Strapline: Research article

Title: The jigsaw model: A biogeographic model that partitions habitat heterogeneity from area

Running Title: The jigsaw model of island biogeography

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Abstract

Species– area models now frequently include habitat heterogeneity. These models often fit real-world data better than models that exclude this factor. However, such models usually link the effects of habitat heterogeneity and study area. Critically, we show that difficulties in quantifying habitat heterogeneity within these models can lead to distortions of the apparent effect of area on species richness . Here, we derive a model that minimises these distortions by partitioning the influence of habitat heterogeneity from that of area, without compromising ease of model application. This 'jigsaw model' achieves this by assuming that different habitats within an area can support similar numbers of species. We compare the behaviour of this model to that of existing models of similar complexity using both simulated island ecosystems and 40 published empirical datasets. The effects of habitat heterogeneity and area on species richness vary independently in our simulations, and these independent effects are recovered by the jigsaw model. This flexibility, however, is not present when the same data are analysed using other models of similar complexity. When applied to real-world data, the jigsaw model demonstrates that the relative importance of area and habitat heterogeneity varies depending on the study system. The jigsaw model provides the best fit to real-world data (according to AICc) of all tested models in logarithmic form, and the second best fit, after the choros model, in power-law form. Our results demonstrate the importance of partitioning the effects of habitat heterogeneity and area on species richness in biogeographic models. The jigsaw model is a simple but powerful tool for such partitioning. It has the potential to elucidate the underlying drivers of species richness patterns, and to be used as a tool in biological conservation projects, where data are often incomplete.

Highlights:
- Existing simple biogeographic models cannot distinguish between the influences of habitat heterogeneity and area on species richness.
- The jigsaw model can determine the relative contributions of the effects of these variables.
- The jigsaw model provides an excellent fit to real-world datasets.
- Determining the relative contributions of habitat heterogeneity and area to species richness is an important step in protecting biodiversity in threatened ecosystems.

Keywords: biodiversity, choros model, habitat heterogeneity, habitat loss, island biogeography, island species– area relationship, species– area relationship, species richness

Introduction

The species richness of isolates, be they true islands or areas of isolated habitat, increases with the area of those isolates (Arrhenius 1921, MacArthur and Wilson 1963, Brown 1971). This increase occurs at a decelerating rate as geographical area increases; larger areas contain more species in total, but fewer species per unit area (Arrhenius 1921, Allen and White 2003, Matthews et al. 2016). The island species–area relationship (ISAR) is a mathematical description of this pattern, supported by decades of empirical research (Rosenzweig 1995, Matthews et al. 2021a). Understanding of this relationship has been refined over time (Rosenzweig 1995, Lomolino and Weiser 2001, Matthews et al. 2016), but the mathematical core of the relationship is more than a century old (Arrhenius 1921).

There are many potential drivers behind the ISAR (Tjørve et al. 2021), but all either propose some direct effect of area (Hutchinson 1957, MacArthur and Wilson 1963, MacArthur and Wilson 1967, Wright 1983, Belovsky et al. 1999, Krauss et al. 2004, Storch et al. 2018), or propose that area is a proxy for some other factor that controls species richness within isolates, often habitat heterogeneity (Hutchinson 1957, MacArthur 1958, Báldi 2008, Stein et al. 2014). These direct and indirect hypotheses are not mutually exclusive: both may operate simultaneously (Kohn and Walsh 1994, Tjørve et al. 2021). Understanding the differing roles of these drivers in different ecosystems is an ongoing challenge (Chase et al. 2019, Liu et al. 2019).

Models
The first mathematical models of species richness within isolates relied upon area as the sole predictor (Arrhenius 1920, Arrhenius 1921, Brenner 1921). The earliest such model was the power-law model (Arrhenius 1921) (equation 1), hereafter referred to as the Arrhenius model to avoid confusion with other models that also use a power-law relationship between species richness and area. Within this model, for any positive constant c, and value of the constant z between zero and one, species richness (S) increases with area (A), but at a decreasing rate.

$$1.\ \ S = cA^z$$

An alternative model uses the same single predictor and constants but proposes an alternative shape for their relationship with species richness (Gleason 1925) (equation 2). This is the logarithmic model, hereafter referred to as the Gleason model to avoid confusion with other models that also use a logarithmic relationship between species richness and area.

$$2.\ \ S = ln(cA^z)$$

Both models are useful in that they have minimal data requirements and provide good fits to real-world data (Tjørve and Tjørve 2021). Furthermore, the constant z captures information about the processes affecting particular island systems and groups of organisms (Brown 1971, Allen and White 2003, Triantis et al. 2012,

Mendenhall et al. 2014, Matthews et al. 2016, Whittaker et al. 2017, Freeman et al. 2018, Matthews et al. 2021b), although the number of biological processes that influence z means it cannot be analogised to any single biological quantity (Tjørve and Tjørve 2017). For example, analyses of groups with restricted mobility between isolates tend to result in higher values of z (Brown 1971, Tjørve et al. 2021), as do analyses of groups comprising specialist, rather than generalist, species (Freeman et al. 2018). Habitat fragmentation can increase z (McNeill and Fairweather 1993, Tjørve 2010), or occasionally decrease it (Tjørve 2010), and z is influenced by the spatial scale of the analysis (Allen and White 2003, Dengler et al. 2020), as well as by the rate of extirpation of species from isolates (MacArthur and Wilson 1967).

More recent models have explicitly included the effect of habitat heterogeneity (H), rather than modelling this factor through an assumed correlation with area. These include the choros model (Triantis et al. 2003) (equation 3) and the Kallimanis model (Kallimanis et al. 2008) (equation 4, presented here in power-law form for consistency).

$$3. \quad S = c(AH)^z$$
$$4. \quad S = cA^{z+dH}$$

The choros model proposes that species richness is better predicted by the product of habitat heterogeneity and area than by either factor individually (Triantis et al. 2003). The Kallimanis model proposes that increasing habitat heterogeneity increases species richness by increasing the slope (on a log-log plot) of the Arrhenius model. Both models frequently provide a significantly improved fit to empirical data when compared to models without habitat heterogeneity (Triantis et al. 2003, Kallimanis et al. 2008, Matthews et al. 2016).

These four models are all mathematically and conceptually simple. More complex models exist, but these typically model species richness as the product of specific mechanisms (Buckley 1982, Rafe et al. 1985, Tjørve 2002, Pereira and Daily 2006). Of these, the countryside model (Pereira and Daily 2006) is perhaps the best known: this model can provide a better fit to empirical data than simpler models (Proença and Pereira 2013) but requires more data and is therefore more difficult to apply. For this reason, simple models continue to be used today in studies of species biogeography (e.g. Ohyama et al. 2021, Triantis 2021).

