Research article

A comparison of random draw and locally neutral models for the avifauna of an English woodland

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Abstract

Background: Explanations for patterns observed in the structure of local assemblages are frequently sought with reference to interactions between species, and between species and their local environment. However, analyses of null models, where non-interactive local communities are assembled from regional species pools, have demonstrated that much of the structure of local assemblages remains in simulated assemblages where local interactions have been excluded. Here we compare the ability of two null models to reproduce the breeding bird community of Eastern Wood, a 16-hectare woodland in England, UK. A random draw model, in which there is complete annual replacement of the community by immigrants from the regional pool, is compared to a locally neutral community model, in which there are two additional parameters describing the proportion of the community replaced annually (per capita death rate) and the proportion of individuals recruited locally rather than as immigrants from the regional pool.

Results: Both the random draw and locally neutral model are capable of reproducing with significant accuracy several features of the observed structure of the annual Eastern Wood breeding bird community, including species relative abundances, species richness and species composition. The two additional parameters present in the neutral model result in a qualitatively more realistic representation of the Eastern Wood breeding bird community, particularly of its dynamics through time. The fact that these parameters can be varied, allows for a close quantitative fit between model and observed communities to be achieved, particularly with respect to annual species richness and species accumulation through time.

Conclusion: The presence of additional free parameters does not detract from the qualitative improvement in the model and the neutral model remains a model of local community structure that is null with respect to species differences at the local scale. The ability of this locally neutral model to describe a larger number of woodland bird communities with either little variation in its parameters or with variation explained by features local to the woods themselves (such as the area and isolation of a wood) will be a key subsequent test of its relevance.

Background

The question of the importance of interactions between species in determining the structure of species assem-blages is one that has occupied ecologists for many decades [1-6]. Direct evidence for the influence of interactions is difficult to garner without intensive field

studies [e.g. desert rodents, [7,8]], and so most of the evidence that has been presented for such effects is indirect. In particular, consistencies in assemblage composition have been interpreted by many as evidence for strong interspecific interactions at the local scale that constrain assemblages to certain structural patterns [9,10]. Apparent regularities in the species compositions of local assemblages are often attributed to locally occurring processes that differentiate between species. Examples include habitat associations, where shared habitat preferences result in repeated associations of particular species [3], and interspecific competition, which is thought to discourage the co-occurrence of particular pairs of species and to favour particular combinations of species that minimise competition whilst ensuring efficient resource use [6,11-13].

An important stage in the development of ecology has been the recognition that regional processes can have a profound influence on the structure of local communities [14,15]. Although the regional species pool is necessarily the sum total of its constituent local assemblages, it does not follow that causality of structure should run solely from the local to the regional level [16]. The nature of the regional pool can influence the structure of local assemblages, as patterns can be propagated from regional to local assemblages through individual dispersal. Demonstrating the role of locally occurring interactions for community structure requires an appropriate null model of the structure that would be expected if communities consisted of non-interacting species assembled at random from the regional species pool [17,18]. This idea has been used explicitly to produce null models in which local communities are generated by random draws of individuals or species from a regional pool, the resulting simulated local communities being then compared to real data. The random draw procedure should exclude local processes, so that any patterns in the resulting simulated assemblages ought to be due to chance, or to be a consequence of the structure of the regional species pool. It is the difference between the real and null-modelled communities that needs to be explained by local processes and not the entire community structure.

One example of the random draw approach is a study by Blackburn and Gaston [19] of the breeding bird community of Eastern Wood, a small (16 ha) deciduous woodland in Surrey, southern England. They demonstrated that this community could be accurately modelled by drawing species at random from a defined pool of British breeding woodland bird species. When the probability of selecting a species was weighted by either its abundance or its range size in Britain, the resulting random assemblages showed a high percentage similarity in species composition with the real Eastern Wood community (76.7% and 72.6%

respectively). One of the limitations of random draw models that select by species, such as that just described, is that they draw a predetermined number of species from the regional pool, and therefore make no predictions about species richness. Clearly, neither can they make any predictions about the local abundances of the species they predict to be present. These shortcomings are addressed by models that select a predetermined number of individuals, rather than species, and then determine how many species are present in the sample, together with the abundance of those species. This type of model was also investigated for Eastern Wood, and found to accurately predict mean annual species richness but to significantly overestimate long-term species richness [20]. One reason for this last result may be a further undesirable feature of such models: the local community is modelled each year by a new random draw of individuals. Hence, the entire community is completely replaced each year, and all recruits to the community come from the regional pool: there is no local recruitment.

Here, we extend these random draw models for Eastern Wood to produce a more realistic model of the breeding bird community, whilst retaining many of the features that allow the model to be referred to as 'null' (the degree to which this model and others like it are truly null is considered further in the Discussion). Specifically, we adopt a neutral model approach, whereby all species are treated as identical on a *per capita* basis, and which incorporates parameters that specify the annual individual death rate in the community and the proportion of those deaths that are replaced by local births rather than immigrants drawn from the regional pool. We model annual changes in an initial population of individuals derived by random draw under the influence of these two parameters, and assess the extent to which this approach can replicate the actual structure of the breeding bird community of Eastern Wood. We evaluate the performance of this locally neutral model relative to that of the simple random draw model, and discuss its usefulness as a null model when investigating community structure.

