Landscape disturbance models consistently explain variation in ecological integrity across large landscapes

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Abstract. The generally negative effect of anthropogenic disturbance on the quality of habitats for species viability makes it a common focus of conservation assessment and prioritization efforts. Although many available spatial models and metrics (e.g., distance to or density of disturbance) characterize impact patterns of anthropogenic disturbance on the landscape, a general evaluation of model performance against empirical measurements of ecological integrity is lacking. We tested both distance-based and disturbance-density models in relation to ecological indicators. The models included roads, residential and commercial development, agricultural land use, mining, energy development infrastructure, and transmission structures as disturbance sources. Model parameters were based on expert input and results from the published literature. The disturbance models were tested against two disparate and independent measures of habitat quality: a floristic quality index and measures of greater sage-grouse population integrity. Floristic quality scores were significantly lower in vegetation plots closer to disturbances in a general distance-based disturbance model across Colorado. Although the proportion of variation in floristic quality explained by anthropogenic disturbance was relatively low (8.5–11.8%), it appeared to represent a ubiquitous baseline negative effect of proximity to anthropogenic disturbance on the quality of vegetation communities. For both distance- and density-based greater sage-grouse models, modeled disturbance indices were significantly lower (10–12 times) near active than historic leks, and numbers of males counted at leks increased significantly (3.2–3.4 times) as modeled disturbance decreased. Our findings indicate that as a general class, geospatial models can depict effects of anthropogenic disturbance on both plant communities and individual animal species. Empirical validation of disturbance models focused on other species or regions is recommended to further evaluate the utility and reliability of these methods.

Key words: anthropogenic disturbance; Centrocercus urophasianus; floristic quality index; greater sage-grouse; landscape integrity models.

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INTRODUCTION

Due to the typically negative effects of anthropogenic disturbance on nearby habitat quality, geospatial models of anthropogenic disturbance on the landscape are useful in a variety of conservation activities, including threat and condition assessment (Di Marco et al. 2013, Haines et al. 2013), prioritization (Brooks et al. 2006), connectivity and core area assessment (Cardoso et al. 2013, Krosby et al. 2015), planning (Bryce et al. 2012), and mitigation (Kiesecker et al. 2009). In most cases, attempts to quantify the effects of anthropogenic disturbance are essentially the obverse of efforts to quantify ecological integrity (i.e., intactness of natural conditions). In recent decades, researchers have focused on streamlining and standardizing landscape-level disturbance or ecological integrity models by developing geospatial representations of impact levels based on geospatial mapping of man-made features. In many instances, the intensity and extent of anthropogenic impacts have been modeled with regard to their effects on composition, structure, or fragmentation of a landscape (reviewed by Cushman et al. 2008, Kindlmann and Burel 2008, and others), generating a plethora of landscape metrics. In addition, connectivity modeling frequently incorporates GIS data layers depicting anthropogenic disturbance as cost- or resistance-surface modifiers for a suite of habitat suitability or permeability factors (Wade et al. 2015).

The effects of anthropogenic disturbance are often modeled using the distance to a particular disturbance or the density of disturbance within an area of concern. Negative effects on wildlife acting beyond the surface extent (footprint) of man-made structures have been documented for roads, fences, and power lines (Palomino and Carrascal 2007, Wolfe et al. 2007, Benitez-Lopez et al. 2010, Stevens et al. 2012), urban and exurban development (Odell and Knight 2001, McDonald et al. 2009, Goad et al. 2014), energy development and production (Pruett et al. 2009, Harju et al. 2010, Sawyer et al. 2013, Gregory and Beck 2014, Shaffer and Buhl 2015), and agriculture (Burel et al. 2004, Ghilain and Bélisle 2008). Because species are believed to vary in their response to disturbance, distance and density effects of anthropogenic disturbance are often specified as applying to a particular taxa or guild.

Results from studies such as those described above have been applied through distance- or density-based geospatial models to represent the cumulative influence of anthropogenic disturbance that reaches beyond an immediate disturbance footprint. The distance approach uses distance-decay methods employing a variety of decay curves to depict the lessening of impact over distance. Distance methods typically summarize the cumulative effects of individual disturbance data layers in an additive model of landscape or habitat integrity (Copeland et al. 2007, Leu et al. 2008), but more complex input layers may be constructed from individual disturbance layers (Leu et al. 2008, Theobald 2013). Density of disturbance is expressed as a measure of impact per unit area significant to the study object and density-based models smooth the actual location of disturbances into “hot spot” estimates (i.e., exceptional concentrations of disturbance). The distance and density approaches offer different ways of aggregating disturbance impacts on the landscape. Regardless of method used, it is important to know if such models are effectively depicting the influence of anthropogenic disturbance on habitat quality.

Despite their growing applications, geospatial models of anthropogenic disturbance have not been widely validated against field data, especially outside of overall resistance-surface model applications. To address this limitation, we tested both general and species-specific landscape disturbance models in Colorado, USA. Our objective was to compare the modeled intensity of disturbance at a selection of locations to an independent measure of habitat quality observed at those same locations. A general distance-based model was compared with floristic quality index (FQI) scores derived from field plot species lists. Species-specific distance- and density-based disturbance models focused on a flagship vertebrate species of conservation concern (*Centrocercus urophasianus*, the greater sage-grouse) and were tested using presence and activity data for this species across its range in Colorado. The greater sage-grouse provided an ideal opportunity to test our spatial models because the species requires large landscapes...
while selecting habitat conditions at multiple scales (Connelly et al. 2011), has a well-documented response to distance and density facets of anthropogenic disturbances (Naugle et al. 2011, Manier et al. 2013), and a long-term index of population data (lek counts) is available. If our models are depicting negative effects of anthropogenic disturbance across the landscape in a realistic fashion, we expect both floristic quality scores and greater sage-grouse presence and activity to decline in areas with higher disturbance index values.

