that are not strictly neutral. There is thus a continuum between strict neutrality and deterministic (niche-based) models, and ecological drift can operate under a broad range of community conditions (Hubbell 2001, 2005; Hu et al. 2006; Vellend 2010, He et al. 2012).

Here we present data from an integrative study aiming to overcome some of the limitations of previous studies. We combine observational data on distributions, mesocosms, field experiments, and modeling to investigate how ecological drift and deterministic factors influence coexistence of congeneric and ecologically similar *Calopteryx* damselfly species at high latitudes near these two species' northern range limits (Svensson 2012; Wellenreuther et al. 2012). Odonates (dragonflies and damselflies) are generalist predators with little detectable climatic (Wellenreuther et al. 2012), thermal (Svensson 2012), or trophic niche differentiation (Siepielski et al. 2010), neither at the larval nor at the adult stage, yet many species co-occur locally (McPeek and Brown 2000). Ecological similarity of closely related odonate species partly reflects the fact that the evolution of reproductive isolation and speciation in this group is largely driven by sexual selection, rather than by niche divergence and ecological speciation (McPeek et al. 2008; Svensson 2012; Svensson and Waller 2013). Many strongly reproductively isolated but coexisting odonate species are ecologically similar, which raises questions about the mechanisms of species coexis-

tence (M'Gonigle et al. 2012) and which also has implications for some models that predict high extinction rates among newly formed ecologically similar species (Rosenblum et al. 2012). The high niche similarity of many odonate species challenges niche theory and raises the question, To what degree are species abundances influenced by ecological drift?

We focus on two interacting and regionally co-occurring species in this study: the banded demoiselle (*Calopteryx splendens*) and the beautiful demoiselle (*Calopteryx virgo*). The expected dynamics of stochastic ecological drift in such simple two-species communities is similar to the process of genetic drift at a single polymorphic locus with two alleles in classical population genetic theory (Hartl and Clark 1997; Hu et al. 2006). Using regional abundance data in the form of local species frequencies and densities from over 100 populations of these two species in Fennoscandia, we test two predictions from models of ecological drift. First, ecological drift should lead to the local loss of one or the other species from sympatric populations. This would be expected to result in a flattening of the distribution of species frequencies and eventually lead to a U-shaped distribution where sites become allopatric ("fixed") for one of the species or at least heavily dominated by one species. Thus, there should be few sympatric sites with equal frequency of the two species. Such a U-shaped distribution expected from ecological drift is analogous to the U-shaped allele frequency distribution in classic population genetic theory of the dynamics of two neutral alleles at a single locus subjected to genetic drift (Hartl and Clark 1997; Hu et al. 2006). A second prediction, shared between the population genetic theory of genetic drift and ecological drift of two ecologically similar species, is that large populations (or communities, in the case of ecological neutral theory) should lose variation (allelic richness or species diversity) more slowly than small populations (Hartl and Clark 1997; Orrock and Fletcher 2005; Orrock and Watling 2010). From this principle, we would expect sympatric sites, where both species co-occur, to have a larger community size (combined number of both species) than less diverse (allopatric) sites, where only one of the two species occurs.

These two predictions about ecological drift are limited since they rely only on biogeographical patterns and distribution data. To complement the observational approach described above, we therefore also carried out experiments in mesocosms and in the field to elucidate possible mechanisms underlying ecological drift and species interactions. First, we manipulated species frequencies and densities in large outdoor mesocosm experiments and recorded survival under different biotic conditions. Strict neutrality predicts no overall survival difference and complete ecological equivalence of these two species (i.e., no main effect of "species" in a statistical model; see Adler et al. 2007). Alternatively, these two species could respond differently to different biotic conditions (their own frequency or total density) due to, for

example, reproductive interference through male-male aggression (Grether et al. 2017; Shuker and Burdfield-Steel 2017). Such differential responses could reflect negative or positive frequency dependence interactions that can influence coexistence and the balance between ecological drift and deterministic (diversity-maintaining) forces (Chesson 2000; Adler et al. 2007). For instance, negative frequency dependence will maintain local diversity if rare species enjoy advantages in a community (Ayala 1971; Wills et al. 2006). Conversely, common species could enjoy advantages through positive frequency dependence, which would lead to the loss of local diversity but which might instead preserve species diversity on larger regional scales through priority effects (Fukami et al. 2007; M'Gonigle et al. 2012; De Meester et al. 2016). Positive frequency dependence has been suggested as a mechanism for maintaining species diversity of ecologically similar species that have been formed through sexual selection alone, without strong niche differentiation (M'Gonigle et al. 2012). We complemented our mesocosm experiments with field experiments aiming to investigate the role of male aggression avoidance as a possible fitness-equalizing factor (Chesson 2000; Adler et al. 2007) that could increase the scope for ecological drift and demographic stochasticity in this system. More specifically, we tested whether the subdominant species (*C. splendens*; see Tynkkynen et al. 2005) avoids aggression from the dominant species (*C. virgo*) in sympatry, thereby reducing the risk of competitive exclusion. Finally, we synthesize and integrate our findings from our biogeographical

survey and mesocosms and field experiments by using simulation models, where we explore how ecological drift and negative frequency dependence could jointly affect species coexistence in this system.