Results

Over the 29 years in the period 1950–1979, a mean (± S.D.) of 32.03 ± 2.29 species were recorded breeding in Eastern Wood per year, and 45 species in total. The random draw model predicts these values poorly: mean estimates derived from 1000 replicates are 38.1 (± 2.35) and 60.58 (± 1.65), respectively, which differ significantly from the true figures. Standard deviations associated with model estimates of species richness indicate variability in model estimates and not the year to year variation indicated by the standard deviation of the observed mean species richness of Eastern Wood. The locally neutral model can perform rather better, accurately predicting both
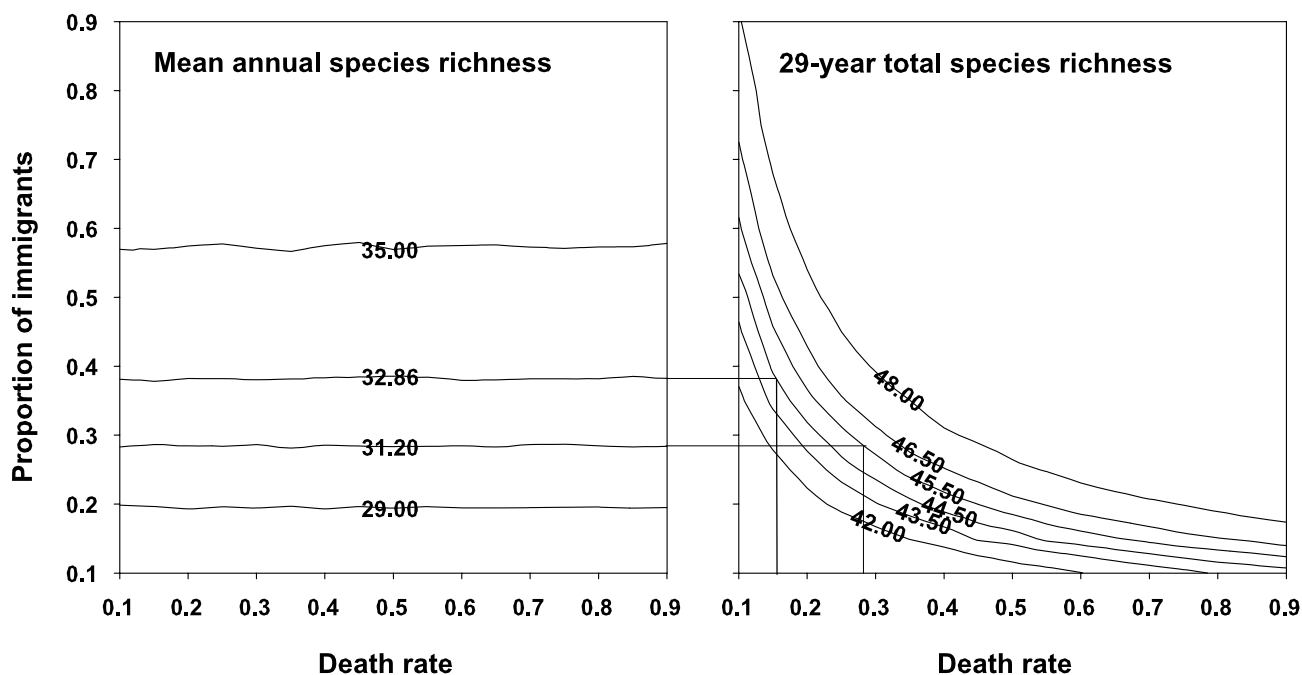
Figure 1
The effect of immigration rate and death rate parameters on neutral model estimates of species richness.
Response of mean annual (left) and total (right) species richness estimates to variation in immigration rate (*m*) and death rate
(*d*) in the neutral model. The area of parameter space between contours 31.20 and 32.86 in the left-hand figure corresponds to
values of *m* and *d* that give estimates encompassing the mean ± 95% probability interval of annual species richness in Eastern
Wood. The area in the right-hand figure between contours 44.5 and 45.5 corresponds to values of *m* and *d* that give integer
total richness values over 29 years of 45 species.

annual and total species richness when appropriate values
for *m* and *d* are used [see also [21]]. Figure 1 shows the
sensitivity of the mean annual and total 29-year species
richness predictions to variation in *m* and *d*. Mean annual
richness predictions are independent of *d* and depend
only on *m*. The number of species predicted in a 29-year
period is dependent on both *m* and *d*, which covary nega-
tively. Mean annual richness is predicted correctly for the
restricted range of immigration rates *m* ≈ 0.28 – 0.38.
Within this restricted range of immigration rates, the
observed total of 45 species is predicted for the restricted
range of death rates *d* ≈ 0.16 – 0.28. In all subsequent per-
formance tests of the neutral model we assume *m* = 0.34
and *d* = 0.22: these values produce the best fit to mean
annual and total species richness within the range of suit-
able values indicated graphically in Figure 1.

Figure 2 shows the species accumulation curve for Eastern
Wood over the period 1950–1979, together with mean

species accumulation curves for a 50-year period, derived
from 1000 replicates of each model. The performance of
the random draw model is clearly poor, and not one of the
Eastern Wood data points falls within the 95% probability
intervals for the model accumulation curve. The neutral
model performs rather better. The values used for param-
eters *m* and *d* were derived from observed values for the
mean annual and total 29-year species richness of Eastern
Wood, so it is no surprise that the predictions made by the
neutral model for these years are accurate. However, the
model predicts species accumulation well over the entire
range of available data; all the Eastern Wood data points
fall well within the 95% probability intervals.