The problem with habitat heterogeneity
There are clear statistical benefits of explicitly incorporating habitat heterogeneity into simple biogeographical models, as demonstrated by the choros and Kallimanis models (Triantis et al. 2003, Kallimanis et al. 2008). If the goal of a study is to describe the species richness of isolates as accurately as possible, then tools such as the choros model may be ideal (Tjørve and Tjørve 2021). However, if the goal is to infer ecological processes from the outputs of models, for example by comparison

of the constant z among systems (Brown 1971, Whittaker et al. 2017, Matthews et al. 2021b), existing simple models are insufficient. The problem stems from an interaction between the mathematics of these models and the difficulty in meaningfully measuring habitat heterogeneity. There is no precise and accepted standard by which habitat heterogeneity should be measured (Panitsa et al. 2006, Stein et al. 2014, Stein and Kreft 2015, Triantis 2021, Loke and Chisholm 2022). Typically, habitat heterogeneity is measured either by counting the number of distinct communities ('biotopes') (Jüriado et al. 2006, Panitsa et al. 2006), or by measuring some number of abiotic environmental factors (Anderson and Ferree 2010, Shi et al. 2010). However, a perfect measure of habitat heterogeneity should theoretically include all axes of variation in a species' Hutchinsonian niche space (Hutchinson 1957, Whittaker et al. 1973, Tews et al. 2004), which is not viable in practice. As such, reported habitat heterogeneity values are, at best, proxies for 'true' habitat heterogeneity values.

If a linear relationship between true (H_t) and reported (H_r) habitat heterogeneity exists (equation 5), it is straightforward to adapt both the choros (equations 6.1–6.5) and Kallimanis (equations 7.1–7.4) models.

$$5.\ H_t = nH_r$$

In the choros model (equation 6.1), replacement of H_r with H_t introduces a new constant n (equation 6.2). This equation can be rearranged to separate the n term from the variables A and H (equation 6.3). Because c_r, n, and z are all constants, the portion of the equation outside of the brackets can be replaced with a single new constant, c_t (equation 6.4). This returns the model to the form that it had before the replacement of H_r with H_t, with only a change in the value of the constant c (equation 6.5).

$$6.1.\ S = c_r(AH_r)^z$$
$$6.2.\ S = c_r(AH_t n^{-1})^z$$
$$6.3.\ S = c_r n^{-z}(AH_t)^z$$
$$6.4.\ c_t = c_r n^{-z}$$
$$6.5.\ S = c_t(AH_t)^z$$

In the Kallimanis model (equation 7.1), replacement of H_r with H_t introduces the same new constant n (equation 7.2). Because n and d_r are both constants, they can be replaced with a single new constant, d_t (equation 7.3). This replacement returns the model to the form that it had before the replacement of H_r with H_t, with only a change in the value of the constant d (equation 7.4).

$$7.1.\ S = cA^{z+d_r H_r}$$
$$7.2.\ S = cA^{z+d_r n^{-1} H_t}$$

$$7.3.\ d_t = d_r n^{-1}$$
$$7.4.\ S = cA^{z+d_t H_t}$$

In both cases, the final models (equations 6.5 and 7.4) have the same forms as the models from which they were derived (equations 6.1 and 7.1). As such, the models will display no change in goodness of fit to any given dataset.

Changing the method by which habitat heterogeneity is measured does change a model constant (either c or d), but this is only a problem if workers compare these constants among systems . This is occasionally done (e.g. Matthews et al. 2021b), but these constants are less likely to be analysed than the constant z, which is unaffected by the replacement of H_r with H_t when these two variables are related linearly. However, there is no reason to assume that the relationship between H_r and H_t is linear in real world systems. Isolates with a greater degree of variation along one (measured) axis of habitat heterogeneity might be expected to have greater variation along other (unmeasured) axes. If the relationship between true and reported habitat heterogeneity is nonlinear (e.g. equation 8), both the choros (Triantis et al. 2003) (equations 9) and Kallimanis (equations 10) models encounter problems.

$$8.\ H_t^n = H_r$$

In the choros model (equation 9.1), replacement of H_r with H_t introduces a new constant n (equation 9.2). This new constant is an exponent of H, but not of A (equation 9.3). Assuming that $n \neq 1$, this means that A and H have different exponents. In this case, the model cannot return to the form that it had before the replacement of H_r with H_t.

$$9.1.\ S = c(AH_r)^z$$
$$9.2.\ S = c(AH_t^n)^z$$
$$9.3.\ S = cA^z H_t^{nz}$$

In the Kallimanis model (equation 10.1), replacement of H_r with H_t introduces the same new constant n (equation 10.2). This new constant is an exponent of H. However, in its original form, the Kallimanis model does not assign an exponent to H. Assuming that $n \neq 1$, this means that the model cannot return to the form that it had before the replacement of H_r with H_t.

$$10.1.\ S = cA^{z+dH_r}$$
$$10.2.\ S = cA^{z+dH_t^n}$$

For both models, there is no way the constants can be changed such that the final models (equations 9.3 and 10.2) have the same forms as the models from which they are derived (equations 9.1 and 10.1). Consequently, the fits of the models to any given dataset will change, as will the values of the fitted constants, including z. In the case of the choros model, the constant n acts directly upon z (equation 9.3), which will result in a systematic increase in the constant z as n decreases (i.e. as habitat heterogeneity is increasingly underestimated). For both models, this makes it harder to infer biological differences by   comparison of z values among datasets , because z is dependent upon both the actual effect of area on species richness and the observer's choice of method to measure habitat heterogeneity.

An additional issue exists with the choros model, even if H_r is assumed to be equal to H_t. The choros model assumes the exponents of habitat heterogeneity and area are identical. However, these factors are expected to influence species richness through different mechanisms (Tjørve et al. 2021). This assumption restricts the ability of the model to fit to data, potentially degrading its utility for providing information about ecological processes acting within systems (Báldi 2008, Travassos-De-Britto and da Rocha 2013).

In short, any non-linear relationship between habitat heterogeneity measured by observers and habitat heterogeneity perceived by organisms in the ecosystem is liable to systematically bias z in the choros and Kallimanis models. This effect makes it difficult to ascribe differences between datasets in choros and Kallimanis z-values to any biological processes (e.g. dispersal, habitat fragmentation, habitat specialisation) that might be expected to influence them (Tjørve and Tjørve 2017).