Material and Methods

Study Organisms

Calopterygid damselflies are sexually dimorphic insects characterized by large melanized wing patches in males (see inserted pictures in fig. 1A). These wing patches serve important functions in intra- and intersexual selection through male-male competition and female choice, respectively (Svensson et al. 2004, 2006, 2010; Verzijden and Svensson 2016). In northern Europe, where this study took place, the banded demoiselle (*Calopteryx splendens*) and the beautiful demoiselle (*Calopteryx virgo*) co-occur regionally and locally (Svensson et al. 2016). Melanized wing patches in Calopterygidae are targets of interspecific male-male aggression (Tynkkynen et al. 2005), function as sexual isolation characters between these co-occurring species (Svensson et al. 2007, 2010), and influence speciation rates (Svensson and Waller 2013). Apart from these interspecific differences in wing melanization, *C. splendens* and *C. virgo* are ecologically and morphologically very similar (Svensson and Friberg 2007), with largely overlapping climatic niches (Wellenreuther et al. 2012) and no detectable fine-scale thermal niche differentiation in sympatry (Svensson 2012). Thus, the genus *Calopteryx*, as with other damselfly
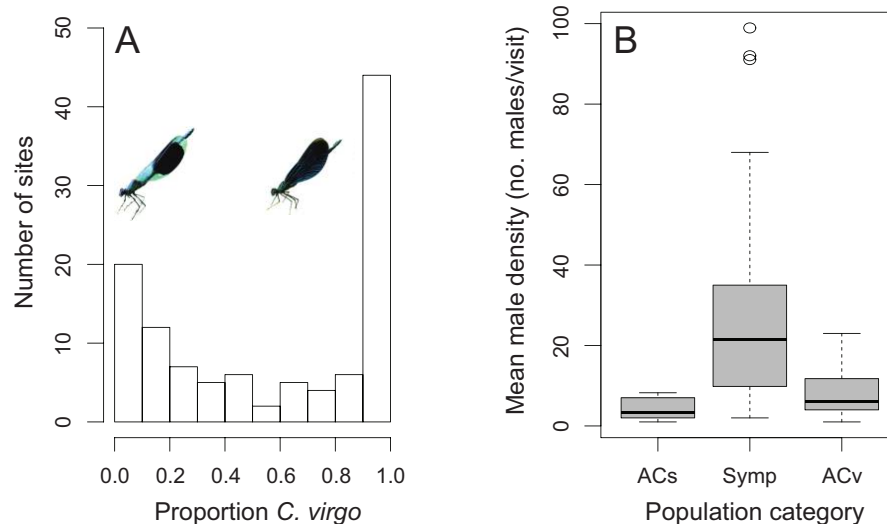
Figure 1: Local species frequencies of *Calopteryx* in Fennoscandia. Inserted figures in A, *Calopteryx virgo* has entirely melanized wings, and *Calopteryx splendens* has melanin patches covering only 50% of the wings. A, The proportion of *C. virgo* showing a U-shaped distribution across 111 sites across Fennoscandia (Wellenreuther et al. 2012), where it is either the common or the rare species. There are relatively few sites where both species are equally common. This U-shaped distribution is also seen if we restrict the analyses to the sympatric zone, excluding northern sites where *C. virgo* is allopatric (fig. B1, available online). B, Sympatric sites (Symp) have higher combined population densities (ANOVA: $F_{2,107} = 14.840$, $P < .001$) than allopatric *C. splendens* (ACs; Tukey: $P = .01$) and allopatric *C. virgo* sites (ACv; Tukey: $P < .001$). This difference is also significant when controlling for latitude and longitude (table A1, available online).

genera such as *Enallagma* (McPeek and Brown 2000; Siepielski et al. 2010), shows weak ecological niche differentiation. Congeneric odonate species are therefore ecologically highly similar, which should increase the scope for ecological drift and demographic stochasticity and reduce the strength of niche-based mechanisms for species coexistence (Chesson 2000; Hubbell 2001; Adler et al. 2007; Rosindell et al. 2011, 2012).

General Fieldwork Procedures

All fieldwork and experiments in this study were carried out during the summers of 2008–2015 in southern Sweden and Fennoscandia. Fieldwork was performed during the reproductive season of *Calopteryx*, which encompasses the summer months of June and July in Fennoscandia (Svensson et al. 2006; Svensson and Friberg 2007; Wellenreuther et al. 2012). Methodological procedures to quantify population abundances and species frequencies at local sites have been described in detail elsewhere (Svensson et al. 2010). Briefly, we recorded the number of observed males and females of both species (in the case of sympatric sites) or the number of *C. splendens* or *C. virgo* (in the case of allopatric sites) along 100-m-long transects in rivers in Sweden and Finland. Parts of these species abundance data have previously been used by us in combination with other species occurrence information from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org) to compare climatic niches of these two congeneric species (Wellenreuther et al. 2012). In our previous work, we used species abundance data from both the field and GBIF to quantify climatic niches separately for each species (Wellenreuther et al. 2012), but we did not present any data on local species frequency variation or local densities in relation to whether sites were sympatric or allopatric. Here, we take our previous work a step forward and present data on local species frequency variation and local density variation between different sites, both in Fennoscandia at large (fig. 1A) and in the sympatric zone of southern Sweden (fig. B1; figs. B1, C1–C3, D1 are available online). In southern Sweden, *C. splendens* and *C. virgo* are sympatric up to the northern range limit Limes Norrlandicus near Dalälven in the Swedish provinces of Uppland and Västmanland (Dijkstra and Lewington 2006; Wellenreuther et al. 2012). Our northernmost sampled population in the sympatric region of southern Sweden comes from the province of Uppland. The total number of sites that are included in this study is 111, adding information on 99 sites to the 12 sites that we have published before (Svensson et al. 2010; Wellenreuther et al. 2010).

Manipulations of Species Densities and Frequencies in Mesocosm Experiments

In the summers of 2014 and 2015 (June and July), we performed experimental manipulations of species densities and frequencies of *C. splendens* and *C. virgo* in large outdoor cages (3 m × 3 m × 3 m = 27 m³) at Stensoffa Ecological Field Station, located 20 km east of Lund in southern Sweden. These large outdoor cages have been used in previous experimental studies on another species of damselfly (*Ischnura elegans*), and the general protocols are described in more detail elsewhere (Takahashi et al. 2014). Each cage contained natural vegetation and two water containers to mimic natural damselfly habitat conditions as closely as possible. The basic rationale for these experiments was to create a common physical environment for both *Calopteryx* species, where subtle micro-environmental niche differences between these species were deliberately minimized. Hence, species-specific survival effects in these experiments should largely be attributed to density- and frequency-dependent effects caused by intra- and interspecific interactions (i.e., interference competition), rather than to subtle microenvironmental niche differences. Although such subtle microenvironmental niche differences might exist in nature, we have not detected them in our previous studies in the zone of sympatry (Svensson 2012; Wellenreuther et al. 2012). Our experiments therefore aimed to investigate the role of density and frequency dependence in maintaining species that are inhabiting a similar physical environment and that share a single underlying resource (McPeek 2012).

