Projected climate-driven faunal movement routes

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INTRODUCTION

In the past, as the Earth’s climates changed, species adapted to new environments, moved to track suitable climates, or went extinct. Many species have already responded to modern climate change in a similar fashion (Parmesan et al. 1999; Pounds et al. 2006; Moritz et al. 2008), and projected changes in climate for the coming century will likewise result in distributional shifts of many species (Thuiller et al. 2005; Araújo et al. 2006) and the loss of others (Thomas et al. 2004). Mounting concern regarding the rapidity of climate change has intensified scientific and conservation interest in connectivity and the need for improved land management and restoration to promote permeable landscapes.

To persist in a rapidly changing climate, much of today’s biota will need to traverse extensive human-dominated landscapes (Kareiva et al. 2007), and thus species attempting to shift their distributions will face many challenges that did not confront their ancestors. By some estimates, less than 17% of the terrestrial landscape has escaped the direct impact of human activities (Sanderson et al. 2002), approximately half of the land surface has been converted to agriculture (Millennium Ecosystem Assessment 2005), and less than 1% of the world’s rivers remain unaffected by humans (Vörösmarty et al. 2010). Organisms attempting to relocate to more suitable climates must contend with expansive agricultural landscapes, road networks, dammed rivers and growing human settlements. These and other human alterations to the landscape create well-documented barriers to movement for some species and reduce movement of others (Sieving et al. 1996; Forman & Alexander 1998).

Conservation efforts that seek to facilitate species movement through these human-dominated landscapes will require an understanding of where species will likely need to move to track suitable climates and what the available and most suitable routes for enabling these movements will be. Projections of both the velocity and the direction of shifting climatic conditions provide a coarse approximation of how many species might need to move to track suitable climates (Loarie et al. 2009; Ackery et al. 2010). Projections of changes in climatic suitability for individual species provide a more targeted assessment of the areas to which species may need to move to track climates (Thuiller et al. 2005; Araújo et al. 2006; Huntley et al. 2008; Cheung et al. 2009). Finally, projected changes in species-specific climatic suitability at multiple time periods can illuminate climatic barriers that may prevent species from tracking climate change (Phillips et al. 2008; Early & Sax 2011). Despite these recent advances, considerable uncertainty remains regarding how human land use may alter movement routes defined by climate suitability alone.

Here, we investigate potential movement routes for vertebrates across human-dominated landscapes of the western hemisphere in response to projected changes in end-of-century climate. By coupling recent advances in species distribution modeling with landscape connectivity analyses, we map routes that would allow 2903 species of mammals, birds and amphibians to track suitable climates while avoiding, when possible, areas that are heavily impacted by human activities. We analyse the resulting maps to highlight areas that will likely provide for species movements in the future and conversely areas through which many species will likely need to move but in which opportunities for movement will be more limited.

MATERIALS AND METHODS

Approach

To identify critical areas for fostering climate-driven species movements, we first projected changes in the distribution of climatically
suitable areas for each species under 10 different projected future climates. We then used a connectivity-modelling approach to plot routes for each species from areas that were projected to become climatically unsuitable to areas that were projected to be climatically suitable and from areas that are currently climatically suitable to areas that were projected to become newly climatically suitable. These routes were mapped in such a way as to avoid the most heavily human-impacted parts of the landscape. For each 50-km by 50-km grid cell in the western hemisphere, we then quantified the projected magnitude of movement across species, the average direction of movement in a cell and the degree of agreement in the direction of movements across species.

**Data**

Climate data were downscaled from the University of East Anglia Climatic Research Unit’s (CRU’s) CL 1.0 (New et al. 1999), CL 2.0 (New et al. 2002) and TS 2.1 (Mitchell & Jones 2005) climate data sets to a 50-km by 50-km grid using locally weighted, lapse-rate-adjusted interpolation. We then averaged monthly climate data from 1961 to 1990 to produce a base-line time period. Future climate data were taken from 10 general circulation model (GCM) simulations archived by the World Climate Research Programme’s (WCRP’s) Coupled Model Intercomparison Project phase 3 (CMIP3) (Table S1). Climate projections were averaged over a 30-year period from 2071 to 2100 and represent climates simulated for a mid-to-high (SRES A2) greenhouse-gas emissions scenario (Nakicenovic et al. 2000). In all, 39 bioclimatic variables were used in the modeling process (Lawler et al. 2009).