T   he jigsaw model
We present an alternative   model for the relationship between species richness, habitat area, and habitat heterogeneity within isolates: the jigsaw model, so named because it models species richness in an area as the sum of the species richness values of several smaller component subareas, which can be visualised as pieces of a jigsaw puzzle. This model is similar in form to the choros model (Triantis et al. 2003), and is mathematically equivalent to the no-interaction (no-INT), trivariate power-law model of Tjørve (2009). We biologically justify the jigsaw model here   as an expansion of the Arrhenius model (Arrhenius 1921), following similar logic to the models of Buckley (1982) and Tjørve (2002).

Like the choros and Kallimanis models, the jigsaw model has minimal data requirements and can be applied readily to real-world datasets and compared to other models. However, unlike previous simple models, the jigsaw model partitions the scaling relationship between species richness and   habitat heterogeneity from that between   species richness and area. This partitioning does not divide species richness into a proportion attributable to area and a proportion attributable to species richness, but rather allows   their relative influences, in terms of the rate at which

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their change produces a change in species richness, to be quantified independently. The jigsaw model also attempts to remove systematic bias from the *z* term, to facilitate comparison of *z*-values among datasets. We compare the behaviour and fit of the jigsaw model to those of existing models using both ecosystem simulations and 40 real-world biogeographical datasets (Table S1).

Materials and Methods

Jigsaw model derivation
Isolates with greater habitat heterogeneity typically support a larger number of species (Triantis et al. 2005, Hortal et al. 2009, Anderson and Ferree 2010). The slope of the relationship between habitat heterogeneity and species richness reflects the degree to which different habitats contain different species (Liu et al. 2019), which itself depends upon the degree to which the environment varies among delineated habitats and the degree to which species are specialised to survive within particular environments (Ricklefs and Lovette 1999). If adjacent delineated habitats are similar, there will likely be substantial overlap in the species they contain. In this case, an area containing many different habitats will not necessarily be substantially more speciose than an area containing only a single habitat (Ricklefs and Lovette 1999). Similarly, if the species inhabiting an area are generalists (Ma and Levin 2006), they are likely to be found in a larger number of habitats and, consequently, an area with multiple habitats will not necessarily be substantially more speciose than an area with only a single habitat (Freeman et al. 2018, Matthews et al. 2021a).

Variation in the rate at which species richness accumulates with increasing habitat heterogeneity can be accounted for mathematically by introduction of a constant, *d* (equation 11). This constant is proportional to the difference in community composition among discrete habitat types.

$$11.\ S \sim H^d$$

Species richness within an isolate also depends upon the area of that isolate. Larger isolates tend to support larger populations of species, which are less likely to go extinct than smaller populations in smaller isolates (Brown 1971, Wright 1983, Schoener and Spiller 1992). Consequently, large isolates tend to be more species-rich than small ones (Nilsson et al. 1988, Krauss et al. 2004). Many mathematical expressions exist that link species richness to area, but the Arrhenius model (equation 1) has been shown to provide, on average, the best fit to empirical data, both on its own (Dengler 2009, Triantis et al. 2012, Matthews et al. 2016) and when used as a component of more complex models (Kallimanis et al. 2008). Thus, we use that form of the relationship here (equation 12).

$$12.\ S \sim A^z$$

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Unification of these two relationships requires an additional step. The existence of a positive relationship between species richness and habitat heterogeneity is predicated on the assumption that different habitat types support different species. If correct, the effective area of the environment, from the perspective of any one species, is not the total study area, but rather the fraction of it habitable to that species (Rafe et al. 1985, Deshaye and Morisset 1988, Kadmon and Allouche 2007, Liu et al. 2019). If we assume that all habitat types comprise equal proportions of the total area, then the area of any one habitat type can be expressed as the total area divided by the number of habitat types. If we further assume that all species inhabit only one habitat type, then the Arrhenius model can predict the species richness of that habitat type (equation 13). The assumption that all species can survive in only one habitat is relaxed by the presence of the constant d, and is therefore absent from the final model. The assumption that each habitat type occupies an approximately equal proportion of the total area of the isolate is not realistic but provides a simplification that removes the need for sigma terms in the model, which reduces data requirements and improves ease of application. The implications of these assumptions for the fit of the jigsaw model are explored in the simulation portion of this study (see "Simulation Experiment 2" in Results).

$$13.\ S \sim \left(\frac{A}{H}\right)^z$$

From these relationships (equations 11 and 13), we construct the jigsaw model (equation 14). To summarise, this model effectively assumes that the area (A) of any isolate can be divided into H subareas (one per habitat type), with each having an area A/H. Within each of these subareas, species richness is assumed to scale according to the Arrhenius model (Arrhenius 1921). The impact of habitat heterogeneity (H) on species richness is modulated by the degree of species overlap between subareas, captured by the constant d. This is conceptually similar to the model presented by Buckley (1982), with the main difference being that the jigsaw model assumes equal areas among habitat types to reduce data requirements and improve ease of use.

$$14.\ S = cH^d\left(\frac{A}{H}\right)^z$$

The influence of habitat heterogeneity in the jigsaw model is controlled by the constant d. When d is equal to one, there is no overlap in community composition among subareas, and each subarea effectively acts as an independent area. In this case, the total species richness of the area is equal to the sum of the species richness of each subarea, as in Rafe et al. (1985). When d is equal to $2z$, the jigsaw model is identical to the choros model (Triantis et al. 2003). When d is equal to z, the jigsaw model is identical to the Arrhenius model (Arrhenius 1921), with no influence of habitat heterogeneity. One consequence of these equivalences is that the jigsaw model cannot have a poorer fit than the choros or Arrhenius models to any given

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dataset, as measured by residual sum of squares (RSS) or R^2; this is because it can adopt values for constants that make identical predictions to those models where this is optimal.

Mathematically, the jigsaw model (equation 14) is a no-INT, trivariate power-law model, as described by Tjørve (2009) (equation 15 or equation 3 in Tjørve (2009)), where x = habitat heterogeneity, y = area, a = c, b = d-z, and c = z. In such a model, the exponents b and c can vary independently, with higher exponents of either predictor variable representing faster scaling of the response variable with that predictor.

$$15.\ f(x,y)\ =\ ax^b y^c$$

Tjørve (2009) suggested this model was one of several that could be used to incorporate habitat into the species–area relationship (equation 16). It is encouraging, therefore, that a model of this form can be derived from a combination of the Arrhenius model and existing ecological theory, as we show (equation 14).

$$16.\ S\ =\ cH^d A^z$$

Tjørve's no-INT, trivariate power-law model can be re-parameterized to derive the jigsaw model by treating the effective area (A_e) of any isolate as the area habitable to that species, as discussed above in our initial derivation of the jigsaw model. Assuming each species can occupy only one habitat type, this yields equation 17.

$$17.\ A_e\ =\ \frac{A}{H}$$

Replacement of area (A) in the model of Tjørve (2009) (equation 16) with effective area (A_e) yields the jigsaw model (equation 14). As in the original derivation, the assumption that all species occupy only a single habitat type is ameliorated by the presence of the constant d.