We caught *C. splendens* and *C. virgo* males and females from two sympatric nearby populations (Klingavälsåns Naturreservat and Omma at Åsumsån). In this study, we report data only on male survival and aggression behaviors. General ecological information about species compositions, geographic positions, and coordinates for these two *Calopteryx* sites have been presented elsewhere (Svensson et al. 2010, 2014). The *C. splendens* populations at these two sites are genetically similar, suggesting a high degree of gene flow and/or recent divergence, which is expected, as they belong to the same metapopulation (Svensson et al. 2014). Nevertheless, males and females from these two sympatric populations were not mixed but kept in separate experimental sessions. Field-caught damselflies were transported to Stensoffa Field Station in small cylindrical netting containers. At the field station, damselflies were marked individually with acrylic paint on the last abdominal segments with a unique three-color combination. Marked individuals were subsequently released in our outdoor cages in various frequency and density combinations (see further below). Small insects could naturally enter through the mesh (2–4 mm) of these cages, whereas *Calopteryx* damselflies could not escape due to their large size (>40 mm). The small prey insects (mainly mosquitoes, flies, and small moths) served as a natural source of food for the damselflies, which are generalist predators (Corbet 1999). Our marked individuals were frequently seen catching and eating this prey during our daily cage visits. During daily cage visits, we recorded the identity of all surviving damselflies and the species composition of the cage. After 7 days we terminated the experiments, and

by then usually most damselflies had died. Damselfly longevities in these cages are similar to the longevities that we have estimated in natural field populations of *C. splendens* (Svensson et al. 2006; Waller and Svensson 2016).

Experimental cages ($N = 8$ in total), identical in size, were randomly assigned to the different treatments. Treatments were rotated between these eight cages. Mean daily temperatures were recorded for each cage using temperature loggers (iButtons). Starting in 2014, we used three sympatric frequency treatments (25%, 50%, and 75% *C. virgo*) and two density treatments (low [$N = 16$ males per cage] and high [$N = 24$ males per cage], both species combined). Thus, we had a completely replicated factorial design for the sympatric treatments with six unique (three frequencies × two densities) environmental conditions. We complemented these sympatric treatments with the allopatric *C. splendens* combination (100% *C. splendens*) and the allopatric *C. virgo* combination (100% *C. virgo*) in 2014 and 2015. Intrinsic species survival differences and species-specific differential responses to the density and frequency manipulations could be statistically analyzed only for the three sympatric treatments. We incorporated the allopatric frequency treatment in within-species tests, together with the three sympatric frequency treatments (four unique frequency treatments), along with the two density treatments (low and high; see above). Again, we used a complete factorial design with eight unique (four frequencies × two densities) environmental conditions.

All males in these experiments were sexually mature, judged by the stiffness of their wings. In addition to the males, we also released three females of each species to stimulate male territoriality and male-male intra- and interspecific competition. Operational sex ratios within this range (3/27 to 3/7; i.e., 57%–89% males) are similar to the natural operational sex ratio range observed in the field (E. I. Svensson, personal observations). Female densities (number of females/m³) were thus equal between the high- and the low-density treatments, but the sex ratios differed (by necessity). However, we assume that female density and thus male-female encounter rate by males is more important than sex ratio for the outcome of these experiments.

Field Experiments on Male Intra- and Interspecific Aggression

In the summers of 2010 and 2012, we performed field experiments aimed at quantifying *C. splendens* male aggression directed toward con- and heterospecific males in allopatry and sympatry. We use *C. splendens* (the subdominant species) as our target species, as our goal was to understand how the subdominant species would cope with a superior and aggressive competitor (*C. virgo*; see Tynkkynen et al. 2004, 2005), potentially through compensatory behaviors. We used field tethering experiments similar to the procedures that we have used

previously to quantify female mating responses to con- and heterospecific males (Svensson et al. 2010). We tied a *C. splendens* male or a *C. virgo* male to a thread that was in turn tied to a 1.5-m-long bamboo stick (Svensson et al. 2010). We then introduced a number of con- and heterospecific males to territorial *C. splendens* males in two allopatric populations (Höje Å: Värpinge and Tolångaån: Näsby) and two sympatric populations (Klingavälsåns Naturreservat and Klingavälsån: Sövdemölla) in the province of Skåne, southern Sweden. The geographic locations and coordinates of these populations are provided elsewhere (Svensson et al. 2014).

We recorded the territory owner's behavioral reactions on a four-point scale, ranging from low to high aggression: 1 = "flying away"; 2 = "remaining still" (after 1 min of presentation time); 3 = "threatening wing display"; 4 = "male attack." Each tethered damselfly was presented three times to each individual *C. splendens* male, and the average score for each male constituted one single data point in the statistical analyses. We analyzed these data using a two-way ANOVA, with site (four levels) and species (of intruder male) as main factors and year included as a fixed-factor control variable.

We followed up these aggression experiments with a phenotypic manipulation experiment aimed at clarifying the role of wing pigmentation as a cue in *C. splendens* male behaviors toward intruding males. We manipulated male wing coloration by painting the wings of both *C. splendens* males and *C. virgo* males entirely black, similar to our previous experimental procedures (Svensson et al. 2007, 2010). These experiments thus aimed to transform *C. splendens* males into *C. virgo* male phenotypes, whereas the manipulation of *C. virgo* males should essentially leave the visual wing phenotype unaffected, since *C. virgo* males already have entirely black wings. If male wing color functions as a cue to recognizing con- and heterospecific competitors and thereby affects *C. splendens*' male decision to escalate or avoid a superior competitor, we would thus expect this identical manipulation to have different effects, depending on which species was being wing-manipulated.

Statistical Analyses

All statistical analyses were made using either various packages in R (R Development Core Team 2014) or Statistica (StatSoft 2004). We used fixed-effects general linear models or mixed generalized linear models depending on the analysis and type of data. In the field experiments on intra- and interspecific male aggression we used two-way ANOVAs where all factors were fixed. These experiments were performed at two allopatric (*C. splendens* only) and two sympatric (*C. splendens* and *C. virgo*) sites. Since sites were chosen not randomly but to obtain behavioral data from both sympatric and allopatric conditions, site was treated as a fixed factor. Post hoc comparisons of how *C. splendens* male aggression differed toward different male phenotypes within sites after wing color ma-

nipulation come from Fisher's least significant difference (LSD) tests. We used Fisher's LSD as a post hoc test rather than the more conservative Tukey honest significant difference (HSD) test, as we were not interested in all pairwise comparisons but only the within-site comparisons of aggressive responses toward con- and heterospecific males, respectively.

When analyzing male survival in relation to species, density, and frequency in the mesocosm experiments, we used generalized linear mixed models assuming a Poisson distribution of the dependent variable (number of days surviving). The main effects of density (high and low) were included as the predictors and all two- and three-way interactions involving species (*C. splendens* and *C. virgo*), density, and frequency. Mean temperature of the days that each male survived was included as a fixed covariate, and cage ID and year (in the case of *C. virgo* survivorship) were included as random factors. Post hoc comparisons of male survivorship of both species in different density and frequency treatments and the within-species differences in survivorship between density and frequency treatments all come from Tukey HSD tests.