Species distribution data were taken from digital range maps for birds (Ridgely et al. 2003), mammals (Patterson et al. 2003) and amphibians (data available online, www.globalamphibians.org). For birds, only breeding ranges were included. Species ranges were mapped to the 50-km by 50-km grid and all grid cells overlapping a range were treated as ‘presences’ and all grid cells that did not overlap the species’ range were considered to be ‘absences’.

To model potential species movements, we used a map of the human influence index representing the cumulative effects of land-use change (e.g. built environments and agriculture), human population density, accessibility (e.g. distance to roads) and night-time lighting (Sanderson et al. 2002). We mapped the human influence index data to the 50-km by 50-km grid used for the climate data using a mean aggregation statistic and a bilinear interpolation technique for projection and re-sampling (Environmental Systems Research Institute 2009).

**Species distribution models**

Bioclimatic models were built using an ensemble-based machine-learning approach (random forest predictors, Cutler et al. 2007) for 6933 species as part of a previous study (Lawler et al. 2009). Random forest predictors were chosen because of their ability to capture interactions among variables without specifying those interactions a priori, because of their ability to handle correlated variables, and most importantly, because of their performance relative to other modeling approaches when tested on the datasets used in this study (Lawler et al. 2006; Olden et al. 2008). One model was built for each species using presence–absence as a binary response variable and the 39 bioclimatic variables as potential predictors. Each random forest was based on 100 classification trees built with subsets of the data and predictor variables. We used 80% of the presences and 80% of the absences for each species to build the models and used the remaining data for model testing. For each model, a threshold for predicting presence was determined using the receiver-operating characteristic curve with the assumption that correctly predicting a presence was as important as predicting an absence (Fielding & Bell 1997). The models were evaluated based on their ability to correctly predict the presences and absences in the test data sets. Of the total number of species examined, models for 2954—1818 birds, 723 mammals and 413 amphibians were able to correctly predict at least 90% of the absences and 80% of the presences in the reserved test data sets. These are the models that were used in this study.

We used the models to project areas that will likely be climatically suitable under the 10 simulated future climates. For each species, we identified areas that are currently climatically suitable and are projected to become climatically unsuitable in a future climate. We treated these as areas of potential range contraction. Similarly, we identified areas that are climatically unsuitable today, but are projected to become climatically suitable in the future. We treated these as areas of potential range expansion.

**Species**

Of the 2954 species for which we had relatively accurate models, 2903 species met a set of additional criteria that allowed us to use them in this study. On average, across the 10 GCM projections, 2765 species were used for calculating species movements into areas of potential range expansion, and 2621 species were used for calculating species movements out of areas of projected range contraction. We did not use any species for which the bioclimatic models projected a complete elimination of climatically suitable space (an average of 133 species across all 10 GCM projections). For modelling movements into areas of potential range expansion, we did not use species for which no range expansions were projected (an average of 43 species across all 10 GCMs) nor did we include species for which historical ranges were disconnected from projected areas of range expansion (i.e. we excluded areas that were projected to be newly climatically suitable but contained no cells that were adjacent to any cell in the species’ historical range). This latter restriction applied to an average of 160 species across the 10 GCM projections. Similarly, for modeling movements out of areas of range contraction, we did not include species for which projected future ranges were disconnected from areas of projected range contraction (an average of 56 species across the 10 GCM projections). By calculating movement routes only for range shifts that resulted in contiguous current and future ranges, we avoided modeling routes to areas that would likely be inaccessible to dispersing individuals. However, this restriction may have obscured some of the routes that species will take to move longer distances as climates change. Finally, all species had some projected range contraction across all 10 GCM projections.

**Movement models**

For each species, we modelled the potential routes of organisms from each grid cell in which the corresponding species-distribution model projected the climate to become unsuitable by the end of the
century to an area in which climate was projected to remain suitable. We likewise mapped potential routes from areas that were suitable in the historical time period (1961–1990) to areas that were projected to become newly climatically suitable by the end of the century.