Use of the jigsaw model requires the same measurements required by the choros and Kallimanis models: species richness, area, and habitat heterogeneity. Furthermore, the jigsaw model can be log-transformed to allow for extraction of the constants d and z from an additive linear model (equation 18   ).

$$18\quad.\ ln(S) = ln(c) + (d - z)ln(H) + zln(A)$$

Under some circumstances, the logarithmic form of a model might be preferable to the power-law form (Gleason 1925). Notably, the power-law form of a model may overpredict species richness in very large areas (Kallimanis et al. 2008). By replacing the Arrhenius model (equation 1) with the Gleason model (equation 2) in

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the derivation of the jigsaw model, it is possible to construct an alternative version of the jigsaw model that follows the logarithmic form (equation 19   ).

$$19 \quad . \; S = H^d ln\left(c\left(\frac{A}{H}\right)^z\right)$$

Unlike the power-law form of the jigsaw model, this logarithmic form cannot be neatly linearised by log-transformation, although this does not preclude the extraction of d and z after the model has been fitted to a dataset. However, this logarithmic form of the jigsaw model lacks the property of the power-law form that allows it to match the predictions of the choros and Arrhenius models.

Simulation analysis
We ran two simulation experiments to determine how the parameters of the jigsaw and other models (choros and Kallimanis) responded to predictable manipulation of ecosystem parameters in simulated biogeographic datasets. The aim of the first simulation was to determine how variation in the degree of species overlap among habitat types affected the parameters of the jigsaw and existing models. We performed the first simulation using a purpose-written Python script (Script S1), which modelled species richness within an isolate of area A as the sum of the species richness of one community of generalist species, and the species richness of H communities of specialist species occupying different habitats, each of area A/H. The richness of each community followed the Arrhenius model, where $z = 0.3$ and c was varied by introduction of the constant b, such that some datasets contained a greater proportion of generalists and some a greater proportion of specialists (equation 20   ).

$$20 \quad . \; S = bcA^z + Hc(1-b)\left(\frac{A}{H}\right)^z$$

In this experiment, we simulated the species richness values of 10,000 isolates for each of twenty-one values of b between 0 and 1 (inclusive). For each isolate, H was an integer chosen at random between 1 and 10 (inclusive), A was an integer chosen at random between 100 and 1000 (inclusive), and c was 10. For each value of b, we fitted the log-log versions of the power-law forms of the jigsaw, choros, and Kallimanis models.

The aim of the second experiment was to determine how robust are the predictions of the jigsaw model to deviations from the model's assumption that each habitat type occupies an equal area. We performed this experiment using the same Python script as in the first experiment (Script S1), but with $b = 0$ throughout (i.e. no generalists), and with random variation introduced in the proportion of the total area of each isolate assigned to each habitat type (equation 21   ).

$$21 \quad . \; S = \sum_{n=1}^{H} c \, A_n^z$$

The maximum possible ratio of the area of one habitat type to another within one isolate was set in Python by the constant Q. In this experiment, we simulated the species richness values of 10,000 isolates for each of 38 values of Q between 1 and 100 (inclusive). For each isolate, H was an integer chosen at random between 1 and 10 (inclusive), A was an integer chosen at random between 100 and 1000 (inclusive), c was 10, and A_n was the area of A assigned to habitat type n within one isolate, which was randomly determined in line with Q. For each value of Q, we fitted the log-log version of the power-law form of the jigsaw model. In both experiments, we fitted the power-law rather than the logarithmic forms of the models because the underlying data were simulated using a model in power-law form (the Arrhenius model).

Real-world analysis

We compiled 40 real-world biogeographical datasets from the published literature. A list of these data sources can be found in Table 1. Each dataset contains measurements of multiple isolates, for which quantification of species richness, area, and habitat heterogeneity exist (see Table 1 for details). Following the method of Triantis et al. (2003), zeros were removed from these datasets to allow log-transformation, as our primary interest was in the fit of models to the data (Triantis et al. 2003), rather than in the shape of the relationship between species richness, area, and habitat heterogeneity (Williams 1996). We recognise that log-transformation and removal of zeros will influence the way in which our models are fitted to the data (Tjørve and Tjørve 2017). However, we performed log-transformation here, in part, because only five of 40 datasets included any number of zeros that needed to be removed, and because it was possible that zeros had already been removed from the other published datasets for previous log-transformations. Some datasets had explicitly excluded very small isolates (e.g. Panitsa et al. 2006) or isolates where species lists were deemed questionably sparse (e.g. Reed 1981, Ricklefs and Lovette 1999), which may have removed isolates with zero species. Log-transformation also helped to rectify dataset violations of assumptions made during model fitting (Tjørve 2009).

We fitted the log-log versions of the power-law forms of the jigsaw, choros, Kallimanis, and Arrhenius models to each of these datasets using the lm() function in R v3.6.3 (R Core Team 2020). Model fit to data was assessed using the corrected Akaike Information Criterion (AICc; Hurvich and Tsai 1989). AICc rewards models for goodness of fit to a dataset and punishes them by a fixed value for each fitted parameter included in the model, plus an additional punishment for more complex models fitted to smaller datasets (Hurvich and Tsai 1989). Model quality was determined by counting the number of datasets for which each model had the best (i.e. lowest) AICc score. This protocol was then repeated using the logarithmic forms of each model, fitted in R using the nonlinear least-squares function nlsLM() from the package 'minpack.lm' v1.2-1 (Mullen 2016).

Because the jigsaw and choros models are identical when $d = 2z$ in the former, the jigsaw model should deviate more from this equality in datasets when it significantly outperforms the choros model than in datasets where it does not. Similarly, the jigsaw and Arrhenius models are identical when $d = z$ in the former. As such, the jigsaw model should deviate more from this equality in datasets when it significantly outperforms the Arrhenius model than in datasets where it does not. We tested both hypotheses using the 40 real-world datasets.