Simulating Ecological Drift and Negative Frequency Dependence

We simulated the effects of ecological drift and negative frequency dependence in our two-species community (*C. splendens* and *C. virgo*) by modifying an R script available on GitHub (https://github.com/aammd/ecotheory/blob/master/vignettes/Box2.Rmd) that was originally developed by Mark Vellend (Vellend 2016). In all of these simulations, we varied three parameters: (1) strength of negative frequency dependence (NF), (2) intrinsic survival differences between species unrelated to frequency dependence (FR = fitness ratio), and (3) total community size (J, the combined population size of both species). The strength of negative frequency dependence varied from no negative frequency dependence and ecological drift operating alone (NF $= 0$) to weak (NF $= -0.2$) and to strong (NF $= -1.2$) negative frequency dependence. Our range of parameters values were chosen to match the strength of negative frequency dependence estimated in our mesocosm experiments and the combined population sizes (community size) estimated in our previous field studies in natural populations (Svensson and Friberg 2007).

The FR reflects the relative survivorship of one species over the other (here *C. virgo* intrinsic survivorship divided by *C. splendens* intrinsic survivorship). For instance, FR = 1.0 indicates complete neutrality and no intrinsic species differences in survivorship, whereas in FR = 1.2 *C. virgo* has 20% intrinsically higher survivorship than *C. splendens* at a site (which would correspond to a significant main effect of species in a statistical model). Such a situation might arise if there are abiotic environmental gradients (e.g., tempera-

ture) that make *C. virgo* intrinsically more adapted to (say) the northern part of the geographic range than *C. splendens* (Wellenreuther et al. 2012). Although our mesocosm experiments did not reveal any such intrinsic species differences in survivorship (i.e., no significant main effect of species; see Results), we nevertheless explored the effects of such intrinsic species differences, should they exist in other parts of the range. Data in this study have been deposited to the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.vj260 (Svensson et al. 2017).

Results

We compared *Calopteryx* species frequency distributions from the 111 sites in northern Europe where these species co-occur regionally (fig. 1). The species frequency distribution among sites was U-shaped, with most sites being dominated by one of these two species, and relatively few sites had an even species frequency (fig. 1*A*). We also found that sympatric sites had higher density of both species combined (a proxy for total community size, *J*), compared to allopatric sites containing only one of these two species (fig. 1*B*). These differences between site categories were not confounded by latitude or longitude (table A1; tables A1–A7 are available online).

To quantify the role of neutrality, frequency, and density dependence, we manipulated species densities and frequencies in mesocosm experiments where we recorded *Calopteryx* male survival (fig. 2; see Material and Methods). *Calopteryx* males are territorial and aggressive against both con- and heterospecific males, and we were particularly interested in frequency- and/or density-dependent survival effects. The abiotic environmental conditions both species experienced were similar in these experiments, as we experimentally sought to exclude any niche-based differences that might exist in natural environments that we might have overlooked in our previous ecological studies (Svensson 2012; Wellenreuther et al. 2012). Such subtle and undetected niche differences could potentially confound our interpretation of neutrality and ecological drift in natural settings (fig. 1). Thus, any frequency- or density-dependent survival effects in these mesocosm experiments should have arisen entirely and intrinsically from interference competition, rather than from undetected niche differences (see Material and Methods).

Survival across three sympatric species frequency treatments and two densities revealed that density and species frequency affected these two species differently (fig. 2*A*). The dominant species *Calopteryx virgo* (Tynkkynen et al. 2005) had high survival when rare and when density was low in one of the six sympatric treatments (fig. 2*A*; table A2). Within-species tests further showed that *Calopteryx splendens* survival was influenced by an interaction between density and frequency (fig. 2*B*; table A3), whereas *C. virgo* exhibited negative frequency-dependent survival only, with no effects of density (fig. 2*C*; tables A4, A5).
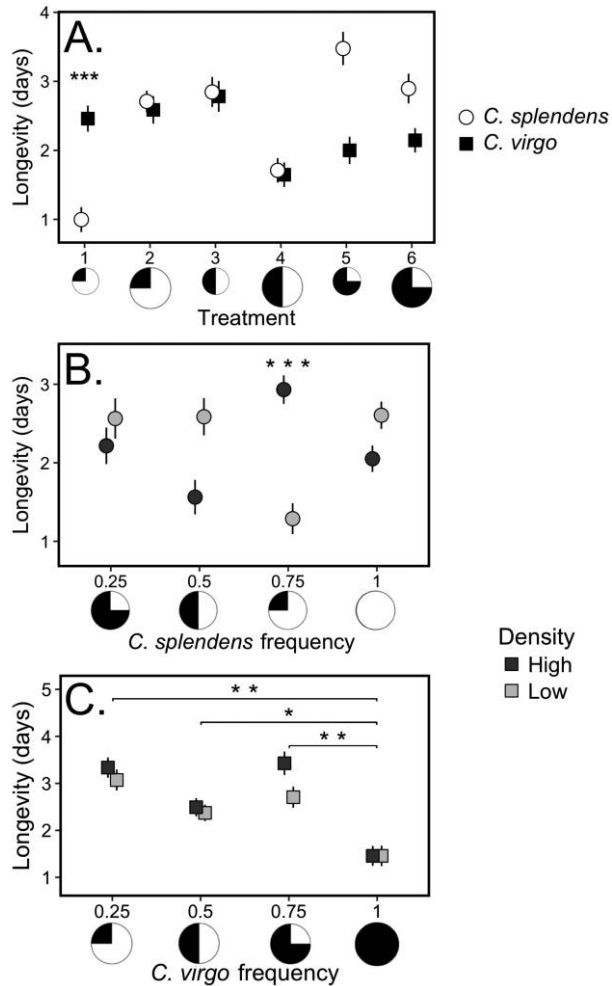
Figure 2: Mesocosm experiments of survival in *Calopteryx* males. Species frequencies (*Calopteryx splendens* and *Calopteryx virgo*) and densities were simultaneously manipulated in a fully factorial design (see Material and Methods). Size and composition of pie charts show total male density (small circles = low; large circles = high) and species composition (black = *C. virgo*; white = *C. splendens*). Shown are mean predictions and standard errors (SEs) from mixed models in tables A2–A5, available online. Raw means and SEs (model-free estimates) are qualitatively similar and are shown in appendix D (fig. D1), available online. *A,* Across three sympatric frequencies, survival in these species are similar (table A2; data from 2014), suggesting near-neutrality and ecological equivalency. *B,* Within-species test for *C. splendens* shows that male survival is influenced by an interaction between density and frequency (table A3; data from 2014), being significantly higher at high density when it was common (75% *C. splendens*). *C,* Within-species test for the dominant species *C. virgo* shows evidence of negative frequency dependence and reduced survival when common (tables A4, A5; data from 2014 and 2015). Note that the within-species tests (*B, C*) contain an additional experimental category (allopatric; far-right symbol in both *B* and *C*) that is not present in the between-species test (*A*). Symbols show significance levels from post hoc tests (Tukey) in the different models (tables A2–A5).

