BIODIVERSITY RESEARCH

Dynamic spatial interactions between the native invader Brown-headed Cowbird and its hosts

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ABSTRACT

Aim We investigated the contribution of parasitism by the Brown-headed Cowbird (*Molothrus ater*) to its host population dynamics at a subcontinental scale. We predicted that the growth rate of cowbirds would be most strongly related to the abundance of forest insectivorous hosts and that landscape fragmentation would have opposite effects on the parasite and its hosts. Furthermore, due to the species' sedentarity and low rates of adult dispersal, we expected that cowbird population dynamics would be structured at local, rather than large spatial scales.

Location The Great Plains, United States.

Methods We modelled jointly the population dynamics of cowbird and its 58 most common hosts, accounting for effects of landscape fragmentation and cowbird dispersal. We used Bayesian inference to evaluate this model on 76 routes of the North American Breeding Bird Survey (BBS), surveyed each year from 2001 to 2011. We then analysed covariations between the demographic dynamics of cowbirds and their hosts in a multivariate ecological trait space.

Results Contrary to most of its hosts, the cowbird had positive growth rates in man-disturbed, fragmented landscapes, which covaried at small spatial scales. The large-scale effects of parasitism were limited, as few host species affected, or were affected by cowbird growth rates. However, significant cowbird–host relationships were structured by ecological traits: cowbird growth rates were most increased by the abundance of ecological generalists, while hosts were affected by cowbird abundance irrespective of their position in the functional space.

Main conclusions Cowbirds parasitize opportunistically the hosts occurring in disturbed landscapes. The large-scale effects of nest parasitism therefore depend probably on landscape structure and other environmental factors operating at local scales. We suggest that efforts to counter the local and continental declines of many passerine species should include parasitism among the biotic components of landscape disturbance.

Keywords
Biotic interactions, bird communities, dispersal, landscape fragmentation, *Molothrus ater*, parasitism.

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INTRODUCTION

The contributions of interspecific interactions to dynamic patterns of species coexistence stand at the foreground of much current ecological research. Local interactions among individuals, including predation, competition and aggression, facilitation, parasitism or host–pathogen relationships, are influenced by larger scale processes of regional species assembly (Ricklefs, 2008) and may translate into patterns of large-scale community dynamics in conjunction with environmental filtering and dispersal (Chase & Myers, 2011). In particular, human-driven species introductions and range

expansion due to climate or habitat change may trigger local extinctions of native species, modify ecosystem structure and ultimately contribute to modify macroscale diversity patterns in conjunction with other environmental disturbances (Shea & Chesson, 2002). Therefore, elucidating the large-scale outcomes of interspecific interactions is a critical component of community ecology and a major issue for biodiversity conservation in the face of global changes (Araújo & Luoto, 2007). However, while the effects of species interactions on individuals and local communities are well documented (Wisz *et al.*, 2013), achieving a better understanding of their larger scale outcomes remains a challenge, especially because they are usually investigated indirectly through spatial co-occurrence patterns and demographic changes (Ricklefs, 2013).

Because they may influence population and community dynamics over continental scales, host–parasite interactions need to be considered among the processes that influence species' conservation status at biogeographical scales (Rivers *et al.*, 2010). Parasites are expected to trigger variability in host occurrence, abundance or demography that cannot be explained by environmental conditions or competitive interactions among the host species (Ricklefs, 2011). For instance, they may create sink host populations in otherwise suitable habitats (Jewell & Arcese, 2008), trigger cyclic seasonal dynamics (Hudson *et al.*, 1998) or population outbreaks (Hudson *et al.*, 2006). The prevalence of parasites in host populations may itself be affected by habitat heterogeneity (Loiseau *et al.*, 2010), local climate (Sehgal *et al.*, 2011), parasite or host dispersal abilities (Boulinier *et al.*, 2001a), co-evolutionary history between parasites and their hosts (Thompson, 2005), and host life history attributes (Servedio & Hauber, 2006). The outcomes of host–parasite interactions are therefore a product of parasite influences on host demography and spatial occurrence patterns and of host influences on parasite dynamics (Horwitz & Wilcox, 2005). At a community level, parasites may trigger the outbreak or loss of key species, change competitive interactions and induce cascading effects through trophic networks, modifying species richness, biomass and ecosystem functions (Summers *et al.*, 2003). However, assessments of regional-level effects of parasitism on species assemblages are scarce (Prenter *et al.*, 2004) or limited to theoretic considerations (Ricklefs, 2013). While this gap usually results from experimental inaccessibility of parasite–host interactions, macroscopic brood parasites such as the Brown-headed Cowbird (*Molothrus ater,* hereafter 'cowbird') offer a chance to investigate the community-level outcomes of parasitism using observation protocols accessible to field biologists.

The cowbird has a broad distribution across North America and has expanded its range for over a century in response to the fragmentation of forested landscapes (Thompson *et al.*, 2000; Morrison & Hahn, 2002; Chace *et al.*, 2005; Hovick & Miller, 2013). Cowbirds are generalist parasites that lay their eggs in the nests of over 130 passerine species (Strausberger & Ashley, 1997; Lowther, 2012), with a preference for hosts living in forests and forest edges, perhaps as a

consequence of the species' recent expansion into forested landscapes (Robinson *et al.*, 2000; Jensen & Cully, 2005). Therefore, cowbird colonization success and persistence depend upon a combination of landscape factors and host community composition, being especially attracted to areas with high host species richness (Cummings & Veech, 2013). In turn, cowbirds have immediate effects on host demography (Arcese *et al.*, 1996; Lorenzana & Sealy, 1999) through egg removal, nest desertion, competition among nestlings and facilitation of host predation (Smith *et al.*, 2002). Hence, the cowbird may locally modify the composition of passerine communities, even more as many of its hosts are declining at a continental scale (Sauer *et al.*, 2011). Cowbirds may especially impair the demography of the rarest and most preferred host species (Strausberger & Ashley, 1997) and drive their local populations to sinks or local extinction (Jewell & Arcese, 2008). Conservation options to reduce the effects of cowbirds on their hosts have included food resource limitation, livestock reduction and cowbird removal (Hartway & Mills, 2012), but have met with mixed success (Hall & Rothstein, 1999).