We used current flow models from electronic circuit theory to plot movement routes for each of the species using Circuitscape software (McRae & Shah 2009). Circuitscape treats landscapes as conductive surfaces, replacing cells connected to their neighbours with nodes connected by resistors. Patterns of current flow can be used to efficiently predict the movement patterns of random walkers across a landscape, where walkers are proportionally more likely to move through low-resistance cells than high-resistance cells (McRae et al. 2008). When 1 Amp of current travels from a source cell to a target cell, the current flowing through each intervening cell represents the likelihood that a random walker would pass through the cell if it started at the source and moved until it reached the target (Newman 2005; McRae et al. 2008). The result is a continuous map of movement probabilities across all possible routes, rather than a single, least-cost path. At the extent of the study area, high densities of current indicate areas through which higher numbers of successful dispersers are predicted to pass.

Resistance to movement through the landscape was based on the distance travelled and the degree to which the landscape along a movement route was dominated by human uses as described by the human influence index (Sanderson et al. 2002). Book-like movements from cell to cell were assigned a resistance of one and diagonal movements were assigned a resistance of the square root of two to account for the difference in the distance between cell centres. The distance-associated resistances were multiplied by the average squared human influence index value of the adjoining cells in question. We chose to use the squared values of the human influence index to ensure that human activities would affect movements. We explored alternative weightings for individual species (e.g. raising the index values to the 3rd or 6th power), which further constrained movements and, in the aggregate, would result in more concentrated projected movement routes.

For mapping movements in potential contraction zones (areas that are climatically suitable today, but projected to become unsuitable in the future), we used each individual cell in that zone as a source, injecting 1A of current into the cell. Areas predicted to remain climatically suitable were set to ground, so that current would flow from contraction zone cells to cells predicted to remain suitable. All routes were constrained to areas that were historically suitable. We applied a similar procedure for modeling movements into expansion zones (areas projected to become climatically suitable as climates change): each cell in the expansion zone was used as a target, with a current source of -1A applied to draw current into the cell from areas that were suitable in the historical time period.

To map movement vectors within each cell, we designed a two-step computation process. First, for each species, we computed a gridded map of current flow directions and magnitudes by calculating the vector sum of currents leaving each cell in each of eight possible directions (Fig. 1). For each cell, we then calculated the mean direction across all species, resulting in a gridded map of vector directions describing a central tendency of species movement (Batschelet 1981). In addition to a directional mean, we also calculated the circular concentration (directional agreement) across species. Second, we added current vector magnitudes across species within each cell. The result was gridded surfaces that described the resultant magnitude and direction of flow across species for each cell location. To account for differences in species richness, we divided the current flow magnitude in a cell by the number of species ranges that currently intersect the cell. We calculated these three statistics for all cells for each of the 10 future climate projections and then produced one set of statistics by averaging the results for the 10 projections.

RESULTS

Several locations in North and South America will likely be critical for species movements in a changing climate (Fig. 2). For example, large numbers of movements are expected relative to the number of species currently at high northern latitudes, in the southeastern United States, northeastern North America, the Amazon Basin and southeastern Brazil. In the southeastern United States, species are projected to track shifting climates by moving northeastward into the southern Appalachian Mountains (Fig. 2a). In central Argentina, species are projected to move poleward into the southern Pampas as well as into the Sierras de Córdoba and Andes (Fig. 2b). Several other mountainous areas are also projected to facilitate movements including the mountain ranges of Central America, the Rocky Mountains of western North America and the southern Brazilian highlands (Fig. 3). Other landforms, such as the Great Lakes in North America and the Atacama Desert in Chile will likely constrain movements as well (Fig. 2).

To address the question of how human land use will likely shape the movements of species in response to climate change, we compared our predictions of species movements that include land-use patterns (Fig. 2) to similar predictions based solely on climatic changes (Fig. S1). The differences in these two forecasts highlight areas to which species movements will be constrained due to human activities (blue areas in Fig. 4a) and conversely, areas in which human activities will likely impede climate-driven shifts in species distributions (red areas in Fig. 4a). These patterns emphasise the effects of potential barriers to movement in the Amazon Basin, south-central Brazil, and the eastern Unites States. They also highlight areas that are likely to be movement corridors due to the relative lack of human activity in the Amazon, along the border between Bolivia and Paraguay, and through the Ozarks and Appalachian Mountains in the eastern United States.