In complementary field experiments, we found that the subdominant species (*C. splendens*) avoided interspecific aggression from intruding heterospecific *C. virgo* males in sympatry (fig. 3*A*). The significant site × species interaction reveals that *C. splendens* males responded differently toward con- and heterospecific males depending on whether the site was allopatric or sympatric (fig. 3*A*; table A6). At the allopatric sites, *C. splendens* males responded equally strongly toward conspecific (*C. splendens*) and heterospecific (*C. virgo*) males, presumably because they had not experienced any previous antagonistic interactions with heterospecific males (fig. 3*A*; Fisher's LSD test). In contrast, in the sympatric populations, *C. splendens* males reduced their aggression toward heterospecific *C. virgo* males compared to conspecific *C. splendens* males, presumably because they had already experienced antagonistic interactions with heterospecific males prior to these experiments (fig. 3*A*; Fisher's LSD test).

We also compared male *C. splendens* aggression responses before and after wing color manipulations in the two sympatric populations. We found that *C. splendens* males use male wing coloration as a cue for competitor recognition and to differentiate between con- and heterospecific males (fig. 3*B*; table A7). Thus, *C. splendens* males in the sympatric populations reduced their aggressive response to *C. splendens* males after they were manipulated to mimic the phenotype of heterospecific *C. virgo* males, whereas there was no significant change in their aggressive responses toward heterospecific *C. virgo* males before and after manipulation (fig. 3*B*; table A7).

Finally, we investigated how ecological drift and frequency dependence could jointly influence species coexistence in this system using simulation modeling (Vellend 2016). We varied local community size (J) and the strength of negative frequency dependence (NF) to explore how long *C. splendens* would be maintained in local communities and when it would be outcompeted by *C. virgo* (fig. 4). Our results show that as long as J is not too low and NF is strong, local species diversity can be maintained even if one species has 20% higher intrinsic survivorship than the other (fig. 4*F*). Increasing J or NF (or both) further increased species co-occurrence and allowed for even higher intrinsic species differences (data not shown).

We varied total community size (J) between 100 (fig. C1), 250 (fig. C2), and 500 (figs. 4, C3). Low community size ($J = 100$ and 250) often led to species loss, as ecological drift then became strong relative to NF. Stronger NF was then required to prevent local species loss (figs. C1, C2). Larger community size ($J = 500$) tipped the balance away from ecological drift and enabled the maintenance of both species longer, even under weak NF (figs. 4, C3). We note that even $J = 500$ can be considered to be a conservative assumption of real community size, since at least some *Calopteryx* sites in southern Fennoscandia contain several thousand sexually reproducing individuals of both species (Svensson and Friberg 2007). When local communities are that
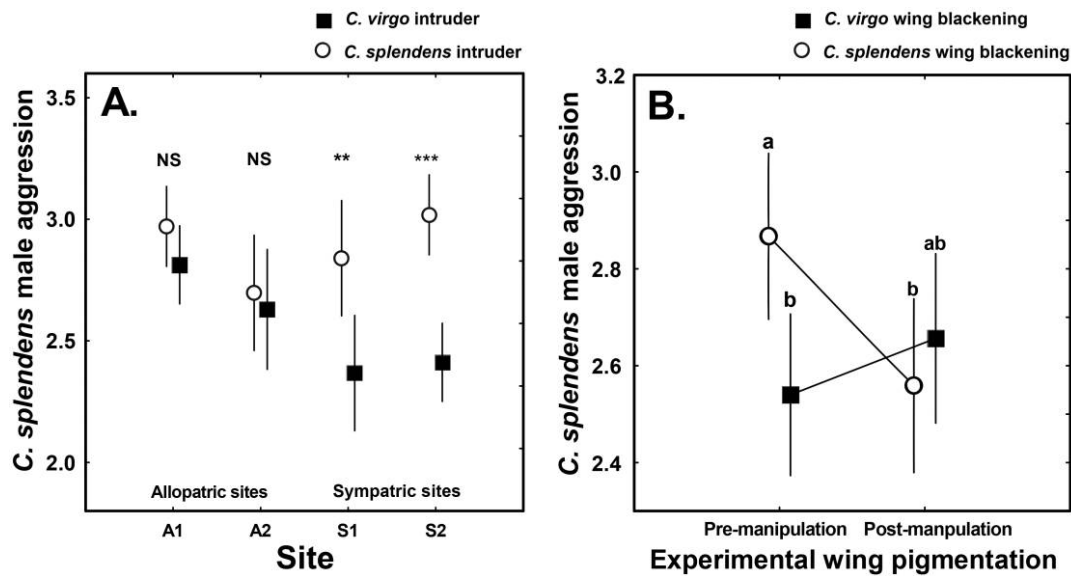
Figure 3: *Calopteryx splendens* male aggression toward conspecific males (circles) and *Calopteryx virgo* males (squares). Means and 95% confidence limits are shown. *A,* Male *C. splendens* aggression levels to intrusion experiments at two allopatric sites (*C. splendens* only) and two sympatric sites (*C. splendens* and *C. virgo*). There is a significant difference in interspecific aggression between sites, with reduced *C. splendens* male aggression toward heterospecific in sympatry (table A6, available online). Symbols show significance levels from post hoc tests (Fisher's least significant difference [LSD]). *B,* Experimental manipulation of male wing color in the two sympatric populations revealed that *C. splendens* males reduced their aggression to manipulated conspecifics who obtained heterospecific male wing coloration (circles), whereas they did not change their response toward manipulated *C. virgo* males (squares), whose visual wing color phenotype was not affected (table A7, available online). Lowercase letters show significant differences between treatments (Fisher's LSD post hoc test).

large, ecological drift becomes a weak or negligible force compared to NF, and species diversity is more likely to be maintained (cf. figs. 1*B*, 4).