Several studies have attempted to evaluate the community-wide influence of cowbirds (Strausberger & Ashley, 1997; Lorenzana & Sealy, 1999; Rivers *et al.*, 2010; Cummings & Veech, 2013), but these have mainly been concerned with the local effects of parasitism on spatial patterns of host species richness or abundance. Hence, the demographic consequences of parasitism on the whole assemblage of common passerine hosts remain to be assessed at regional and continental scales. The only attempt (to our knowledge) to evaluate cowbird parasitism at such large scales failed to find any direct association between cowbirds and host population attributes, and interpreted the observed correlations as shared effects of environmental determinants rather than to parasitism *per se* (Peterjohn *et al.*, 1999). However, annual and spatial variation in host species abundances was not explicitly accounted for, possibly underestimating the role of parasitism on demographic changes. Indeed, biotic interactions, being primarily local processes, are expected to leave fine-grained signatures into species distribution patterns and dynamics that are easily blurred by coarser environmental gradients, although they also sometimes translate into clearer large-scale effects (Wisz *et al.*, 2013). The recent extension of spatial metapopulation models to multispecies frameworks incorporating host–pathogen relationships (Soubeyrand *et al.*, 2009) allows to overcome limitations imposed by the multiplicity of hosts and interplaying environmental factors; however, to our knowledge, such models have never been used to study the effects of host–parasite interactions in vertebrate communities.

In the present study, we searched for signatures of parasitism in the dynamic abundance patterns of cowbirds and its hosts in the Great Plains of the United States. To this aim, we developed a multispecies model similar to Soubeyrand *et al.* (2009)'s, which reflects the covariations between the population dynamics of cowbirds and their hosts in the

Great Plains of North America, accounting for the dominant gradients of landscape structure and composition, and cowbird dispersal. We hypothesized that direct effects of cowbird parasitism and indirect habitat-driven cowbird–host associations would leave contrasting signature on host demographic changes at a subcontinental scale. We tested four specific predictions on how cowbird–host relationships should leave a signature on species' subcontinental population dynamics:

1. As a consequence of parasitism, cowbird population growth rate is positively related to host species' abundances, while cowbird abundance is negatively related to host population growth rates. Convergence (divergence) in habitat preferences would instead lead to symmetric positive (negative) correlations in the growth rates and abundances of the parasite and its hosts.

2. Cowbirds and their hosts have opposite responses to landscape-level habitat structure. Habitat fragmentation and human disturbance improve cowbird colonization success because they provide higher access to resources and a wider host diversity (Morrison & Hahn, 2002; Chace et al., 2005; Hovick & Miller, 2013), but affect most of their hosts negatively (Boulinier et al., 2001b).

3. Cowbird and host dynamics are spatially correlated at small scales (below 100 km) because of the reluctance of adult cowbirds to undertake long-distance dispersal movements (Anderson et al., 2012).

4. The strength of relationships between cowbirds and their hosts depends on the host species' ecological characteristics, including body size, diet and nesting habitat (Mason, 1986). We expected the smallest hosts, those with insectivorous diets and living in semi-open, shrub-dominated habitats to most enhance cowbird growth rates and, in turn, to suffer most from parasitism.

MATERIALS AND METHODS

Study area and period

We restricted our spatial scope to the historical core range of the Brown-headed Cowbird (Thompson et al., 2000; Cummings & Veech, 2013) to ensure that host–parasite relationships did not interfere with recent range fluctuations, range border effects or any other idiosyncratic process resulting from individuals wandering in unsuitable areas. Hence, our study area encompassed the six Bird Conservation Regions of the Great Plains: Prairie Potholes, Badlands and Prairies, Shortgrass Prairie, Central Mixed Grass Prairie, Oaks and Prairies, Edward's Plateau (Fig. 1, North American Bird Conservation Initiative, 2000). Bird data from the BBS were available for all years back to 1966, but we restricted the time span of our analysis to the decade 2001–2011 to take advantage of detailed land cover information, which were available only for the median year 2006 (Small et al., 2012). In the absence of relevant data on habitat temporal changes, we assumed that no substantial habitat shift occurred during the time period covered in our study.

Bird data

Our bird sampling units were the routes of the BBS (Sauer et al., 2011). This long-term monitoring programme provides abundance data for all bird species encountered on 50 point counts spread along 25-mile (39.4 km) routes resampled annually by skilled volunteers. We removed the first sampling year of an individual observer on a given route to limit learning effects (Jiguet, 2009). Although we could not account for the effects of detection errors on bird population dynamics and spatial patterns due to the absence of within-year replicates in the BBS, the absence of any consistent signature of species' detectability is reassuring for the validity of our results. We eventually retained the 76 routes (Fig. 1) that were censused in each of the 11 years of the survey period, to avoid missing data. For each year and route, we retrieved the route-level sum of cowbird and 58 host species counts over the 50 survey points as a measure of bird abundance. To be considered, a host species had to be listed among known hosts of the Brown-headed Cowbird in a compilation of published sources (Lowther, 2012), and to occur each year on at least 10% of the routes (rarer species triggered convergence failures in our model). Although a few host species were relatively abundant locally, none had both low numbers of occurrences and high local abundances to a point raising concern for the design and interpretation of our model.