Results

Simulation Experiment 1
The jigsaw model consistently provided a good fit to the simulated data in Experiment 1 ($R^2 \geq 0.989$ for all values of b); this experiment tested model response to differences in the proportions of generalist and specialist species (Figure 1a). The choros and Kallimanis models also usually provided good fits, but their fit varied with the relative contribution of generalists to the community (b) (Figure 1a). Variation in b had no impact on the value of the constant z adopted by the jigsaw model. However, the values of the constant z in the other models were affected by variation in b (Figure 1b). The constant d in the jigsaw model was negatively correlated with b (Figure 1b).
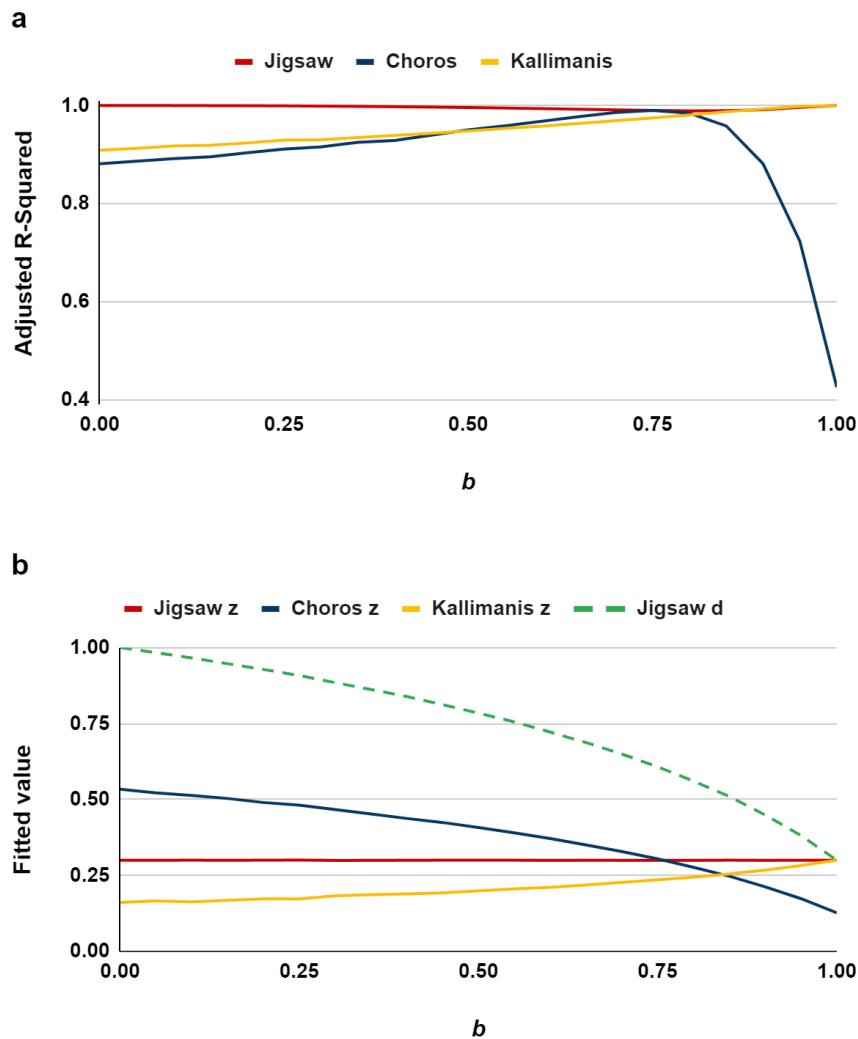
a

b

Figure 1. The relationship between the relative contribution of generalists to the community in the simulated isolates (*b*) in Experiment 1 and a) the fit (adjusted R²) of the choros, jigsaw, and Kallimanis models; b) the values of the fitted *z* constants of the choros and Kallimanis models, and the fitted *z* and *d* constants of the jigsaw model. The fitted *d* constant of the Kallimanis model is not included because it varies over a small range (0≤*d*≤0.03). At *b* = 0, all species are habitat specialists and are found in only a single habitat type; at *b* = 1, all species are habitat generalists and are found in all habitat types.

Simulation Experiment 2
The jigsaw model provided a good fit to the data in Experiment 2, which aimed to test the model's response to violations of its assumption that each habitat type occupies an equal area. The quality of the model's fit declined as inequality in the relative areas of different habitats within isolates increased (i.e., as the model's assumptions became less accurate). However, the jigsaw model fitted with $R^2 > 0.996$ for all tested values of Q (1–100) (Figure 2a). The mean area of a habitat within this experiment was 100 units. The mean within-isolate standard deviation of this area varied between 0 (at $Q = 1$) and 50.5 units (at $Q = 100$). Changes in Q did not result in a systematic change in the value of z estimated by the fit of the jigsaw model, which always fell within a highly restricted range ($0.2991 < z < 0.3011$) around the value used to seed species into the simulation ($z = 0.3$) (Figure 2b). Unlike z, the constant d declined systematically as Q increased (Figure 2a). However, this decline was of a low magnitude ($0.982 < d \leq 1$ for all $Q \leq 100$).
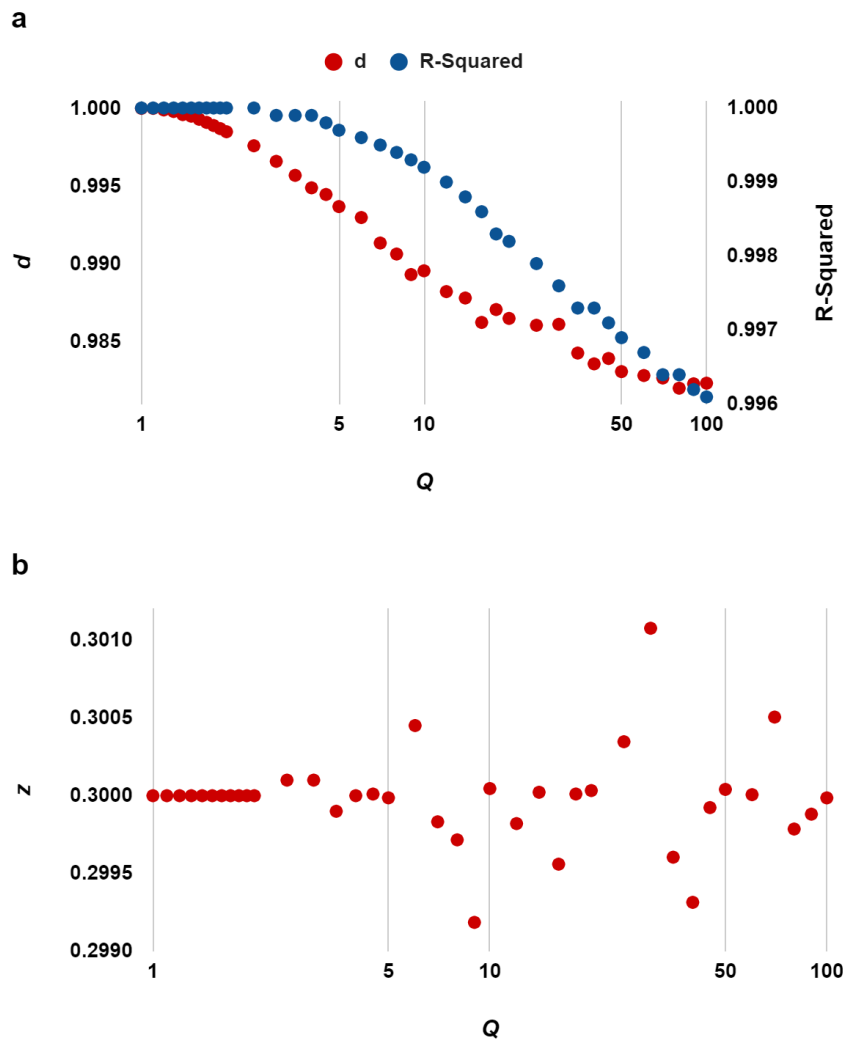
a