In any given simulated assemblage, some of the 45 species
observed breeding in Eastern Wood in the period 1950–
1979 will be correctly modelled as present, some will be
incorrectly modelled as absent, while further species that
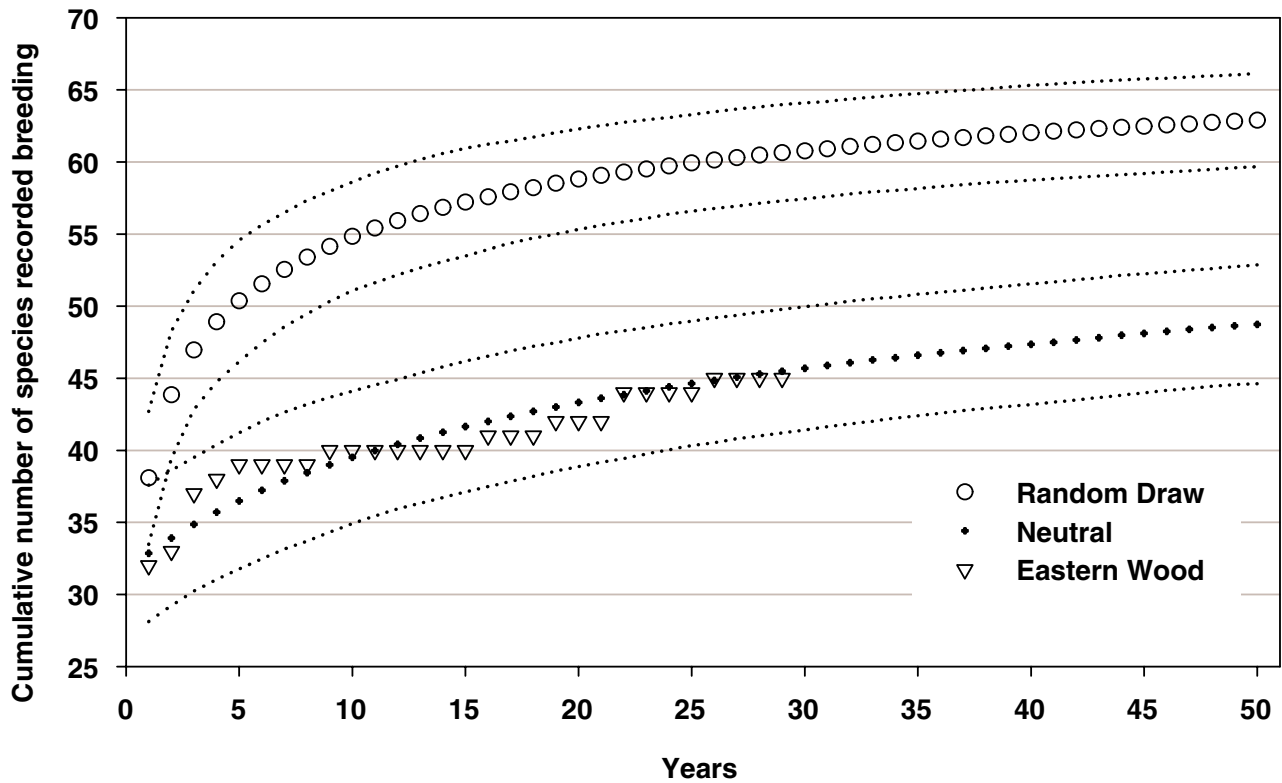were not observed in the real assemblage will be present

Figure 2
Species accumulation curves. The observed species accumulation curve for Eastern Wood together with curves predicted by the random draw and neutral models. Dashed lines delimit the zones within which the models predict that the curves should fall for 95% of replicates.

Table 1: Species composition predictions.

	Random draw model	Neutral model
Mean (± SD) number of species correctly predicted as present	42.1 ± 1.12	33.9 ± 1.69
Mean (± SD) number of species incorrectly predicted as absent	2.87 ± 1.12	11.08 ± 1.69
Mean (± SD) number of species incorrectly predicted as present	17.5 ± 1.29	10.6 ± 1.41
Mean (± SD) number of correct predictions (absences and presences)	60.7 ± 1.68	59.3 ± 2.21

The performance of the random draw and neutral models with regards to predicting the species composition of Eastern Wood. Note that care is needed when interpreting these statistics, as they simulate assemblages of differing mean species richness. Comparisons based on the number of species correctly or incorrectly selected by a model are biased towards models that generate assemblages with higher and lower species richness, respectively. The last comparison is unbiased with respect to simulated species richness.

in the model assemblage. Table 1 summarises this information for 1000 runs of each model. The percentage of those species actually observed breeding in Eastern Wood that were present in replicates was higher for the random draw model: 93.6% on average, compared to just 75.4%

for the neutral model (Table 1). However, the average number of species predicted to have bred after 29 years by the random draw model is much higher than that for the neutral model (60.5 versus 45.5). Therefore, as a consequence of its lower accuracy in predicting the 29-year spe-

cies total, there are more opportunities for the random draw model to pick species. Consequently, it also selects a greater number of species that were not observed breeding in Eastern Wood (Table 1). The percentage of those species predicted to breed in Eastern Wood actually observed breeding during the period studied was higher for the neutral model (76.3%) than for the random draw model (70.7%). The two models perform almost equally well when comparing the total number of correct predictions (species in the woodland pool correctly predicted as present plus the number correctly predicted as absent; Table 1).

Mean annual abundance predictions for each species are presented in Additional file 1 for each model, together with the observed mean annual abundance of the species in Eastern Wood in the period 1950–1979. If the abundance observed in the Eastern Wood data falls within the 95% probability interval for a model, we consider the pre-

diction to be correct. The random draw model underestimates the abundances of 28 species in the regional pool, and overestimates a further 28. Thus, 69.1% of species abundances differ from random draw model predictions. The neutral model underestimates the abundances of 13 species, and overestimates for just 10, giving 28.4% incorrect predictions.