In figure 4 we show species maintenance for up to 2,000 generations, corresponding to 4,000 years, assuming a 2-year generation life cycle of *Calopteryx* in Fennoscandia (Sandhall 2000). Increasing the time to 5,000 generations (10,000 years) gave qualitatively similar results (fig. C3). This suggests that this strength of NF would have the potential to maintain these two species in Fennoscandia since they colonized northern Europe, which happened sometime after the last Ice Age, about 10,000 years BP.

When species are completely neutral (i.e., no intrinsic fitness differences or strict ecological equivalence), ecological drift should operate unopposed (fig. 4*A*). In this scenario, all sympatric sites will diverge gradually in species frequencies until they are replaced by a series of allopatric sites (fig. 4*A*; cf. fig. 1*A*). Fixation or loss of species through ecological drift will happen in less than 2,000 generations, conservatively assuming a moderate-sized community ($J = 500$). Although we did not find any intrinsic species differences in survival (i.e., no significant intercept; Adler et al. 2007; see table A2; fig. 2*A*), we nevertheless relaxed the assumption of neutrality and strict fitness equivalence of these two species by investigating how a 20% higher survival rate of the dominant *C. virgo* would influence the outcome. In such a scenario,

C. virgo would quickly drive *C. splendens* to extinction at all sites (fig. 4*B*).

Incorporating negative frequency dependence alongside ecological drift changes the outcome considerably (fig. 4*C*–4*F*). Under a weak negative frequency-dependent advantage of *C. virgo* when rare, both species are maintained for at least 2,000 generations (fig. 4*C*) and up to 5,000 generations (fig. C3). Weak frequency dependence is not sufficient, however, if there are strong intrinsic species differences in survival, as *C. virgo* will then quickly replace *C. splendens* (fig. 4*D*). Finally, under strong frequency dependence both species can be maintained for thousands of generations, both when having equal intrinsic survival rates (fig. 4*E*) and when intrinsic survival rates differ up to 20% (fig. 4*F*). Increasing community size further extends co-occurrence times (figs. C1–C3).

Discussion

The expected dynamics of stochastic ecological drift in two-species communities is similar to the process of genetic drift at a single polymorphic locus with two alleles in classical population genetic theory (Hartl and Clark 1997; Hu et al. 2006). If community size (total number of individuals, both species combined) is limited, ecological drift should result in a flattening of the species frequency distribution and even-

tually a U-shaped distribution, consistent with what we found in this study (cf. fig. 1*A*). Sympatric sites should thus lose local species due to ecological drift, resulting in a march toward multiple allopatric single-species populations, as long as local community size (*J*) is not infinite (Orrock and Fletcher 2005). Ecological drift is also expected to slow down with larger local community size, just as the process of genetic drift is slower when effective population size (*N*$_e$) is high (Hartl and Clark 1997; Orrock and Fletcher 2005; Hu et al. 2006). This latter prediction is consistent with our findings that sympatric sites have higher local community size (fig. 1*B*).

The U-shaped species frequency distribution (figs. 1*A*, B1) is thus partly consistent with the expectation from ecological drift. Alternatively, these geographic patterns reflect habitat segregation of these species along an ecological latitudinal gradient (fig. 1*A*), possibly in combination with sympatric sites being more productive (fig. 1*B*). However, we consider this latter interpretation unlikely to entirely explain the pattern we have found here, as a similar U-shaped distribution is also seen in the sympatric zone in southern Sweden, where these two species have no detectable climatic or thermal niche differences (Svensson 2012; Wellenreuther et al. 2012; fig. B1).

As a caveat, we note that species abundance distributions like the ones in figure 1*A* can result from multiple and not mutually exclusive processes of which ecological drift is only one such process (McGill 2003; McGill et al. 2006). For instance, positive frequency dependence and priority effects (Fukami et al. 2007; M'Gonigle et al. 2012; De Meester et al. 2016) are also expected to result in a pattern by which a series of sympatric populations are replaced by a series of allopatric populations containing either species. This is a strong argument for complementing biogeographical surveys with direct experimental manipulations, which we did in this study (see further below).

We provide experimental evidence for negative frequency-dependent survival in the dominant and more aggressive species *Calopteryx virgo* (Tynkkynen et al. 2005; fig. 2*C*; tables A4, A5). Such negative frequency dependence is not expected under a model of pure neutrality and complete ecological equivalency of these two species. However, such negative frequency dependence is consistent with a model where the dominant species (*C. virgo*) increasingly interacts with itself as it becomes more common and hence will potentially regulate its own frequency. In the subdominant species *Calopteryx splendens*, we found evidence for a significant interaction between density and frequency (fig. 2*B*). At present, we do not know the mechanisms behind this density and frequency interaction in *C. splendens*, and further studies would be needed in this species. Recent theoretical work shows that positive frequency dependence can maintain diversity of ecologically similar species at regional scales, although it reduces diversity locally through priority effects (M'Gonigle et al. 2012). Interactions between density and frequency are also consistent with "conditional

neutrality," as these species might be nearly neutral in some density environments but not in others (fig. 2*A*; table A2).

Our field experiments on antagonistic interactions suggest that behavioral avoidance by the subdominant *C. splendens* might counteract interference from its dominant competitor *C. virgo* (fig. 3*A*, 3*B*). Our results suggest that sympatric *C. splendens* males use the extent of black wing coloration of intruders as a cue in competitor recognition and in their decision to attack or avoid an intruding male. These findings are consistent with regulatory behaviors buffering organisms against external selection pressures in challenging environments (Huey et al. 2003; Losos et al. 2004). Behavioral plasticity (West-Eberhard 2003) could mitigate costly interspecific interactions, which in turn might increase the scope for neutrality by functioning as a fitness-equalizing mechanism (Chesson 2000; Adler et al. 2007). Given often low heritabilities of behavioral traits (Mousseau and Roff 1987), it is likely that these interspecific territorial behaviors are not completely genetic, although we emphasize that we do not yet have any direct experimental evidence that these behaviors either have a strong genetic basis or are plastic.