b

Figure 2. The relationship between the maximum size ratio of two habitats within one simulated isolate (Q) in Experiment 2 and a) the   fit (adjusted R^2) and value of the fitted d constant of the jigsaw model; b) the value of the fitted z constant of the jigsaw model. Note the logarithmic x-axis.

Real-world analysis

Regardless of whether the model was used in the power-law or logarithmic form, the jigsaw model was competitive with other models in terms of the number of datasets for which it provided the best fit, based on AICc scores. The jigsaw model had the second-best performance of the four models in power-law form, and the best

performance in logarithmic form (Table 2). See Dataset S1 for the model properties for each real-world dataset.

Table 2. The number of real-world datasets to which each model provided the best fit according to AICc. Model comparisons were made exclusively between models with the same form (power-law or logarithmic) and, as such, each dataset is represented twice (once by the model that provided the best fit to that dataset in power-law form, and once by the model that provided the best fit to that dataset in logarithmic form.

Model and Form	Choros	Jigsaw	Kallimanis	Arrhenius / Gleason
Power-Law	16	13	3	8
Logarithmic	7	22	4	7

The jigsaw and choros models make identical predictions (in power-law form) when $d = 2z$ in the jigsaw model. As predicted, the difference between d and $2z$ in the jigsaw model tended to be greater in those datasets where the jigsaw model outperformed the choros model than in those datasets where it did not (Wilcoxon rank sum test: W = 377, p = 1.432×10^{-9}) (Figure 3a). Similarly, the jigsaw and Arrhenius models make identical predictions (in power-law form) when $d = z$ in the jigsaw model. As predicted, the difference between d and z in the jigsaw model tended to be greater in those datasets where the jigsaw model outperformed the Arrhenius model than in those datasets where it did not (Wilcoxon rank sum test: W = 354, p = 1.198×10^{-8}) (Figure 3b).

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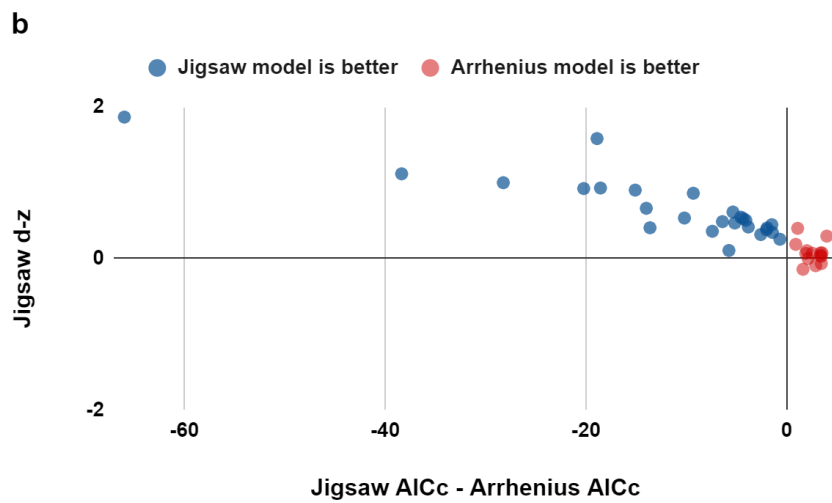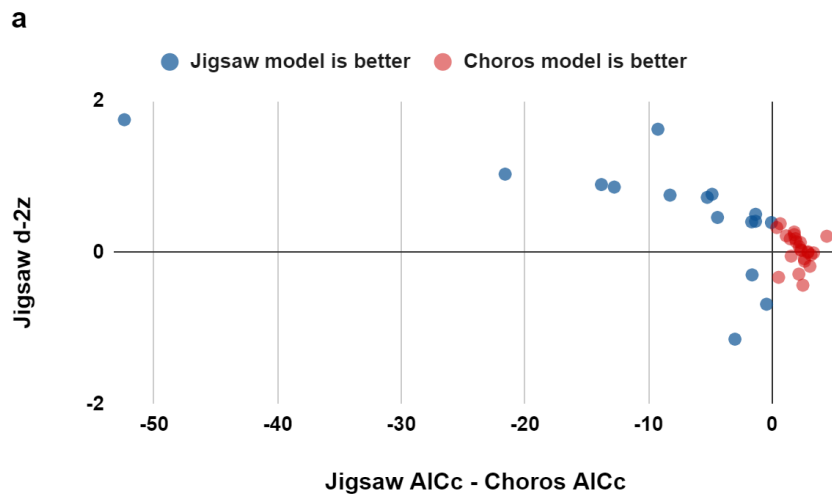
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Figure 3. The relationship between the difference in exponents of habitat heterogeneity and area in the jigsaw model and the relative fits of a) the jigsaw and choros models; and b) the jigsaw and Arrhenius models, to real-world datasets. In both cases, the jigsaw model tended to provide a better fit to the data than the alternative model when the equality assumed by the alternative model ($d = 2z$ in the case of the choros model, and $d = z$ in the case of the Arrhenius model) is less accurate.

Discussion

Jigsaw model fit
In Experiment 1, the fit of the jigsaw model is excellent (Figure 1), although as our simulations make similar ecological assumptions to the model itself, this result is unsurprising. Of more significance is the observation that the fit is consistent, and the value of z is constant for all values of b (i.e. as the underlying influence of habitat heterogeneity varied) (Figure 1a). This contrasts with the choros and Kallimanis models, which display variable qualities of fit and values of z, and demonstrates that, in its final form, the jigsaw model does not assume that species occupy only a single habitat type. The fit of the jigsaw model does decline slightly as its underlying assumptions become less accurate in Experiment 2 (i.e. as the term Q increases; Figure 2a). However, even when the assumption of equal habitat areas was wildly inaccurate, this decline in quality of fit is very small ($R^2 > 0.996$), and thus shows the model is robust to violations of this assumption.