Although the areas with many projected movements reflect the constraints imposed by human land use, they are not necessarily pristine landscapes or even conducive to movement. We identified potential areas for protecting movement and areas in which land use will likely act as a barrier to movements by overlaying a map of projected species movements (from Fig. 2) with a map of the same measures of human impact used in our original analyses. The far northern latitudes, the Amazon Basin, and southeastern Bolivia and northern Paraguay (orange areas in Fig. 4b) are important for movement and less impacted by human activities. In contrast, large portions of the southeastern United States, southeastern Brazil and the Pampas lowlands are projected to experience many movements through highly impacted landscapes (the maroon-coloured areas in Fig. 4b).

As expected, the relative amount of climate-driven movement and the general direction of movement varies regionally. When
expressed as a proportion of the current species richness, the Tundra, Boreal Forest and Taiga, North Temperate Broadleaf and Mixed Forests, and the Tropical and Subtropical Moist Broadleaf Forests are projected to experience the greatest flux of species movements compared to less-trafficked southern hemisphere Montane Grasslands and Shrublands and Temperate Broadleaf and Mixed Forests, as well as the Tropical and Subtropical Coniferous Forests (Fig. 5a). When absolute numbers of movements are considered, the patterns, at least in part, reflect patterns of vertebrate species richness, with the tropical regions projected to experience the most movement (Fig. S2).

We used simple linear models to test whether the number of movements (adjusted for current species richness) and the variance in the direction of movements were associated with elevation. In general, mountainous biomes (those with larger ranges of elevations) tend to have fewer projected movements than biomes with less topographical relief ($P < 0.01, r^2 = 0.44$, Fig. 5b). Our models also forecast greater variance in the direction of movement in mountainous regions ($P < 0.05, r^2 = 0.42$, Fig. 5c). The ecoregions with the greatest variability in the directions that species are projected to move are in the tropics – the Tropical and Subtropical Dry Broadleaf Forests, southern hemisphere Deserts and Xeric Shrublands, and the Tropical and Subtropical Coniferous Forests. Indeed, in the tropics, species are not consistently projected to move poleward as in the temperate regions (where, as expected, species are projected to move north and south respectively, Fig. 5a). Movements in the tropical broadleaf forests and the montane grasslands tend to be westward, in part towards higher elevations in the Andes.

Finally, we found that when analysed separately, the three taxonomic groups that we modelled all showed similar patterns of movement across much of the western hemisphere (Fig. S3–S5). Nonetheless, the taxa differed with respect to movements in particular areas. For example, movements into the Andes and across the southern portion of the Great Basin in the southwestern United States were particularly important for amphibians and there were far fewer movements projected in the Amazon Basin for mammals.

**DISCUSSION**

**Projected movement**

Our results depict projected climate-driven, land-use constrained movements of almost 3000 species across the western hemisphere. Several areas are likely to experience high concentrations of movements either because many species will experience changes in climatic suitability there or because land use will constrain their movements. There are potentially simple explanations for many of the specific patterns highlighted by the models in our study. Many
of the movements are to higher elevations or latitudes and many skirt areas with intensive agriculture or development. The southern Appalachian Mountains in the southeastern United States and the Atlantic Forest in Brazil were two prominent areas highlighted by our models as likely to have high concentrations of species movements. Both of these areas are suspected to have served as climate refugia in the past. For example, the central and northern Atlantic Forest in southeastern Brazil have been identified as refugia in which these forest systems likely persisted through the Pleistocene (Carnaval & Moritz 2008). Whereas the projected movements into southeastern Brazil may imply that this area will again be a stronghold for species in a changing climate, the movements in the southern Appalachians are northward, out of the areas that served as refugia in the past.

The seemingly large impacts of land use on projected movements at high northern latitudes largely reflect that we have mapped the number of movements as a fraction of the current species richness in a cell (Figs 2 and 4). The high latitudes have few species but are projected to experience a large influx of species (Lawler et al. 2009) and thus the number of movements – and the difference between the number of movements accounting for and ignoring human land use – is high relative to the number of species in a cell. Patterns of raw species movements are more reflective of hemispheric patterns of species richness (Figs. S2 and S6).