Land cover data

We retrieved three landscape configuration variables aimed at reflecting habitat fragmentation and the relative covers of 13 land use categories within 2-km buffers around each BBS route from the remote-sensing-derived National Land Cover Database 2006 (NLCD, Fry et al., 2011) compiled by Small et al. (2012; variables retained are described in Table 1). Our buffer size is consistent with the known restriction of cowbirds to areas within three kilometres of an agricultural patch (Robinson, 1999). We summarized these variables using a Principal Component Analysis (PCA), and retrieved the route scores on the first component, which accounted for 27% of the total variance (second component: 17%). The newly created variable, referred to as 'landscape fragmentation' below, was dominated by configuration variables, and ranged from fragmented landscapes with moderate or high levels of urbanization and deciduous forest to more homogeneous agricultural areas with higher proportions of crops and pastures (Table 1). The cowbird is expected to range widely along this synthetic gradient following its recent range expansion towards forested habitats, although its historical habitats are located at the positive extreme. This first principal component therefore summarized the habitat information required to test our prediction on the effects of habitat fragmentation on cowbird–host dynamics. Thus, we did not take into account the other principal components or other habitat descriptors.
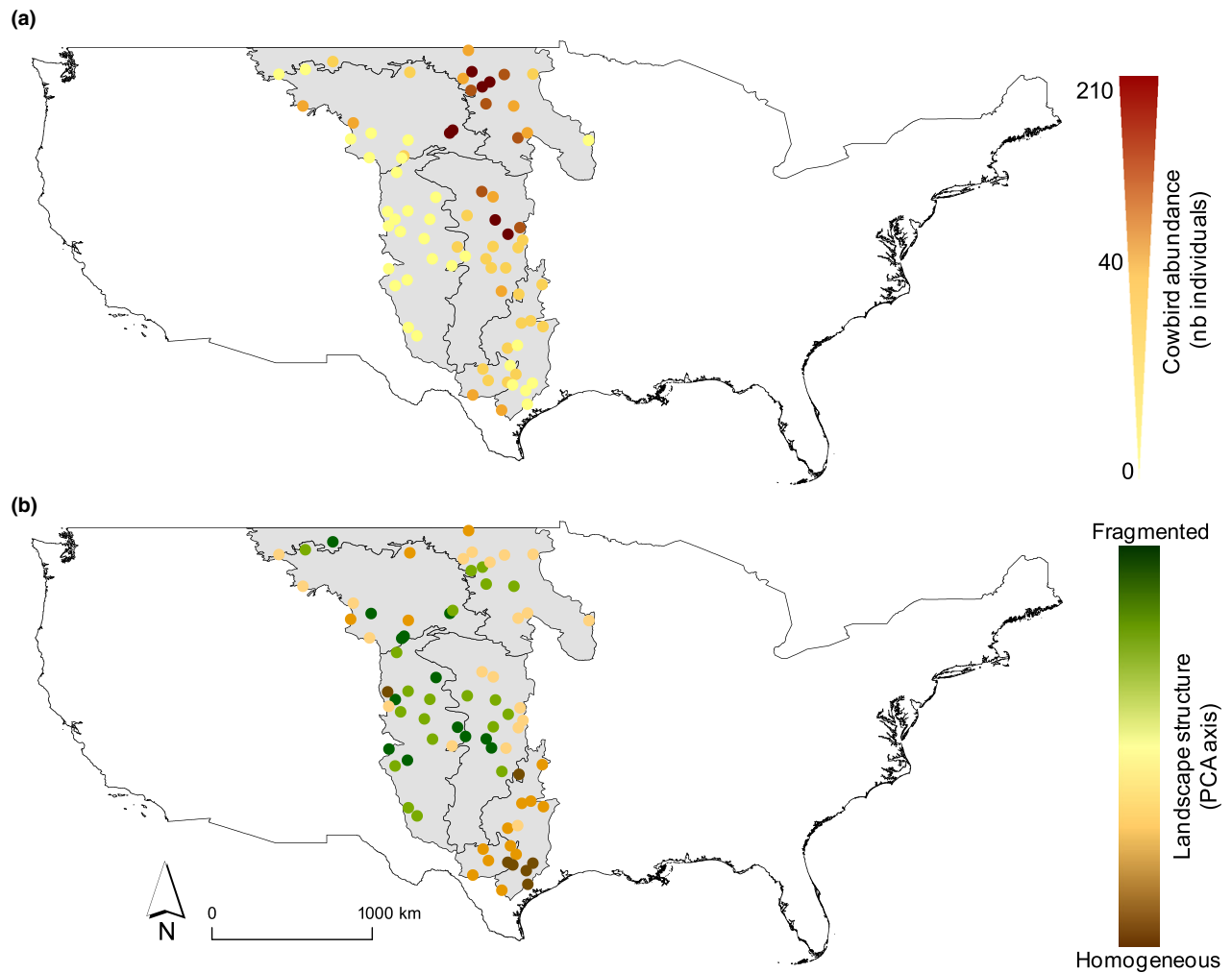
(a)

(b)

Figure 1 Map of the 76 breeding bird survey routes included in the study. The study area (Great Plains Bird Conservation Regions) is greyed out. Colour gradients reflect (a) the route-level counts of Brown-headed Cowbirds, (b) the position of each route on a principal component analysis (PCA) axis ranging from highly fragmented landscapes dominated by forest and urban areas (green) to homogeneous, agricultural landscapes (brown).

Trait data

We compiled nine life history traits of host species from the Encyclopedia of Life (www.eol.org): number of broods per year, number of eggs per clutch, mating behaviour, main habitat category, nest location, nest type, dietary guild, foraging method and body mass (see Table S1 in Supporting Information for details). We assumed this suite of traits to be representative of host ecology and productivity, and to reflect their susceptibility to cowbird parasitism.