When applied to real-world datasets, the fit of the jigsaw model, as measured using AICc, is competitive with that of existing published models of similar complexity (Arrhenius 1921, Gleason 1925, Triantis et al. 2003, Kallimanis et al. 2008). Indeed, the logarithmic form (Gleason 1925) of the jigsaw model substantially outperforms all other tested models of the same form (Table 2). While these results alone do not provide an unequivocal argument for the use of the jigsaw model, they demonstrate that AICc performance is at least on a par with alternative models, and model fit is not the only consideration when it comes to determining the utility of a model (Tjørve and Tjørve 2021).

The z parameter
A great deal of attention has been paid to the z parameter of the species–area relationship (Brown 1971, Allen and White 2003, Matthews et al. 2016, Matthews et al. 2021b). This attention is largely predicated on the assumption that the z parameter is controlled by some amalgamation of biological processes, and that differences in z among systems reflect differences in the scale and/or nature of those biological processes (MacArthur and Wilson 1963, Ricklefs and Lovette 1999, Halley et al. 2013). Processes that influence the z parameter in the Arrhenius model include immigration rate (Brown 1971), local extinction rate (MacArthur and Wilson 1967), habitat heterogeneity (Tjørve and Tjørve 2017), species habitat selectivity (Freeman et al. 2018, Liu et al. 2019), spatial scale (Tjørve and Tjørve 2017), altitude (Tjørve and Tjørve 2017), habitat fragmentation (McNeill and Fairweather 1993), and, if not accounted for, sampling effects (Chase et al. 2019). For any model that seeks to be used for explicative, rather than descriptive, purposes, it is important that the model constants should not be influenced by arbitrary factors that introduce noise or bias into measurements that might otherwise be used to infer ecological differences between systems, such as z (Chase et al. 2019, Tjørve and Tjørve 2021).

Experiment 1 demonstrates that   the jigsaw model shields the z parameter from the influence of habitat heterogeneity, whereas the choros and Kallimanis models do not. The z parameter of the jigsaw model, like those of other models, still represents a combination of biological processes, including immigration rate, local extinction rate, and spatial scale. However, removing the influence of habitat heterogeneity from the z parameter of the jigsaw model   is important for two reasons. First, given that   there are many different factors that can influence z (Matthews et al. 2021b, Tjørve et al. 2021), partitioning these factors in a predictable way between two variables makes it easier to infer how ecological processes differ between systems. Second, because measurements of habitat heterogeneity are imprecise and unstandardised (see 'The problem with habitat heterogeneity' above), differences in sampling technique between studies could introduce arbitrary variation into the value of z if it was influenced by habitat heterogeneity. The shielded z constant of the jigsaw model therefore provides a standardised approach with which biogeographical phenomena, such as the scaling of the species–   area relationship with the spatial scale of analysis (Allen and White 2003, Anderson et al. 2010, Dengler et al. 2020), can be evaluated.

The d parameter
Under ideal conditions, the d parameter of the jigsaw model will be influenced by both community disparity among habitat types, similar to between-patch variation beta diversity (Whittaker 1960, Anderson et al. 2010), and any dispersal limitation between disconnected fragments of the same habitat within the isolate (Holt 1992, Freestone and Inouye 2006, Makoto and Wilson 2018, Saupe et al. 2019). Such dispersal limitation would effectively increase the number of compositionally-distinct habitat areas within the isolate without increasing the measured habitat diversity, which would lead to an increase in d (McNeill and Fairweather 1993). However, comparison of the d parameter between datasets will be hampered by nonlinear error in the quantification of habitat heterogeneity (equation 8), which would increase or decrease d to bring the measured habitat heterogeneity value closer to that experienced by organisms in the ecosystem. This complication means that it might be difficult to make reliable   inferences from between-study differences in the d parameter, unless habitat heterogeneity is quantified in the same way in both studies. This also explains the high variation in d in the jigsaw model that we observe in our real-world datasets (0.16–2.0) relative to variation in the jigsaw model z term (-0.04–1.0).

Flexibility
Real differences in the dominant processes that structure richness within systems mean that we should not expect to find a single model that provides the best fit to all datasets (Tjørve and Tjørve 2021). However, the mathematical flexibility of the jigsaw model means that it can provide a good fit to area-dominated systems (e.g. Travassos-de-Britto and da Rocha 2013), habitat heterogeneity-dominated systems

(e.g. Sfenthourakis 1996), and any system on the continuum between these extremes (e.g. Herrault et al. 2016). By contrast, other models are not as flexible: the Arrhenius model assumes that habitat-heterogeneity is either unimportant or is well predicted by area, and the choros model assumes that the effects of habitat heterogeneity and area on species richness can be described well by a single, shared exponent (z).

Unsurprisingly, the jigsaw model tends to outperform these other models when real-world systems display behaviour that deviates from the aforementioned assumptions (Figure 3). For example, the power-law form of the jigsaw model outperforms the power-law form of the choros model when fitted to the dataset of Sfenthourakis (1996), which describes species richness of terrestrial isopods on Greek islands (ΔAICc = 13.8). In this instance, the choros model fits a z-value of 0.172, but the jigsaw model fits values of z = 0.027 and d = 0.921. This partitioning suggests that the measure of habitat heterogeneity used here is a more consistent driver of isopod species richness than is area in this system, which matches the conclusions of the original study (Sfenthourakis 1996). Although this conclusion can be reached without the use of the jigsaw model, the jigsaw model also provides model constants that can be used to make comparisons between datasets. Given that the jigsaw model cannot provide a worse raw fit to real-world data (i.e. a greater residual sum of squares) than either the choros or Arrhenius models, and given real-world systems vary on a continuum from area-dominated to habitat-heterogeneity-dominated, the jigsaw model should outperform both of these models as a descriptive and predictive tool regardless of the processes at work within real-world ecosystems.

Caveats and assumptions

The jigsaw model is structured to shield the z parameter from the influence of habitat heterogeneity, and our simulations show that it does so effectively. However, this shielding is only possible if measured habitat heterogeneity is better than area as a predictor of actual habitat heterogeneity. This need not always be the case, as habitat heterogeneity correlates with area (Báldi 2008), and so this condition represents a significant caveat for the application of the jigsaw model, particularly in studies where habitat heterogeneity has been measured in a questionable way (Stein and Kreft 2015). The jigsaw model can still be used as a curve-fitting tool if this condition is not met, but our caution in these cases relates to interpretation of the parameters.