The higher number of movements projected for flatter landscapes relative to more mountainous regions likely reflects, in part, the projected velocity of climate change (the instantaneous local rate of movement needed to maintain constant climatic conditions; Loarie et al. 2009). In mountainous areas where climate gradients are steep (e.g. coniferous forests and Montane Grasslands and Shrublands), climates will move more slowly across the landscape and thus species will need to move shorter distances to track suitable climates. In flatter regions (e.g. Tropical and Subtropical Broadleaf Forests and the Northern Temperate Broadleaf and Mixed Forests) with higher velocities of climate change, more species will be required to move greater distances and thus we might expect to see more movement in these areas. Similarly, the contrast between the more consistently projected latitudinal movements in ecoregions at mid to high latitudes and the less consistent directional movements of the species in the tropics likely reflect that elevational temperature gra-

Figure 2 Projected climate-driven species movements averaged across 10 future climate projections. Arrows represent the direction of modelled movements from unsuitable climates to suitable climates via routes that avoid human land uses. The sizes of the arrows represent the number of projected species movements (current flow) as a proportion of current species richness. The colours of the arrows reflect the level of agreement in the direction of movement across species and routes. The insets are maps of (a) a high concentration of movements through southeastern North America and into the Appalachian Mountains and (b) areas of movement through the Sierra De Córdoba and into the Andes and the southern Pampas. Lighter blue shading in these topographical overlays indicates more intensive human activity.
Differences are generally stronger than latitudinal temperature gradients in the tropics and thus are more likely to drive species movements in the future (Bush 2002).

In general, our projected movement patterns have some expected similarities with studies that have modelled connectivity based solely on measures of human impact on the landscape (e.g. Theobald et al. 2012). Theobald et al. (2012) identified several corridors in the southern and eastern United States and parts of corridors in the western United States that correspond with the routes that we identified. The differences between the maps produced by these two studies are

Figure 3 Projected climate-driven species movements averaged across 10 future climate projections for three specific areas (a). These are the same data presented in Fig. 2. The squares on the map in panel (a) correspond to areas in Central America (b), the Rocky Mountains (c) and the southern Brazilian Highlands (d).

Figure 4 Areas in which human land use will likely impede climate-driven movements (a, red areas) and where human land use will likely concentrate movements (a, blue areas). Values are based on differences in the number of projected climate-driven faunal movements between models that include human land use and those that do not. Some areas with many projected movements are highly impacted by human land use (b, dark purple areas) and some are much less impacted (b, light yellow areas). In both maps, movements are calculated as the amount of current passing through a cell divided by the number of species’ current ranges that overlap the cell.
largely due to the fact that our routes account for climate-driven movements. The results of our analysis of where climate-driven movement routes are likely to be more or less impacted by human land uses (Fig. 4b) also correspond well with areas that have been identified as providing more or less connectivity for terrestrial mammalian carnivores in general (Crooks et al. 2011).

A matter of scale

This study provides a continental-scale perspective of climate-driven species movement routes. Our goal of intensively modelling movement for many species across a large extent required that we limit our analyses to a relatively coarse resolution to facilitate computation. Nonetheless, there is ample opportunity for analytical innovations that could lead to more fine-grained analyses in the future. The spatial resolution of our analyses likely obscures finer scale patterns that might highlight other areas through which species will be able to move. The circuit theory-based algorithm we used took an average value of human impact as a measure of resistance to movement that would only be resolved at finer spatial scales.

Given the coarse resolution of the data used in our analyses, the areas we identified as being important for the movement of species in a changing climate are indeed very likely to be important for many species. However, they will not be the only important areas for providing connectivity. Finer scale regional analyses will likely reveal additional (and possibly alternative) routes where conservation efforts can be directed. Thus, although conservation investments in the areas highlighted by our analyses will likely be useful, finer scale analyses will be important for revealing additional investment options – choices that in some cases will be more cost-effective. Moreover, the analyses presented here are most appropriate for locating general areas in which connectivity could be preserved or enhanced to facilitate species movements in a changing climate. They could, for example, be used to identify where new, large-scale projects such as the Yellowstone to Yukon (Gailus 2001) effort could be located or for directing resources to such ongoing efforts. However, given the limitations of their coarse resolution, they cannot be used to identify where in those general regions specific investments should be made. Finer scale analyses will be necessary for informing such decisions. Nonetheless, broad-scale analyses such as those presented here are critical for addressing the impacts of climate change, which, in many cases, will be unconstrained by regional and national borders (Hannah 2010).