Fewer abundance estimates are classified as incorrect for the neutral model because the probability intervals for those predictions are wider. Whilst differences between consecutive years within a replicate are smaller in the neutral model than the random draw model, differences between mean communities (averaged over 29 years) from separate replicates are greater in the neutral model, resulting in larger probability intervals. Figure 3 illustrates this property for the two most abundant species in the regional pool: the wren, *Troglodytes troglodytes* and chaffinch, *Fringilla coelebs*.
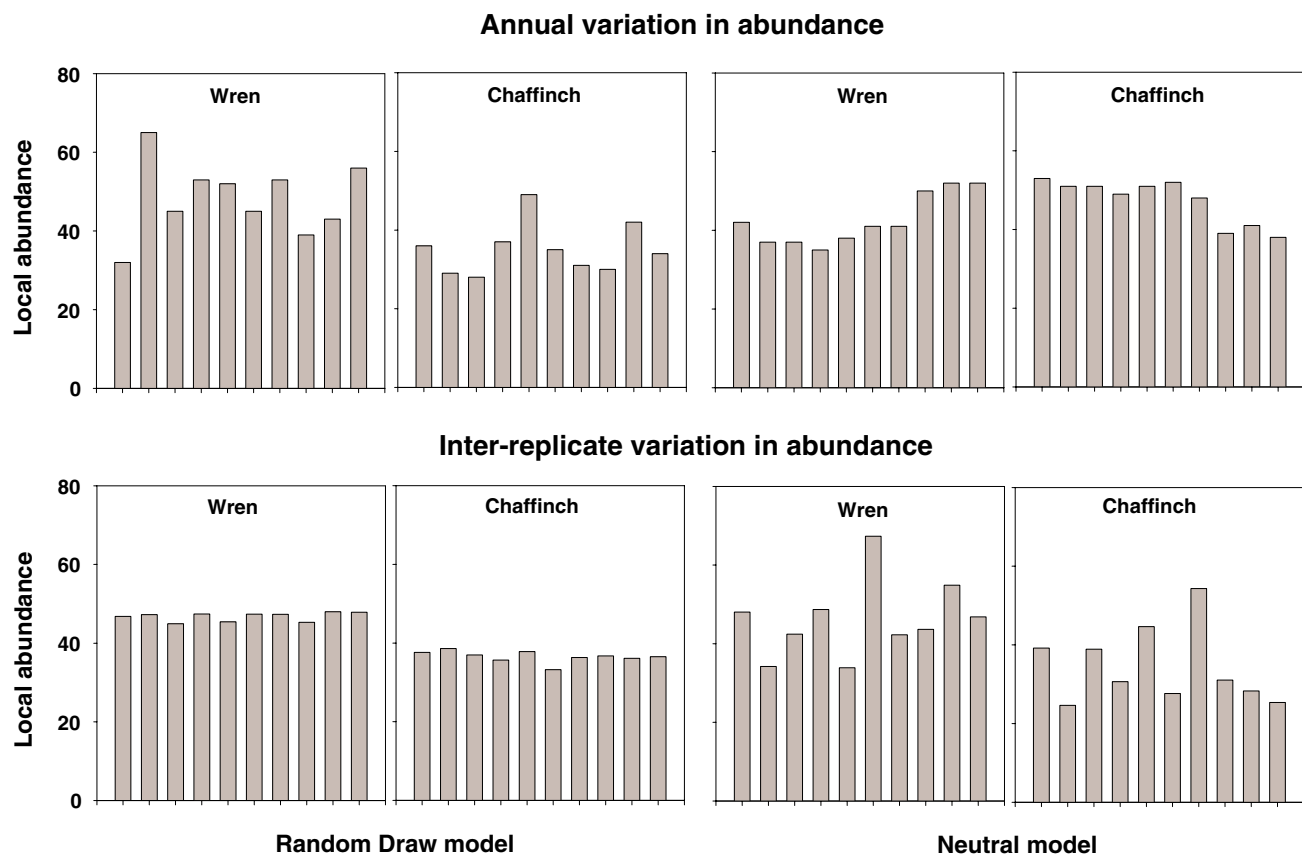

Figure 3
Inter-annual and inter-replicate variation in the random draw and neutral models. Top: the abundance of the wren and chaffinch in 10 consecutive years from a single replicate of each model. Year to year fluctuations in the abundances of species are greater for the random draw model than the neutral model. **Bottom:** the abundance of the wren and chaffinch in 10 independent replicates of either model. Conversely, inter-replicate variation in abundance is greater in the neutral model than the random draw model.
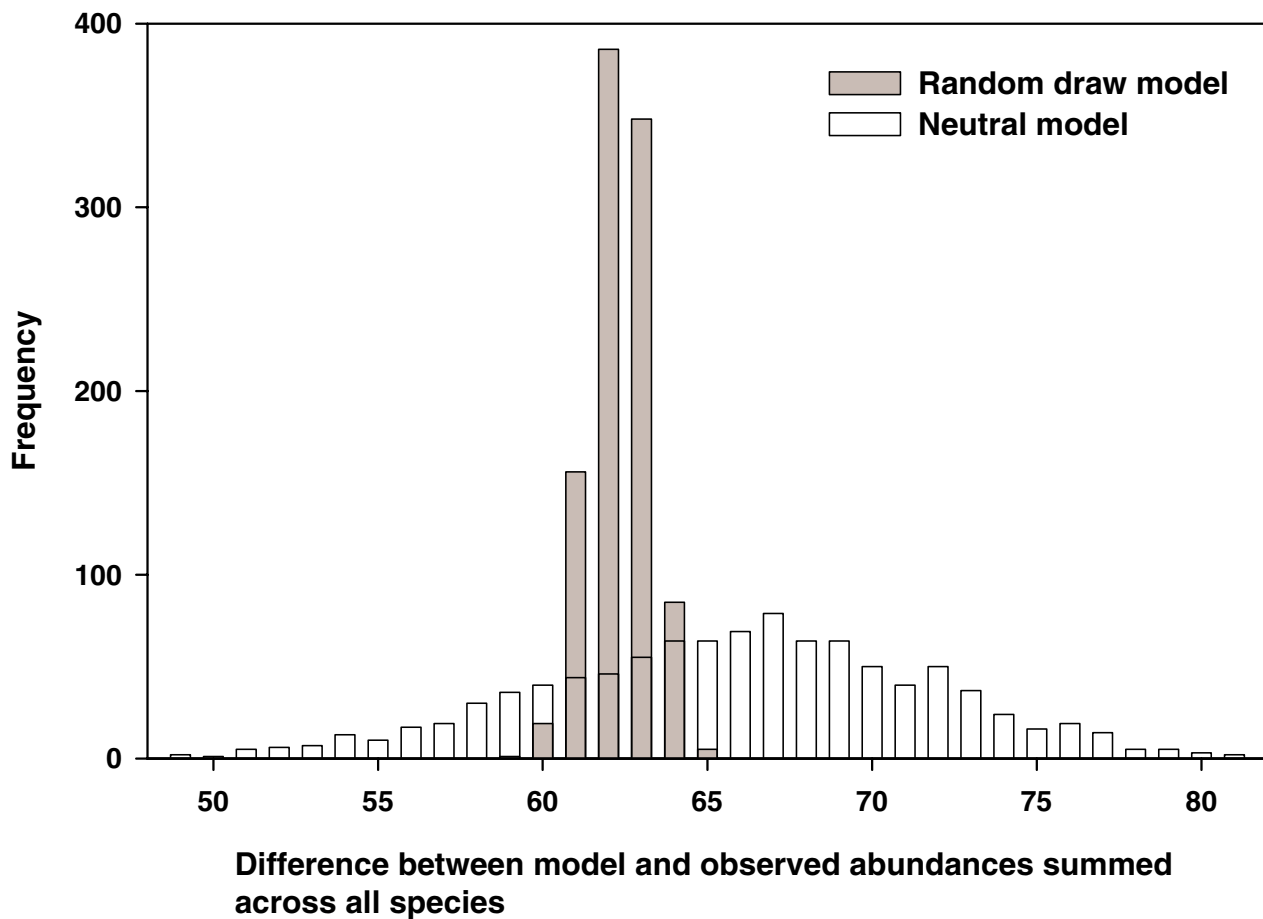
Figure 4
Overall model deviation from the observed Eastern Wood community. The superimposed frequency distributions of differences between predicted and observed abundance summed across all species, for the random draw model (grey) and the neutral model (white). Individual differences were squared and then the sum was back transformed by square rooting.