Our biogeographic data, experimental results, and simulation modeling jointly suggest that stochastic and deterministic factors interact in shaping co-occurrence of these two species over regional scales. We suggest that ecological drift pushes species frequencies away from sympatry (figs. 1*A*, 4*A*, 4*B*), whereas large community size (fig. 1*B*) and negative frequency dependence (fig. 2*C*) delays or prevents the local loss or fixation of the dominant species *C. virgo* (fig. 4*C*, 4*E*, 4*F*). The simultaneous operation of stochastic and deterministic forces in this system illustrates that the traditional dichotomy between neutrality and deterministic models is misleading (Tilman 2004; Ricklefs 2006; Adler et al. 2007) and that ecological drift should be seriously considered in empirical studies (Gilbert and Levine 2017). As ecological drift is likely to be ubiquitous (Hubbell 2001; Rosindell et al. 2011, 2012), it is mainly an empirical issue to quantify its strength to understand how it interacts with stabilizing and equalizing mechanisms in shaping local species diversity (Chesson 2000; Adler et al. 2007; Levine and HilleRisLambers 2009).

Ecological drift is thus unlikely to operate alone but is likely opposed by deterministic factors maintaining species locally (Vellend 2016). Based on our experimental results and simulations, we suggest that interference competition can create negative frequency dependence and maintain diversity through rare-species advantage, even if interspecific ecological niche differences are weak (McPeek 2012). This is similar to how negative frequency-dependent selection maintains genetic polymorphisms within species (Le Rouzic et al. 2015), although in the case of community ecology, negative frequency dependence maintains species diversity rather than genetic diversity (Ayala 1971; Wills et al. 2006; Harpole and Suding 2007). Even though some previous correlative studies on
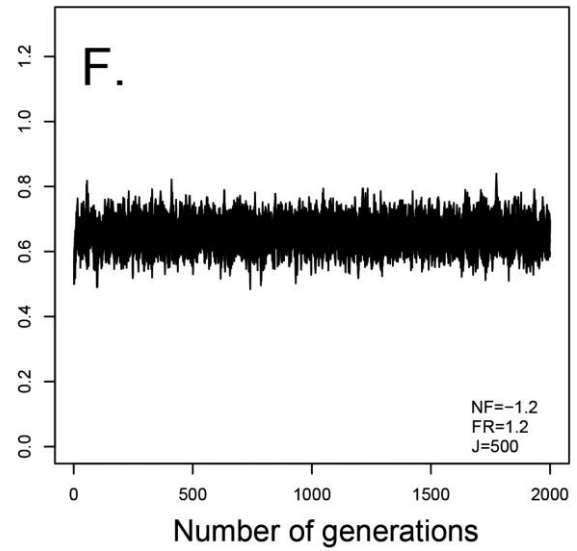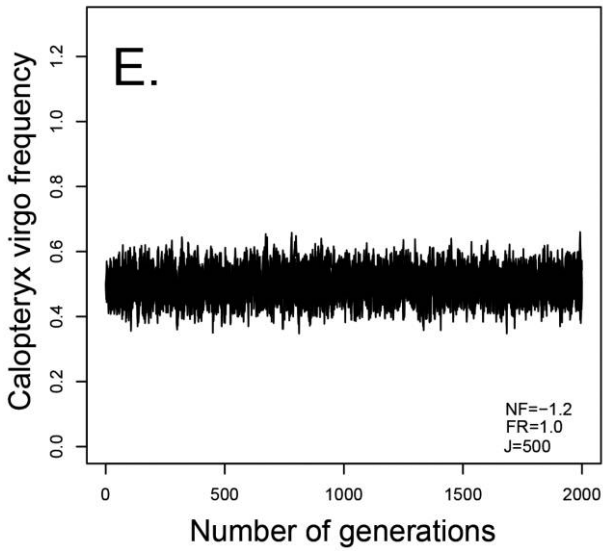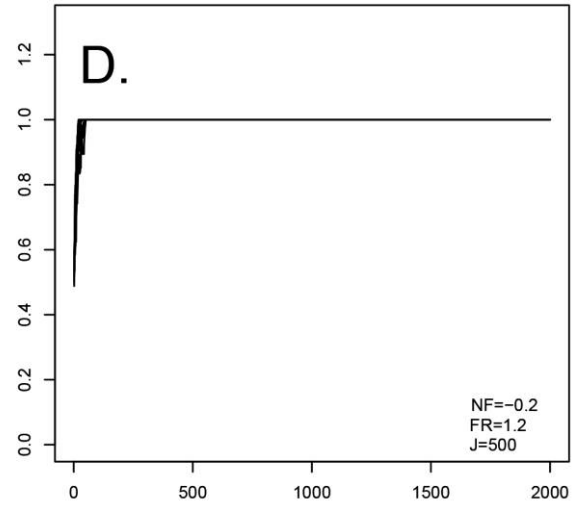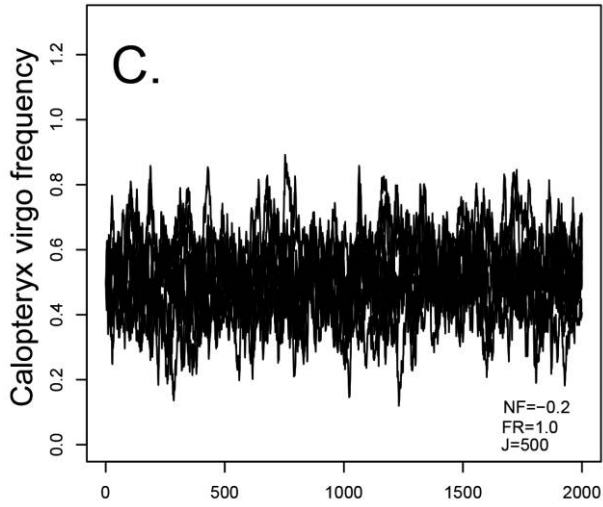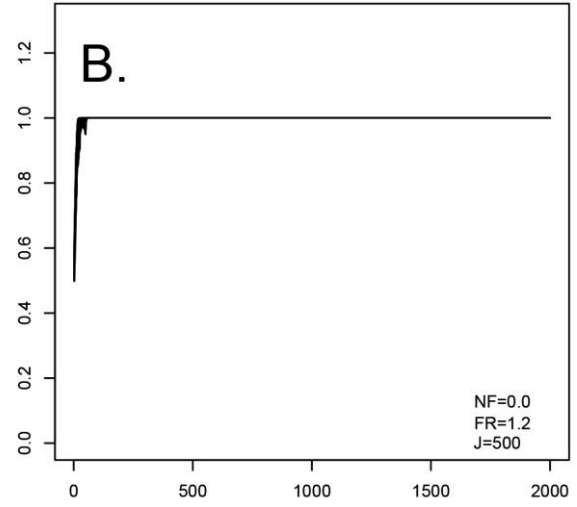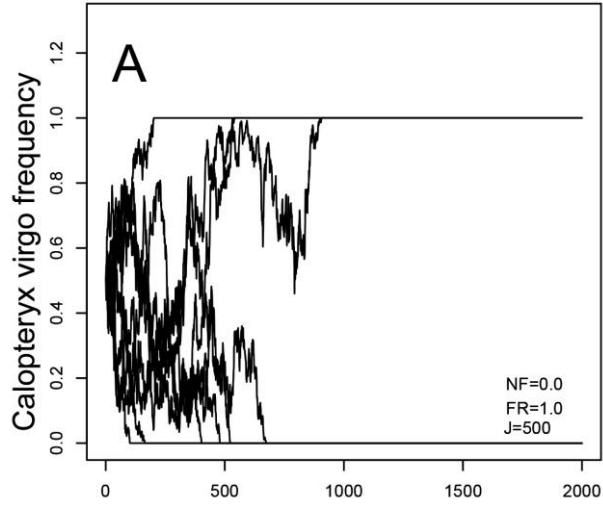
tropical and temperate tree communities suggest rare-species advantage (Volkov et al. 2005; Wills et al. 2006), experimental tests for negative frequency dependence maintaining species diversity are rare (but see Ayala 1971; Harpole and Suding 2007; Levine and HilleRisLambers 2009). In *Calopteryx* damselflies and other odonate taxa, negative frequency dependence could act as a stabilizing mechanism (Chesson 2000; Adler et al. 2007), as these insects are characterized by strong interspecific reproductive interference, even between ecologically similar species (Tynkkynen et al. 2004, 2005; Drury et al. 2015). Nevertheless, on the continuum between neutrality (i.e., fitness equivalence) and stabilizing mechanisms (i.e., negative feedbacks) that preserve diversity, *Calopteryx* damselflies are likely to be closer to the neutrality end of the spectrum, given the lack of any significant intrinsic survival differences between these two species (i.e., no significant effect of species in table A2). We also note that in previous empirical studies in this area, niche differences were inferred based on the existence of stabilizing mechanisms, rather than demonstrated directly (Levine and HilleRisLambers 2009). However, we have argued above that such stabilizing mechanisms can arise even in the absence of strong niche differentiation, provided that reproductive interference competition generates some form of negative frequency dependence.