Host–parasite model

Model overview

The central part of our study consisted of a spatially explicit multispecies model reflecting the dynamic relationships between cowbird abundance and the abundance of its host species, accounting for the effects of landscape fragmentation. In the model, cowbird abundance in a given year t and BBS route i ($NP_{i,t}$) influenced the population growth rates of host species (h) on this route for that year ($coloH_{i,t,h}$) through a host-specific parameter called $cp2_h$. In turn, host species' abundances ($NH_{i,t,h}$) affected cowbird growth rates ($coloP_{i,t}$) through a host-specific parameter called $ch2_h$. Both cowbird and host dynamics were affected by landscape fragmentation. The annual growth rate of cowbirds on a given BBS route also depended on cowbird abundance in the neighbouring routes through a spatial kernel function; yet, for computational reasons, we had to assume that host growth rates were not spatially structured (see Appendix S1). We estimated model parameters through a Bayesian inference procedure. We subsequently analysed the estimated species-specific host–parasite relationships $cp2_h$ and $ch2_h$ within a multivariate trait space.

Table 1 Loadings of land use types on the first axis of a principal components analysis (PCA) based on 76 breeding bird survey routes. Original data are extracted from Small *et al.* (2012). Variables are ranked according to their contribution to the axis. The first column gives National Land Cover Database (NLCD) acronyms as a reference

NLCD code	Land use variables	PCA loadings
Landscape configuration		
AI	Aggregation index (*area weighted mean aggregation index (AI) across all land use classes within a buffer. AI is defined by the number of like adjacencies involving a given class/maximum possible of like adjacencies involving this class*)	0.85
PD	Patch density (*number of patches per unit area*)	−0.83
LPI	Largest patch index (*percentage of total landscape area comprised by the largest patch*)	0.68
Landscape composition classes		
N71	Grassland/herbaceous	0.61
N41	Deciduous forest	−0.56
N81	Pasture/hay	−0.54
N22	Developed, low intensity	−0.49
N23	Developed, medium intensity	−0.48
N21	Developed, open space	−0.45
N24	Developed, high intensity	−0.44
N90	Woody wetlands	−0.4
N43	Mixed forest	−0.38
N82	Cultivated crops	0.31
N52	Shrub/scrub	−0.3
N42	Evergreen forest	−0.3
N95	Emergent herbaceous wetlands	0.07

Cowbird dynamics

We modelled cowbird abundance on a route i and a year t, $NP_{i,t}$, as a Poisson distribution with the mean, $\lambda P_{i,t}$, depending on the growth rate of route i at time $t-1$ ($coloP_{i,t-1}$), immigration from the others routes through parameter $D_{i,t-1}$ and a lognormal overdispersion term ($\varepsilon_{i,t}$):

$$\begin{cases} NP_{i,t} | \lambda P_{i,t} \sim \text{Poisson}(\lambda P_{i,t}), \\ \lambda P_{i,t} = \delta_{i,t-1} \times coloP_{i,t-1} \times D_{i,t-1} + \varepsilon_{i,t}. \end{cases} \quad (1)$$

The variable $\delta_{i,t-1}$ prevented cowbirds to colonize routes without any host species by equalling 0 when no hosts were recorded on the route i at time $t-1$, and 1 otherwise. We then regressed the growth rate against a function of landscape fragmentation at route i (L_i) and host abundances $NH_{i,t,h}$ ($h = 1,\ldots,58$), with an intercept $cp0$ and slope coefficients $cp1$ and $cp2_h$:

$$\log(coloP_{i,t}) = cp0 + cp1 \times L_i + \sum_h (cp2_h \times NH_{i,t,h}). \quad (2)$$

Finally, $D_{i,t-1}$ was the summation over all the routes j of a product of dispersal rate from route j to i ($m_{j,i}$) and the number of cowbirds on that route ($NP_{j,t-1}$):

$$D_{i,t-1} = \sum_j (m_{j,i} \times NP_{j,t-1}). \quad (3)$$

We assumed dispersal rates to be an exponentially decreasing function of the distance $d_{i,j}$ between routes i and j:

$$m_{i,j} = \frac{1}{2 \times \text{dist}M} \times \exp\left(-\frac{d_{i,j}}{\text{dist}M}\right), \quad (4)$$

where $\text{dist}M$ was the mean dispersal distance of cowbirds. Note that this parameter should not be viewed as a direct measure of individual cowbirds' effective dispersal, but rather as an indication of the spatial scale at which the population processes are structured. The route-level abundances of cowbirds were highest in the species' historical area of presence (Northern Great Plains), but there was no clear pattern justifying further complexity in the spatial structure of our model (Fig. 1).

Host dynamics

As for cowbirds, we modelled host species' route-level abundance ($NH_{i,t,h}$, $h = 1,\ldots,58$) as a Poisson distribution, with the mean, $\lambda H_{i,t,h}$, depending on host growth rate ($coloH_{i,t-1,h}$), host abundance at time $t-1$ and a lognormal overdispersion term ($\varepsilon'_{i,t,h}$):

$$\begin{cases} NH_{i,t,h} | \lambda H_{i,t,h} \sim \text{Poisson}(\lambda H_{i,t,h}), \\ \lambda H_{i,t,h} = coloH_{i,t-1,h} \times NH_{i,t-1,h} + \varepsilon'_{i,t,h}. \end{cases} \quad (5)$$

A complementary analysis did not reveal any spatial covariance pattern in host species' growth rates (Appendix S1). We therefore assumed that effects of host dispersal on their growth rates were negligible and that host–parasite interactions were primarily local. We regressed the growth rate against a function of landscape fragmentation and cowbird abundance on the route i, in which we allowed the intercept $ch0_h$ and slope coefficients $ch1_h$ and $ch2_h$ to differ per species:

$$\log(coloH_{i,t,h}) = ch0_h + ch1_h \times L_i + ch2_h \times NP_{i,t} \quad (6)$$

Model specifications and performances

We computed a Bayesian joint posterior distribution for inference on the parameters (Gelman *et al.*, 2004), via a Markov chain Monte Carlo (MCMC) method under JAGS software (Plummer, 2003). We specified non-informative priors for all the parameters and computed three MCMC-chains of 101,000 iterations (the run took 15 days on a computation server with 2 × 2.93 GHz, 48GB of RAM under

Microsoft Server 2008 64bits). We discarded an adaptation period of 1000 iterations and a burn-in of 50,000 iterations, and used the remaining 50,000 iterations, thinned by 50, for inference (hence, our inference was based on 3×1000 iterations). As assessed by Gelman and Rubin statistic $\hat{R}$ (Gelman *et al.*, 2004), these settings resulted in acceptable convergence for all parameters except five $cp2$, all below a $\hat{R}$ of 1.3 (see Appendix S2). Bayesian *P*-values (Gelman *et al.*, 2004) based on a comparison of observed and replicated *NP* and *NH* revealed an acceptable fit (see Appendix S3).