Whilst the neutral model tended to estimate the abundances of fewer species incorrectly than did the random draw model, neutral model species abundances actually differed slightly more on average from those of the Eastern Wood assemblage than did those of the random draw model communities. Figure 4 shows the frequency distributions, for 1000 model replicates, of the differences in species-specific abundance between the Eastern Wood community and each model run, summed across all species. The mean difference in abundance summed across all species is higher for the neutral model than the random draw model (65.3 individuals versus 61.8). How-

ever, because of the greater variability between replicate runs in the neutral model, some neutral model communities are more similar to the Eastern Wood community than are the most similar random draw communities (Figure 4).

The rank abundance curves for the real and simulated assemblages are presented in Figure 5. The random draw model underestimated the abundance at 7 out of 81 possible ranks and overestimated abundance at 35, a total of 51.9% of possible ranks. The neutral model underestimated and overestimated abundance at 5 and 4 ranks
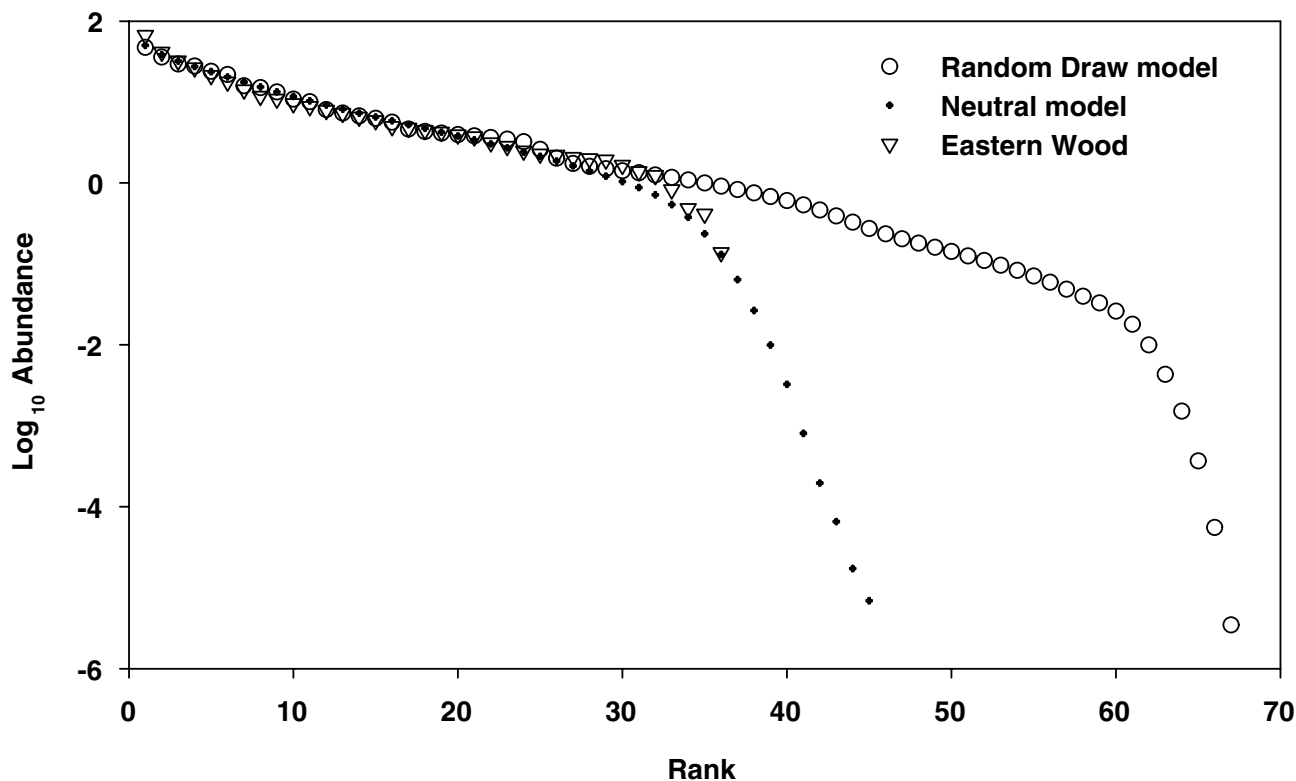
Figure 5
Rank-abundance plots for Eastern Wood and the random draw and neutral models. Abundances were ranked in descending order each year so that the abundance at rank *i* is the mean abundance of the *ith* species and not the abundance of any one species in particular.

respectively, meaning that just 11.1% of rank abundances were incorrectly estimated. Once again, this was largely due to the larger probability intervals associated with neutral model predictions. However in this case, differences between model and observed abundances, summed over ranks 1 to 36 (as in no year were more than 36 species recorded breeding in Eastern Wood) were smaller for the neutral than the random draw model (19.9 versus 22.1).