If this condition is not met, it would be expected that the exponent of measured habitat heterogeneity (d-z) would fall close to zero. This prediction could be used to evaluate the usefulness of different methods of habitat heterogeneity measurement, an exercise that would be of utility more generally (Stein and Kreft 2015). However, it must be noted that d-z ≈ 0 is also expected in systems where habitat heterogeneity is relatively unimportant as a driver of species richness, and so such a condition is not a sure sign of poor measurement of habitat heterogeneity.

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The jigsaw model's assumption that habitat types occupy equal proportions of the area of any given isolate is undoubtedly violated in real systems. While it is clear from our simulation analysis that violations of this assumption have little impact on the output of the model (Figure 2), it is also possible to construct a similar model without this assumption, by introduction of a sigma term (equation 22).

$$22.\ S = c_1 A^z + \sum_{n=1}^{H} c_2 A_n^z$$

Here, the species richness of an isolate is calculated as the sum of a generalist component and H specialist components, where each specialist component is derived from applying the Arrhenius model to an area of size A_n, which represents the fraction of the total area identified as a given habitat type. This model is similar to those used to test the jigsaw model's response to violations of its assumptions (equations 20 and 21). Although this equation lacks the constant d, a measure of the importance of habitat heterogeneity to species richness can be derived from the ratio of $c_2:c_1$. An even more general model, which allows for variable degrees of species' specialisation to distinct habitat types, can be found in the habitat-unit model of Buckley (1982), which is derived using similar ecological theory to the jigsaw model.

Adding value to existing datasets

Application of the jigsaw model to existing real-world datasets demonstrates its ability to provide additional information about the relationship amongst species richness, habitat heterogeneity, and area in those   systems, beyond that provided by previous methods of analysis. By identifying the nature of these relationships, the jigsaw model may facilitate further research to determine the mechanisms driving these relationships. As an example, Fattorini (2011) found that the addition of habitat heterogeneity to a species–   area model did not significantly improve predictions of species richness and, as such, concluded that species richness was primarily driven by area. However, the jigsaw model, which provides the best fit to this dataset of all tested models, suggests that habitat heterogeneity may have a greater effect than was originally suggested   ($z = 0.09$, $d = 0.95$). In this case, a doubling of area has almost no effect on species richness, whereas a doubling of habitat heterogeneity results in an almost doubling of species richness. This also suggests, more generally,   that not all variance that can be explained statistically by area should necessarily be ascribed to area. This is a repeated pattern in existing datasets, where correlations between habitat heterogeneity and area may have masked the importance of habitat heterogeneity (Sillén and Solbreck 1977, Kitchener et al. 1980b, Panitsa et al. 2006, Fattorini 2011). In such systems, habitat-based mechanisms such as environmental filtering (Liu et al. 2019) may have been overlooked as drivers of species richness.

In other cases, the jigsaw model corroborates previous, more detailed analyses where other simple models do not. For example, Deshaye and Morisset (1988)

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studied a system in which species– area relationships were well-supported when no distinction was made between habitat types, but where relationships between area and species richness within individual habitat types were weaker or absent, depending on the habitat. In this case, the species– area relationship was driven primarily by a correlation between area and habitat heterogeneity. The Arrhenius model, applied to this system, supports the observation of a species– area relationship when habitat heterogeneity is ignored ($z = 0.74$), but the jigsaw model reveals that this relationship is, on average, driven by habitat heterogeneity rather than area ($z = -0.04$, $d = 1.53$).

Conservation applications
Biogeographic models of species richness have applications to conservation biology in the face of habitat loss resulting from land use and/or climate change (Rosenzweig 2004, Pereira and Daily 2006, Chase et al. 2019). The explicit use of habitat heterogeneity in biogeographic models is useful for conservation science, because it removes any assumption that smaller areas act as representative subsamples of larger areas with respect to habitat type (Fattorini et al. 2021).

The countryside model is a biogeographic model that explicitly includes a measure of habitat heterogeneity that is designed specifically to model species richness in landscapes impacted by habitat loss (Pereira and Daily 2006, Proença and Pereira 2013). The countryside model achieves this by dividing species into groups based on their affinities for particular habitat types (Pereira and Daily 2006). When this information is available, the countryside model is likely to outperform simpler models such as the jigsaw model (Proença and Pereira 2013). However, when insufficient data exist to fit models such as the countryside model, the jigsaw model may be able to provide a useful first estimate of the potential species loss that could occur from habitat loss. The jigsaw model's ability to partition the effects of area and habitat heterogeneity means that the potential impacts of their loss can be considered independently. This partitioning could inform the design of reserves to ensure the importance of habitat heterogeneity and area are both considered in conservation (Tjørve 2002, Tjørve 2010, Fattorini et al. 2021).

Conclusions
The jigsaw is a biogeographic model that provides an ecological justification for the use of the no-INT, trivariate power-law model of Tjørve (2009), which can partition the impacts of habitat heterogeneity and area on species richness in island systems in a way that other models of comparable complexity cannot. The jigsaw model can be fitted to systems where either area or habitat heterogeneity are dominant drivers of species richness, and it is mathematically flexible enough to conform to other simple models when appropriate. The ability of the jigsaw model to partition the effects of area and habitat heterogeneity is important not just because they are liable to have effects of different magnitudes, but also because habitat heterogeneity, as a concept, is much less well understood than area. This model

can act as a tool for the initial assessment of both habitat heterogeneity metrics and potential species loss from habitat degradation in environments, such as the tropics, where habitat data are often limited.

Acknowledgements

Author contributions

ENF and EES conceived the ideas; ENF collected and analysed the data; ENF led the writing, with contributions from all authors; all authors read and approved of the final manuscript.

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Data availability

The real-world datasets used for comparison of model fits are published and available online, associated with their corresponding publication. A list of these publications and associated metadata are available in the supporting information (Table S1). All publications from which data were derived are cited in the reference list. The raw data associated with experiments 1 and 2, and the analysis of model fits to the real-world datasets, have been uploaded as supporting information. The python script used in experiments 1 and 2 is available in the supporting information (Script S1).

Supplementary Information

The following materials are available as part of the online article:

Script S1. The python script used to generate simulated species richness values to test the response of the jigsaw model to various conditions.

Dataset S1. Details of the model fits to real-world datasets.

Table S1. Datasets used in model comparisons, with associated metadata.

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