Effect of host traits on host–cowbirds relationships

We explored trait-mediated differences in host–cowbirds dynamic relationships by plotting $cp2_h$ (effect of host abundance, NH, on cowbird growth rates) and $ch2_h$ (effect of cowbird abundance, NP, on host growth rates) in a functional space built with the two-first components of a Hill & Smith analysis (an equivalent to Principal Component Analysis mixing continuous and categorical data, Hill & Smith, 1976), summarizing the nine host life history traits. The first axis of this multivariate analysis ranged from larger species nesting in shrubs, with omnivorous or seed-based diets (negative values), to smaller species living in forested or arid habitats, nesting in closed nests or cavities and feeding mostly on fruits and invertebrates (positive values, see Table S1 for trait loadings). We therefore interpreted this first component as an axis separating ecological generalists from specialist species more tightly related to one of the two extremes of a moisture-habitat gradient. The second component ranged from open or rocky habitat species with cooperative breeding behaviour (negative values) to forest species (positive values). We interpreted it as a gradient of habitat preference.

We categorized $cp2_h$ and $ch2_h$ as positive (negative) on the basis of their posterior probability being larger (smaller) than 0. We defined a third class for parameters not differing from 0, defined as those which probabilities were below 0.95. We then grouped host species using ellipses centered on the centroids of each category, with axes representing $1.5 \times$ the standard deviation of species' coordinates on the two components of the functional space. We assessed the significance of ellipses separation on the functional axis with a MANOVA taking species' coordinates as the response variables and either $cp2$ or $ch2$ sign categories (positive, negative, non-significant) as the predictor. All analyses were implemented under the *ape* and *ade4* libraries in R 3.0.1 (R Development Core Team, 2011).

RESULTS

Spatial scale of cowbirds population dynamics

The estimated mean dispersal distance of cowbirds was well below the average distance between adjacent routes (Fig 2; dist*M*: median = 43.5 km, 95% credibility interval [35.6 km, 53.6 km]). The predominance of small-scale patterns of covariation among cowbird growth rates suggested that cowbird population dynamics are influenced by local rather than large-scale environmental drivers and that breeding dispersal occurs mainly over short distances.

Effects of landscape on growth rates

Cowbirds had higher population growth rates in routes located within fragmented landscapes with high levels of human development (Fig. 3), as only did three host species (Orchard Oriole *Icterus spurius*, Brewer's Blackbird *Euphagus cyanocephalus*, Grasshoper Sparrow *Ammodramus savannarum*). Most host species either did not respond to landscape configuration ($n = 30$) or had higher growth rates in less fragmented, less human-altered landscapes ($n = 25$).

Effects of host abundance on cowbird population dynamics (*cp2*)

The abundance of eight hosts increased cowbird growth rates, among which two were related to homogeneous habitats (Western Meadowlark *Sturnella neglecta* and White-eyed Vireo *Vireo griseus*), while only one (Grasshoper Sparrow *A. savannarum*) shared cowbirds' positive response to more heterogeneous landscapes with higher levels of human presence (see Table S2a for an overview of cowbird demographic responses to landscape and hosts abundance and Table S3 for species-specific parameter credibility intervals). The five others did not respond to habitat. Cowbird negative growth rates were related to high abundances of eight hosts that favoured homogeneous landscapes or without any landscape response (Baltimore Oriole *Icterus galbula*, Tufted Titmouse *Baeolophus bicolor*, Horned Lark *Eremophila alpestris*, Lazuli Bunting *Passerina amoena*, Eastern Phoebe *Sayornis phoebe*, Eastern Wood-Pewee *Contopus virens,* Rose-breasted Grosbeak *Pheucticus ludovicianus* and Rock Wren *Salpinctes obsoletus*). The 43 remaining hosts did not affect significantly cowbird demography. The effects of host abundance on cowbird growth rates significantly depended on host traits, although the ellipses overlapped partly in the functional space (Fig. 4a, MANOVA: $F_{4,58} = 3.57$, $P < 0.01$). Host species positively affecting cowbird growth rates tended to be generalist species occurring in open habitats, while negative effects were associated with ecological specialization and preference for forest (see Table S1 for the Hill & Smith loadings).

Effects of cowbird abundance on hosts population dynamics (*ch2*)