Discussion

Our findings are consistent with the view emerging from the field of macroecology, and from ecology in general, that much apparent local community structure may be attributed to processes that act on much larger scales than the immediate local community, and influence local communities through the dispersal of individuals across the wider landscape [14-16,20,22,23]. They are also in keeping with findings from both sides of a long-running debate over the use of null models in the analysis of com-

munity structure [24-29]; although the effects of species interactions can be readily demonstrated using null models for pairs of species or narrowly defined guilds, these effects have been hard to detect when analysis is carried out at the level of the whole community [30] although more powerful recent analyses have succeeded [31,32]. To us this indicates that whole community structure is largely dominated by the influence of the regional species pool; with local processes adding the finer detail. Null models that reflect this can generate much of the structure observed in local assemblages.

Both the random draw and locally neutral models reproduce the Eastern Wood assemblage with a surprising degree of accuracy when it is considered that Eastern Wood comprises just 0.0014% of the British deciduous/mixed woodland of which the regional pool consists [statistic from [19]]. When differences in the number of species selected are accounted for, the accuracies of the

random draw and neutral models, in terms of correctly predicting the identities of the species inhabiting Eastern Wood, are almost identical (Table 1), as are species' mean predicted abundances (see Additional file 1). This is to be expected, as both models use the same regional source pool and the expected abundance of a given species in a replicate of either model is determined by its relative abundance in the source pool. Differences between the models arise because the local recruitment present in the neutral model allows species to spend a greater proportion of time away from their expected local population size, and to drift away from this expected population size to a greater degree.

The neutral model's superiority as a null model comes not then from closer estimates of mean species abundances, or a greater mean percentage correspondence in species composition, but rather from a more accurate representation of temporal patterns of species' presence and abundance in the local community. A replicate of the random draw model consists of 29 independent samples of 340 individuals from the regional pool: there is no continuity between communities from one year to the next. A replicate of the neutral model on the other hand consists of 29 annual communities that are correlated through time as a result both of shared individuals (as only part of the community is replaced each year) and local recruitment (new individuals are assigned to species according the local relative abundances of species already present in the local community). Species that are relatively rare in the regional pool appear less frequently in the neutral model (in fewer replicates) because there are fewer immigration events from the regional pool, and hence lower annual and 29-year species richnesses. When these rare species do immigrate from the regional pool, they can persist for a number of years because the entire community is not replaced each year. They can also increase in local abundance because replacements are made from the local community, where the rare species in question has a temporarily elevated relative abundance and hence an increased probability of selection (see also Hubbell 2001).

The abundances of all species show reduced year-to-year variability within replicates of the neutral model due to the temporal correlation in community composition described above. However, their abundances between replicates are more variable for the same reason. Whereas in the random draw model any unusually high or low abundances are averaged out over 29 independent samples, in the neutral model if a species is unusually abundant in one year, it is likely to remain so in subsequent years (e.g. Figure 3). It is this realistic level of inter-replicate variation, brought about by the incorporation of basic demographic rates, that makes the neutral model a better candidate for a null model of woodland bird com-

munities in England. We would not expect two woodlands to have identical avifaunas, and neither would we expect the same woodland to contain the same avifauna during separate time periods. Therefore, the best null model is not one that generates a mean avifauna identical to that of any one specific woodland, but rather a model that will produce a distribution of expectations within which the majority of woodland avifaunas fall.

The values for the proportion of immigrants, $m = 0.34$, and the death rate, $d = 0.22$, used to calibrate the neutral model were those that resulted in accurate estimates of annual and 29-year species richness. These values can be thought of as an average for all the species present in the woodland (see also below), and since most estimates of such parameters are for individual species, it is therefore difficult to assess to what degree they are realistic. Nevertheless, reported annual death rates for small-bodied bird species are usually greater than the 0.22 used here: 0.35–0.70 for small bodied land-birds [33], and a mean of 0.48 with range 0.37–0.71 for European passerines [34]. Likewise, the two reported estimates that we found in the literature of the proportion of new recruits to woodlands that were immigrants were also higher than the 0.34 used here, albeit that both referred to great tits, *Parus major*: 0.46 in Wytham Wood [35] and 0.69 ± 0.15 (1 S.D.) on Vlieland Island, Holland [[36]: cited in Gill, 1999].

Using values for m and d that are closer to these observed values does not result in wildly inaccurate estimates of species richness (Figure 1). Nevertheless, we used values that produced the best fit as there is reason to believe that estimates of required immigration rate and death rate will be systematically underestimated by the model. The real species pool from which Eastern Wood receives immigrants is spatially structured: species distributions are patchy at the national scale [37]. Related to this, the species compositions of woodlands become more distinct the further they are apart [38]. Frequency distributions of both natal and breeding dispersal distance are highly right-skewed [39] so that an immigrant to a real woodland is much more likely to have come from a nearby woodland with a similar species composition, than from a distant one with a more distinct species composition. A limitation of both the random draw and locally neutral models is that they use a non-spatial regional species pool, such that either the species populations are assumed to be evenly distributed across the region for which the species pool is compiled (in this case Britain), or immigrants are equally likely to arrive from all points across the region. A given number of immigrant individuals probably produce more new species in the non-spatial model than they would if spatial structure in the pool was taken into account, because they are drawn with equal probability from the whole of Britain, rather than prefer-

entially from local, similar, woodlands. This will have the effect of lowering both the death rate and proportion of immigrants required by the model to produce the observed species richnesses.