Finally, dispersal could counteract local ecological drift by homogenizing species frequencies across large spatial scales (contra the pattern seen in fig. 1). Hence, high dispersal would make it more difficult to detect the U-shaped distribution of species frequencies that we have detected in this study (fig. 1). That we have detected such distribution in spite of the fact that *Calopteryx* damselflies disperse over long distances (Karjalainen and Hämäläinen 2013) is encouraging and strengthens the case for ecological drift. Other models of the competition-colonization trade-off that incorporate demographic stochasticity (i.e., ecological drift) suggest that the scope for species coexistence increases with smaller community size because the dominant competitor would become effectively neutral under such circumstances (Orrock and Watling 2010). However, this model is unlikely to apply in our case, given the positive relationship between species diversity and community size (fig. 1*B*).

Conclusions

Negative feedbacks can maintain species diversity (Chesson 2000), but such feedbacks do not necessarily require strong niche differentiation, as long as some mechanisms such as behavioral interactions and interference competition (Grether et al. 2017; Shuker and Burdfield-Steel 2017) cause negative frequency dependence and rare-species advantage (this study). Thus, negative frequency dependence could arise even if species have similar ecological niches, as is the case for many odonate species (McPeek and Brown 2000; Siepielski et al. 2010; McPeek 2012; Svensson 2012; Wellenreuther et al. 2012; this study). Niche and neutral perspectives are increasingly recognized as not being mutually exclusive (Chesson 2000; Tilman 2004; Adler et al. 2007; Vellend 2010), and community ecologists are paying increased attention to how mechanisms such as negative frequency dependence, higher-order interactions, interaction chains, and intransitive competition can maintain species diversity even in the absence of strong ecological niche differentiation (Levine et al. 2017; Maynard et al. 2017). We have suggested that negative frequency dependence can arise independently of the physical environment if there are antagonistic interactions between species that differ in dominance relationships (Tynkkynen et al. 2005), provided that such interactions lead to rare-species advantage (Ayala 1971; Chesson 2000; Wills et al. 2006; Harpole and Suding 2007; Levine and HilleRisLambers 2009; this study). Our study and other recent work suggests that ecological drift and demographic stochasticity deserve more attention in empirical and theoretical studies of both macroecology and macroevolution (Hubbell 2001; Chevin 2016; Gilbert and Levine 2017).

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Figure 4: Opposing effects of ecological drift and negative frequency dependence (rare-species advantage) on species coexistence. Simulations of the frequency of *Calopteryx virgo* under pure neutrality (*A*, *B*) and weak (*C*, *D*) and strong (*E*, *F*) negative frequency dependence during 2,000 generations. The right column shows the proportion of *C. virgo* when species have unequal baseline survival rates (FR = fitness ratio between *C. virgo* and *Calopteryx splendens*, here a 20% intrinsic survival difference; i.e., species are not completely neutral). NF shows the strength of negative frequency dependence being 0 in *A* and *B* (ecological drift operating alone), weak to moderate (−0.2) in *C* and *D*, and strong (−1.2) in *E* and *F*. In all these simulations local community size (*J* = both species combined) is set to 500 and generation number is 2,000. Scenarios with different parameter values are simulated in appendix C (figs. C1–C3), available online.

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Left, typical habitat of *Calopteryx* demoiselles: a slow-flowing river in southern Sweden (province of Blekinge). *Above right*, beautiful demoiselle (*C. virgo*): males of this species have entirely melanized black wings. *Below right*, banded demoiselle (*C. splendens*): males of this species have a smaller melanin wing patch, covering only 50% of the wing, but are otherwise morphologically and ecologically very similar to the close relative the beautiful demoiselle (*C. virgo*). Photo credits: Erik I. Svensson.