The growth rates of 32 host species were unrelated to cowbird abundance, among which 17 exhibited no response to habitat, 14 occurred more in homogeneous landscapes and one in disturbed areas (see Table S2b for an overview of hosts demographic responses to landscape and cowbird abundance and Table S3 for species-specific parameter credibility intervals). Twelve hosts had negative growth rates where cowbirds were abundant, among which eight did not respond to landscape,
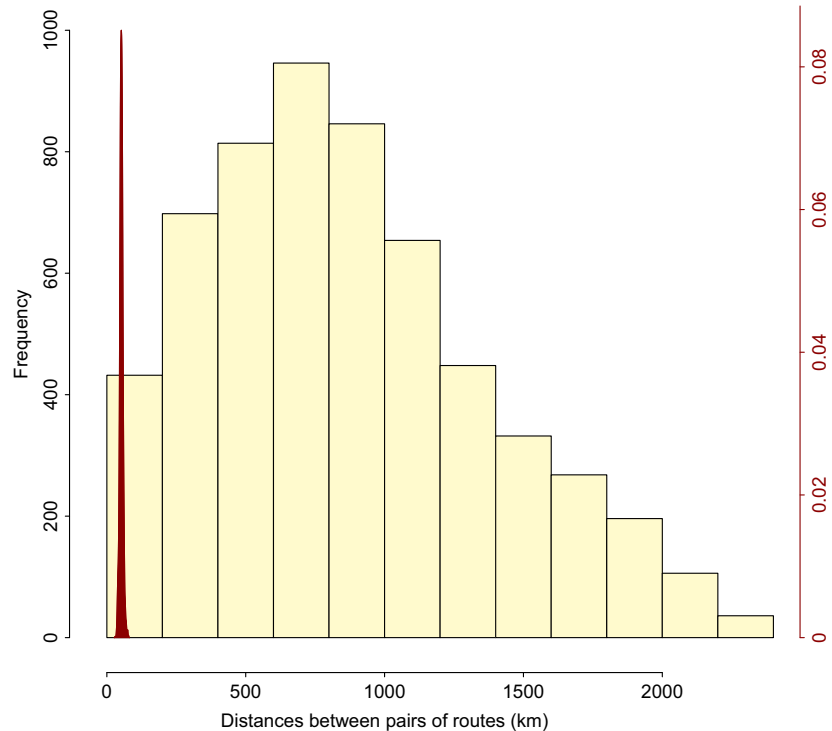
Figure 2 Distribution of pairwise distances between 76 breeding bird survey routes in the US Great Plains Bird Conservation Regions. The red curve represents the posterior probability density function of cowbirds' mean dispersal distance (distM), as estimated by our host–parasite model. It reflects the spatial scale of covariance in cowbirds' colonization rates among neighbouring locations.

one lived in fragmented areas (Brewer's Blackbird *Euphagus cyanocephalus*) and three in homogeneous habitats (Northern Cardinal *Cardinalis cardinalis,* Ovenbird *Seiurus aurocapilla* and Eastern Meadowlark *Sturnella magna*). Fourteen other hosts had positive growth rates in locations where cowbirds were abundant, including eight species favouring homogeneous landscapes (Red-winged Blackbird *Agelaius phoeniceus,* Tufted Titmouse *Baeolophus bicolor,* Northern Mockingbird *Mimus polyglottos,* Lazuli Bunting *Passerina amoena,* Eastern Bluebird *Sialia sialis,* Clay-coloured Sparrow *Spizella pallida,* Western Meadowlark *S. neglecta* and Warbling Vireo *Vireo gilvus*) and only one living in more disturbed areas (Grasshopper Sparrow), the latter probably reflecting shared habitat preferences with cowbirds. However, the low proportion of species responding both to landscape and to cowbird abundance suggests that the opposite habitat preference of the hosts and their parasite cannot be invoked as the sole explanation for their covariation patterns. The effects of cowbird abundance on host dynamics were independent of host traits (Fig. 4b).

DISCUSSION

Dynamic relationships between cowbird and its hosts

Host–parasite interactions have the potential to affect patterns of community dynamics (Horwitz & Wilcox, 2005; Ricklefs, 2011, 2013), but have been poorly studied at large scales because such hard-to-observe process can most often be investigated only through their signatures in correlative

patterns (McGill & Nekola, 2010; Wisz *et al.*, 2013). Modelling the covariation between cowbirds and their multiple hosts enabled us to assess the large-scale effects of an antagonistic interaction on large-scale bird population dynamics. We showed that interactions between cowbirds and hosts are highly variable. Contrary to our prediction (*i*), host species positively affecting cowbird growth rates did not systematically exhibit negative growth rates where cowbirds are abundant, which is consistent with the low community-wide effects of cowbird parasitism observed in local studies (De Groot & Smith, 2001). Cowbirds have been shown to be a primary factor of local population decline for both common species such as the Song Sparrow (*Melopsiza melodia*) (Smith *et al.*, 2002) or rarer hosts such as the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Whithfield, 2000); yet, these specific species did not exhibit large-scale dynamic responses to parasitism in our analyses. Several hosts even had positive growth rates in cowbird-rich areas, suggesting that the relative influences of habitat suitability and parasitism on host population dynamics vary on a species-per-species basis. Identifying the specific processes that blur direct parasitism effects at large scales is beyond the capacities of our correlative model, but may include host immigration into sink populations triggered by locally high parasitism levels or interactions between other biotic or non-biotic processes (Donovan *et al.*, 1995; De Groot & Smith, 2001).