Whilst the locally neutral model seems to provide an acceptable first order explanation for the observed community structure of the Eastern Wood breeding bird community, it makes at least two assumptions that seem hard to justify in the context of a bird assemblage comprising species from different feeding guilds and trophic levels. First, this neutral model, along with those of Hubbell and Bell [40-42], operate under what Hubbell has termed "zero-sum dynamics". This means that there is a hard upper limit to the total number of individuals that can be present in the community – in this case, 340. Once this limit is reached, any increase in the abundance of one species must be offset by corresponding decreases in the abundance of one or more other species: changes in abundance summed across all species must equal zero. Hence, if a particular species is unusually abundant in one replicate sample of individuals, it follows that the other species must have correspondingly lower abundances. The biological interpretation of zero-sum dynamics is that all species in the community are competing for a common resource, such as food or nesting sites. This seems unlikely in an assemblage such as the avifauna of Eastern Wood, which contains species with lifestyles as different as hawks (Accipitridae), woodpeckers (Picidae) and tits (Paridae). Nevertheless, all random draw based methods that select a predetermined number of individuals for generating a null community contain the same assumption. Therefore, the neutral model is no less justifiable than more conventional random draw null model techniques in this respect.

The second unlikely assumption of neutral models is that all the species have equal *per capita* demographic rates of birth, death and migration. Interspecific differences in the birth and death rates of British birds are well documented [e.g. [34,43-45]], while differences in species longevity and site fidelity suggest that migration rates may also differ between species. However, while this assumption may be unrealistic, it is an intentional feature of the neutral modelling approach. Neutral models are defined as treating all species as identical on a *per capita* basis [42]. It is this that makes them 'null', with respect to interspecific differences in the interaction of individuals with their local environment, both abiotic and biotic. The question here is less whether or not this assumption is likely to be true (it is not), but more whether it leads to unrealistic predictions of community structure. That it does not suggests that interspecific variation in demographic rates is not an important influence on community structure, and that the assumption of 'average' rates is sufficient.

It is important to be clear at what spatial and temporal scales and at what level of habitat specificity these models are indeed neutral. The definition of a woodland species pool is an admission that habitat features are important determinants of species composition. Only those species known to breed in woodland in Britain have been included. Thus, at a very low resolution of habitat classification the model does recognise species differences, as it excludes all those not known to breed in woodland. It is at higher resolutions of habitat classification that the model is neutral. There are many documented examples of species with associations to particular types of woodland or woodland feature [46]. It is this type of association that is excluded from the model.

Both the locally neutral and random draw models take as their major input estimates, gained through fieldwork, of the British breeding population sizes of those species present in the regional pool. The processes that have led to those species obtaining the abundances they have are not controlled for in the model. There is therefore a risk that the very processes with respect to which the model is supposed to be null are actually intrinsic to the data upon which the model is built. This is the "Narcissus effect" [47] whereby null models are constructed by sampling from a regional pool that is already post-competitive: that is, the effects of competition are already reflected in the abundances of the species present in the pool, and in those species that are absent from the pool, the 'ghosts of competition past' [48]. Therefore, whilst the model is neutral with regard to processes occurring at the scale of the local community it is not necessarily so with regard to processes occurring at the regional level.

In assessing the success or otherwise of the neutral model developed here, the conclusion drawn depends on what it is that we seek to achieve in pursuing this line of research. If the aim were to develop a model that could accurately predict the particular community structure of Eastern Wood, then success would have to be judged as limited. The neutral model is only marginally better at this than the random draw model. Moreover, the greater success of the neutral model derives in part because its abundance predictions are less precise, providing more variation within which to encompass the values observed for species in Eastern Wood. However, it is just this variation that would seem to make the neutral model a superior candidate for a first order model of the structure of woodland bird communities in Britain in general.

Conclusions
Woodlands like Eastern Wood have breeding bird communities that resemble, to a large extent, what would be expected were they a random selection of individuals from the regional woodland avifauna. In turn locally

neutral models resemble random draw models, with the distinction that they contain parameters that define the proportion of the community replaced each year (due to deaths and emigrations) and the proportion of new individuals recruited locally. The result of these two additional parameters is a qualitatively improved model of local communities, particularly with respect to their temporal dynamics and the variation in community structure that might be expected in a group of woodlands. A key subsequent test of this neutral model will be its ability to describe a larger number of woodland bird communities with either little variation in its parameters, or with variation explained by features local to the woods themselves, such as their area and isolation. We are currently engaged in applying neutral models to other woodland communities to help ascertain further whether or not this is the case.

Methods
The breeding bird community of Eastern Wood was quantified during the period 1949–1979 by annual censuses carried out by the London Natural History Society (LNHS). They resulted in a data set of exceptionally high quality that gives reliable estimates of the annual breeding abundance of all bird species found in the wood over this period [49,50]. No census was made in the year 1957 and the data for 1949 were excluded because abundance estimates were not made for all species that year, giving a total of 29 years of complete bird population data (given in Appendix II of Gaston and Blackburn 2000). We used this LNHS data to assess the abilities of two models to reproduce the breeding bird community of Eastern Wood observed during this period: a pure random draw model, where the entire assemblage is redrawn each year, and a modified random draw model where only a portion of the assemblage is replaced each year, and where some of those individuals are replaced by locally recruited birds rather than immigrants from the regional pool. Hereafter these models are referred to simply as the random draw model and locally neutral model respectively. The neutral model can be regarded as a more complex version of the random draw model and so we will first explain the functioning of the random draw model and then describe the alterations that lead to the neutral model.

The random draw model
In the case of the random draw model, communities were assembled by drawing individuals with replacement at random from a pool of individual birds of species known to breed in woodlands in Britain, where the probability of an individual of species i being drawn was equal to that species' relative abundance in the source pool. Species included in this pool of individuals were those present in the British breeding woodland bird species pool defined by Blackburn and Gaston [[19], Appendix 1]. They included all species indicated by Ehrlich *et al.* [51] to typically or frequently breed in deciduous woodland. Estimates of their abundances were taken from Stone *et al.* [52] and are also published as Appendix III in Gaston and Blackburn [20]. A mean (± S.D.) number of 169.8 ± 28.5 pairs of birds were recorded breeding each year in Eastern Wood during the 29 years of census data, so annual assemblages consisted of 340 individuals; this differs slightly from the method of Gaston and Blackburn [20], who selected pairs rather than individuals. Separate sets of 340 individuals were drawn from the regional pool for each of the 29 consecutive years that were modelled.