Bioclimatic and movement models

Previous studies have projected the potential rates and directions of local climatic changes (Loarie et al. 2009; Ackerly et al. 2010). In contrast, the bioclimatic models used in our study integrate multiple climatic variables to provide species-specific forecasts. In addition, our movement models, which account for coarse landscape patterns, provide a more biologically meaningful estimate of where species will likely need to move in response to climate change. Nonetheless, much like their application in past studies, these models make several simplifying assumptions. First, bioclimatic models like those used in this study can provide an informed, but imperfect

Figure 5 Average number and direction of climate-driven species movements per 50-km by 50-km grid cell across major biomes (a), the relationship between the average number of movements and elevation range in each biome (b), and the relationship between the variance in movement directions across each biome and the range of elevations in the biome (c). Movements are calculated as current flow through a cell divided by the number of species’ ranges that overlap the cell. Biomes are depicted in Fig. S9.
approximation of how some species will move in response to climate change (Araújo et al. 2005) because they rely on empirically derived relationships between species distributions and climatic conditions and because they do not directly model biotic interactions – for example, predator–prey interactions or habitat associations – or evolutionary processes (Botkin et al. 2007). Second, our models do not account for dispersal distances and thus some of the movements included in our results may be unrealistic as they may be in areas that a given species will not be able to reach in a 100-year period. Many moles, shrews and primates, for example, may not be able to disperse fast enough to keep pace with climate change in the Western Hemisphere (Schloss et al. 2012). Third, we have used static models to investigate a dynamic process; more dynamic modelling could potentially reveal different patterns of species movements and barriers to those movements (Early & Sax 2011). Fourth, our models use a static map of the human influence index. Given that human land use will continue to change, and potentially have a greater influence than climate change on species in some regions (Jetz et al. 2007), using projected changes in the patterns of human influence on the landscape would likely improve the ability to project critical movement corridors and to anticipate where connections could be lost due to future development.

Perhaps most importantly, our models do not account for species-specific habitat requirements. Thus, some of the areas of projected climatic suitability may not have suitable habitat. In addition, by not accounting for species’ habitat requirements, our models make the simplifying assumption that all species respond to human land use in the same way and that human impacts on the landscape (and large rivers which are incorporated into the human influence index we used to represent human impacts) are the only factors that limit movement. This clearly is not the case. Many birds, for example, will be able to fly over areas that will serve as barriers to many amphibians and small mammals. Because we do not take species-specific habitat requirements, barriers to movement and dispersal behaviours into account, our models likely overestimate the number of movements through a given cell. Nonetheless, although it necessarily obscures the routes that will be needed to provide connectivity for specific species, using a simple measure of the condition of the landscape has the potential to reflect species movement patterns when summarising potential movements across a wide range of species with disparate habitat preferences (WHCWG 2010).

Finally, our analyses gave equal weight to movements in areas of potential range expansions and those in areas of potential range contractions. However, for many species, the critical movements will be those into areas that become newly climatically suitable. Movements out of areas that become climatically unsuitable and into already occupied areas will likely be less important for species persistence. When examined separately, many of the projected movements into areas of potential range expansions are similar to the projected movements highlighted in Figs 2 and 3 (Fig. S7). Nonetheless, there are some significant differences between the projected movements into potential expansion zones and those out of potential contraction zones (Figs. S7 and S8).

CONCLUSIONS

Fostering species movements by increasing connectivity is one of the most often-cited adaptation strategies for conserving biodiversity in a changing climate (Heller & Zavaleta 2009). Thus, identifying where large numbers of species will need to move has the potential to guide critical land use and conservation planning. To date, most connectivity planning has focused on connecting patches of suitable habitat for one or more focal species. However, planning for connectivity that will allow species to track changes in climate will require new approaches that address multiple species, changing landscapes and plan for movements outside of species’ current distributions (Phillips et al. 2008; Nuñez et al. 2013). Broad-scale conservation efforts such as the Yellowstone to Yukon and Mesoamerican Biocorridor projects have the potential to facilitate the types of movements projected by our models. However, our results highlight other areas in which there are no clear corridors and where restoration efforts and land-management practices could be used to either develop such corridors or to create more permeable landscapes in general. What is perhaps most clear, is that many species will likely move in response to climate change, and human activities on the landscape have the potential to greatly facilitate or inhibit those movements.

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AUTHORSHIP

JL conceived of the study, AR and BM conducted the analyses, and JL, AR, JO and BM designed the analyses and wrote the manuscript.

REFERENCES


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