Spatial and environmental effects

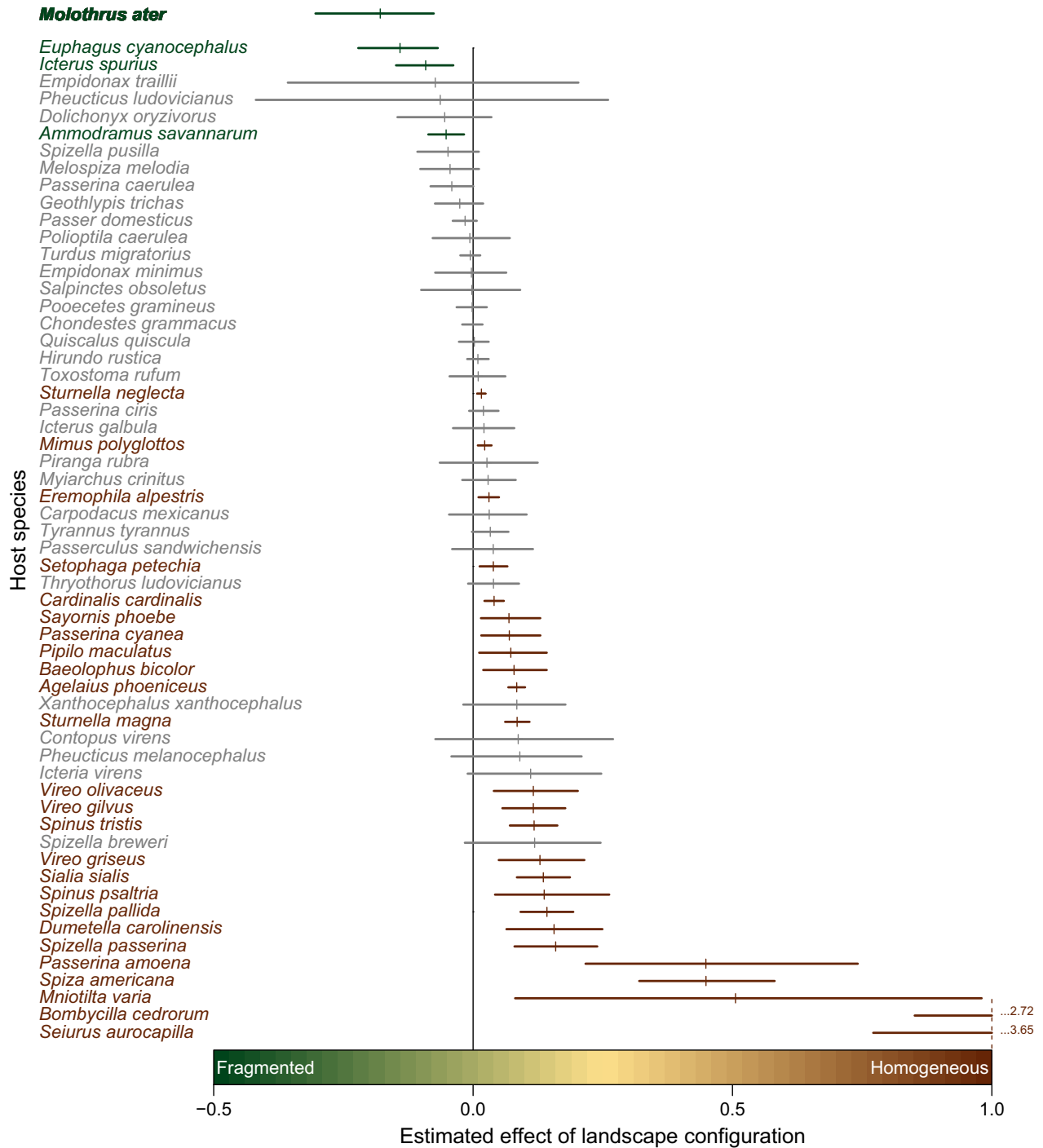Our estimates of the cowbird dispersal distance are consistent with their predominantly local movements as adults

Figure 3 Effect of landscape composition on the growth rates of Brown-headed Cowbirds and 58 of its host species (green: significant negative coefficient, brown: significant positive coefficient, grey: non-significant coefficient). Landscape composition ranges from fragmented to homogeneous landscapes (see Table 1 and Fig. 1b for details).

(Anderson *et al.*, 2012). Accordingly, cowbird occupancy and density have been related to local factors including host richness, landscape fragmentation and increasing urbanization, but not to climatic factors or other large-scale environmental gradients (Robinson, 1999; Chace *et al.*, 2005; Cummings & Veech, 2013). We consistently showed that cowbirds had higher growth rates in fragmented landscapes, while most host species either did not respond to landscape configuration, or had higher growth rates in less disturbed, more homogeneous habitats with preserved grasslands and forest. As a livestock-related species, cowbirds avoid large expanses of homogeneous forest (Morrison & Hahn, 2002) and have
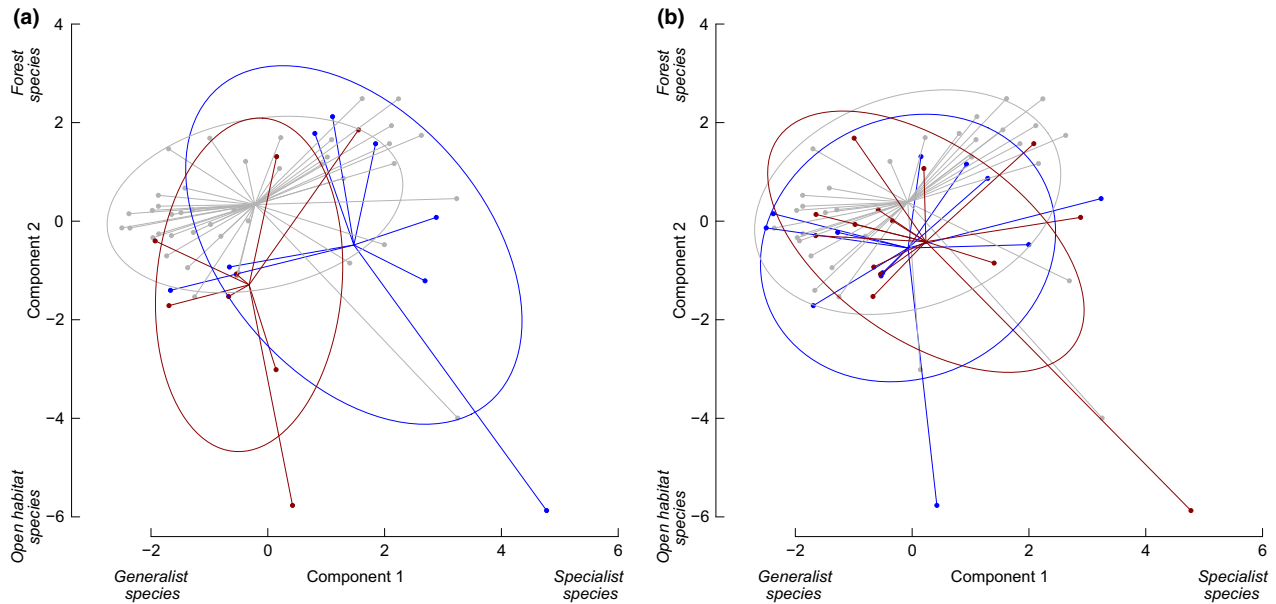
Figure 4 Distribution of host effects on cowbird growth rates ($cp2$: a) and of cowbird effects on host growth rates ($ch2$: b) on a multivariate functional space built from nine ecological traits representing key aspects of bird life history: habitat and dietary preferences, nest type and location, foraging method, mating, productivity and body size (see Table S1 for the loadings of each trait on principal component axes). Grey, blue and red dots represent, respectively, non-significant, negative and positive responses.