The locally neutral model
The random draw model (where all recruits to the local community are immigrants from the regional species pool and the entire local community is replaced each year by 340 immigrants), was modified so that only a proportion d of the community is replaced each year. The total number of replacements = $D = d*340$. Of those D individuals, only a proportion, m, are replaced by immigrants from the regional pool, while the rest derive from locally recruited birds, so that local communities contain a mixture of local recruits and immigrants. The inclusion of local recruitment allows local communities to diverge to a certain extent from the regional species pool. We refer to this modified model as the 'neutral model' (c.f. Bell 2000; Hubbell 2001). A similar model has recently been published by McGill [53] to investigate the effect, on estimates of species abundance distributions, of accumulating repeated, partially correlated, samples from a regional pool.

For each replicate of the neutral model, the random draw model was used to generate an initial assemblage of 340 individuals. Then a process was initiated in which individuals are killed at random and replaced by immigration from the source pool with probability m, or by local recruitment with probability $1-m$. Where individuals are replaced by local recruitment, the probability of the new individual belonging to species i is the relative abundance of species i in the local community. Immigrants are drawn from the regional pool as above. Sufficient deaths followed by recruitment are made (normally 10,000) until local extinction and colonisation are at equilibrium and the mean species richness of the local assemblage does not vary systematically through time. The local abundance of each species is then recorded at intervals of D replacements due to deaths or emigrations, where D replacements occur annually. Twenty-nine such recordings are made representing twenty-nine consecutive annual censuses. This model is very similar in construction to that outlined in Hubbell [[42] chapter 4].

Unlike the random draw model, the predictions of the neutral model can be altered by varying its parameters, m

and *d*, which need to be assigned values. The neutral model was run for a large number of combinations of *m*, the immigration rate, and *D*, the number of replacements per year, expressed as *d* (1000 replicates for each combination). Contour plots were produced to assess the response of mean annual and long-term species richness predictions to variation in *m* and *d*. From these we determined the values of *m* and *d* that gave the best fit to the observed mean annual and long-term (29-year) species richness of Eastern Wood. It was these values that were then used when generating model data for all subsequent analyses.

Analysis
Ten thousand replicates of each model were performed to generate the data used to compare the ability of the two models to predict accurately the Eastern Wood breeding bird community for the period 1950–1979 [49,50]. As stated above, the parameter values used in the neutral model were those values of *m* and *d* that gave the best fit to the observed mean annual and long-term (29-year) species richness of Eastern Wood.

The data being modelled comprise of 29 consecutive annual censuses (with the exception of 1957) for a single woodland breeding bird community. These data are equivalent to just a single replicate of either model. We cannot know how close to the true mean, or the mean of a larger sample of woodlands, are the values for the Eastern Wood community. Therefore it is not meaningful to compare community descriptors derived from this single replicate with mean values of descriptors derived from many replicates of the models. Instead, we generate 95% probability limits for the range in which each model predicts that a statistic derived from 1 replicate (i.e. 1 real woodland surveyed for 29 years) should fall 95% of the time. If the statistic for Eastern Wood falls within this range then we consider that the model fits the observed data for that statistic.

The neutral model was calibrated using the observed mean annual species richness and total species richness after 29 years for Eastern Wood, and therefore would be expected to produce accurate predictions of cumulative species richness at 1 and 29 years. To assess the species accumulation pattern during the intervening 27 years and beyond, a plot of cumulative species richness was made showing the actual pattern of species accumulation observed in Eastern Wood together with patterns predicted by both the random draw and neutral models for 1 to 50 years. The predicted patterns were shown as mean curves calculated from 1000 replicates of each model, along with dashed lines representing the boundaries of zones in which the models predict that real curves should fall 95% of the time.

Using models that select individuals rather than species allows us to compare those models in terms of their predictions for the local abundances of species in Eastern Wood, as well as the identities of those species. The comparison of species abundances in simulated and real assemblages can be made from two separate theoretical perspectives, a species-specific perspective and a community structure or process perspective [54]. For example, we can compare the predicted and observed abundances of the robin, *Erithacus rubecula*, which happens to be the most abundant species in Eastern Wood but usually is not so in the simulated assemblages, or we can compare the abundance of the most abundant species in Eastern Wood with that of the most abundant species in a given simulated assemblage, regardless of whether they are the same species. Comparisons were made from both perspectives.

The predicted abundances of species in each of the 10,000 replicates of the random draw and neutral model were analysed. Abundance predictions were considered correct if the range of abundances that a model predicted a species should obtain 95% of the time encompassed the observed abundance value. To assess the overall deviation of the simulated assemblages from that observed in Eastern Wood, the differences between real and model abundances were summed across all species for each replicate and for each model. The abundance structures of the real and simulated assemblages were compared using rank-abundance plots. Species were ranked in descending order of abundance each year, so an individual data point represents the mean annual abundance of the species at rank '*i*' rather than the mean annual abundance of species '*i*'. The mean abundance of each rank was then calculated along with its 95% probability intervals, and predictions were again classified as being correct if these probability intervals encompassed the observed abundance value.

Authors' contributions
AMD wrote the C++ programs that execute the random draw and neutral models and performed the simulations. AMD performed the analyses with guidance from TMB. The manuscript was drafted by AMD with contributions and advice from TMB.

Additional material

> ### Additional File 1
> *Species abundances in Eastern wood with abundances predicted by random draw and neutral models.*
> Click here for file
> [http://www.biomedcentral.com/content/supplementary/1472-6785-4-8-S1.pdf]

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