recently expanded into partially deforested areas, where they find suitable perches to detect hosts (Thompson *et al.*, 2000). Habitat fragmentation has thus recently favoured local sympatry among cowbirds and hosts with which they have little recent co-evolutionary history (Morrison & Hahn, 2002; Servedio & Hauber, 2006), and increased the length of forest edges in landscapes, enhancing parasitism rates (Thompson *et al.*, 2000). Man-mediated disturbance and management of forest may therefore increase parasitism effects on passerine communities in addition with increased rates of predation (Tewksbury *et al.*, 2006), competition, aggressiveness (Robertson *et al.*, 2013) and decrease in resource availability.

Effect of host ecological traits

We found that high abundances of larger, habitat generalist species with omnivorous diets tended to be associated with positive cowbird growth rates, while species more specialized for food and habitat had negative effects. Furthermore, the effects of cowbirds on hosts were indistinct in the functional space. These results counter local studies showing that large-bodied and productive species tend to be less parasitized because their more numerous and larger host chicks out-compete cowbird nestlings (Lorenzana & Sealy, 1999), while canopy nesters and forest species have been reported to be more negatively affected by cowbirds than grassland, shrubland and ground-nesting species (Robinson *et al.*, 2000; Jensen & Cully, 2005). From our large-scale results in the heavily man-impacted Great Plains, cowbird abundance seems to primarily increase in suitable landscape configurations and may be influenced by

specific hosts' ecological traits at fine spatial grains within landscapes. Hosts responding negatively to cowbird abundance had no particular effect on cowbird population dynamics, further indicating that cowbirds select hosts as a consequence of their nest availability and habitat preference rather than through targeted parasitism (Strausberger & Ashley, 1997).

Methodological perspectives

Although our model is a step towards a better understanding of large-scale dynamic covariation of host species with their parasites, this comes at the cost of a number of limitations dictated by our current computational restrictions. In particular, we had to assume no influence of host dispersal, which is supported by supplementary results (see Appendix S1), but is nevertheless a simplification. Host dispersal may, in particular, compensate local negative growth rates triggered by cowbirds or allow to escape cowbird-infested areas (Boulinier *et al.*, 2001a), and thus decrease the strength of host–parasite interactions at the community level. In addition, incorporating interactions between landscape structure and the host–parasite relationships in our model may help better deciphering the relative influences of parasitism and habitat on passerine dynamics. Last, allowing spatial variability and temporal lags > 1 in host–parasite interactions could increase the capacity of our model to reflect spatial and temporal dependencies in cowbird–host interactions. These considerations point to challenging, but necessary next steps for improving our understanding of large-scale host–parasite dynamics and their implications in community assembly.

CONCLUSION

While the Brown-headed Cowbird has been the focus of an extensive literature on both local conservation issues and more basic behavioural processes, our study is, so far, among the few that investigate its dynamic relationship with hosts over large spatial scales. We found a large-scale signature of cowbird parasitism in a limited number of host species' population dynamics. Our results thus suggest that cowbird growth rates and their effects on hosts are driven over large spatial extents by a combination of indirect, landscape-mediated effects, short-distance adult dispersal and a secondary, perhaps more local, influence of host ecological traits. We therefore support the recommendation that cowbird management should focus on landscape-scale habitat suitability (Robinson *et al.*, 2000; Thompson *et al.*, 2000) and that individual removal will only be a short-term local solution to threats posed by high cowbird density to rare species (Smith *et al.*, 2002). Overcoming the current technical limitations for spatially explicit modelling of host–parasite dynamics will allow to link and compare the effects of parasitism on passerine population dynamics to those of climatic changes and other biotic interactions, for example pathogens (Ricklefs, 2013). Nevertheless, our results bring out that parasitism can be an important biotic component of habitat loss and fragmentation effects on bird communities at large spatial scales.

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SUPPORTING INFORMATION

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

Appendix S1 Spatial autocorrelation of growth rates in host species.

Appendix S2 Convergence of parameters as reflected by Gelman's R-hat.

Appendix S3 Evaluation of model fit: comparison of observed and replicated data.

Table S1 Loadings of the Hill and Smith analysis on hosts life history traits.

Table S2 Comparison of landscape effects with host-cowbirds demographic covariations.

Table S3 Estimated relationships between the Brown-headed Cowbird and 58 of its host species.

BIOSKETCH

The Center for Informatics Research on Complexity in Ecology is a research centre established at Aarhus University in 2012 to study the importance of complexity for how ecosystems function and respond to environmental change, by employing an informatics approach, analysing large ecological data sets using advanced statistical and mechanistic modelling. CIRCE focuses on three major complexity factors: species interactions, dispersal and environmental variability (http://projects.au.dk/circe-center-for-informatics-research-on-complexity-in-ecology/).

Author contributions: J.-Y.B. and J.-C.S. conceived the study; J.P., J.-Y.B. and O.G. built the model and analysed the results; J.-Y.B. led the preparation of the manuscript; all authors contributed significantly to the writing.

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