**METHODS**

**Generating spatial models of landscape disturbance**

Although our three geospatial disturbance models draw on a common set of input data, the combination process is distinct for each model (Fig. 1).

**General distance-based disturbance model.**—Using methods developed for landscape integrity models (Colorado Natural Heritage Program 2008), we created a general distance-based disturbance...
model (DistI) for Colorado (Fig. 2A), incorporating anthropogenic disturbance sources that could be mapped consistently at a statewide level. We obtained the best publicly available raster datasets covering six categories of anthropogenic disturbance: roads, residential and commercial development, agricultural land use, mining, energy development infrastructure, and transmission structures. For each disturbance type, distance effects were modeled by assigning an impact weight to the mapped extent (footprint) of the disturbance, and decaying this weight across adjacent raster cells through a decreasing sigmoid function whose steepness and spread were specified individually for each disturbance type. The resulting individual disturbance rasters were additively combined to produce a cumulative anthropogenic disturbance effect index, where values of 0 represented no impact. Further details are provided in Appendix S1.

Greater sage-grouse disturbance models.—We developed two separate spatial disturbance indices for greater sage-grouse (GRSG) habitat across the species’ range in Colorado. Our GRSG distance-based disturbance model (SG-DistI) is a composite index of the distance effects of mappable infrastructure on GRSG habitat across the landscape and was created using methods similar to those described for the general model (Fig. 3A). Literature associated with studies of radio-equipped GRSG was used to establish distance effects for transmission lines, highways, unpaved roads, and producing natural gas/oil wells; thus, the distance-based model represents

Fig. 2. The general disturbance index across the State of Colorado (A) and an example comparison of the general distance-based index (B) with the greater sage-grouse distance-based index (C) illustrating the potential for varying results depending on inputs and methods used to generate the index.
the response of individual GRSG to disturbance. For other anthropogenic features, we applied literature-derived distances established for what we considered the most similar feature type. In contrast to the general disturbance index, the GRSG-specific indices focused on depicting the degradation of otherwise suitable GRSG habitat due to anthropogenic disturbance. Distance effects were applied to each disturbance feature individually using decaying sigmoidal functions, and normalized to range from 0 to 1 before being multiplied together to produce the SG-DistI which ranged from 0 (no value for GRSG) to 1 (value for GRSG not reduced). Note that the method of combining individual disturbance layers (multiplicative instead of additive) and the scale direction of the GRSG model differ from the general model described above due to different original intended uses of each model. These differences are mentioned for clarity but do not affect the analyses presented here, as the general and GRSG-specific models were not directly compared. Further details are provided in Appendix S1.

Our density-based disturbance model for GRSG habitat (SG-DenI) indexes the cumulative surface disturbance associated with a unit area (Fig. 3B). The SG-DenI summarized the density of disturbance at each raster cell location using a 3.2 km radius moving window (32.2 km², the median best distance from GRSG studies that evaluated disturbance-density effects over multiple window sizes). All anthropogenic feature types (e.g., well pads, roads, towers) were represented spatially by their typical extent (i.e., footprint), providing a measure of the actual area of surface disturbance per 32.2 km² associated with each raster cell location. We then applied minimum and maximum values (thresholds) to each location to indicate negligible vs. exclusionary levels of disturbance (above which we expect GRSG to be excluded from the landscape). Levels were based on a literature review of GRSG lek response to roads and oil and gas wells. These thresholds were applied across all disturbance types, because the literature was lacking to describe responses of GRSG to densities of other disturbance types. We relied on the lek-based literature because GRSG responses, as measured via facets of lek ecology (e.g., peak attendance, lek activity status), represent long-term and large-scale population responses to cumulative
impacts on the surrounding landscape; thus, the density-based model represents the response of GRSG leks to disturbance. The upper and lower thresholds were based on numbers of well pads and lengths of road and were translated into associated disturbance areas. For the final SG-DenI, zero corresponded to locations that were highly disturbed and likely no longer provide suitable GRSG habitat (i.e., above an upper disturbance threshold of 3.07 km² disturbance per 32.2 km²), one corresponded to locations with no or minimal disturbance (i.e., below a lower disturbance threshold of 0.82 km² of disturbance per 32.2 km²), and values greater than zero or less than one continuously represented intermediate levels of disturbance. Further details are provided in Appendix S1.

Validating disturbance models with field observations

General distance-based disturbance model.—Publicly available vegetation plot datasets from the National Park Service (NPS) Vegetation Inventory Program and the Colorado Wetland and Riparian Classification were used to calculate an index of floristic quality for a selection of plots across Colorado using the methods of Rocchio (2007). The NPS data were drawn from within 10 NPS units within Colorado. The Colorado Wetland and Riparian Classification (Wetland-Riparian) data were collected throughout Colorado, although a majority of plots were in montane areas. We used a spatially stratified random sampling procedure to select 299 NPS plots and 201 Wetland-Riparian plots from the available data. We analyzed the two plot datasets separately as independent tests of the general DistI, since field methodology and geographic location in Colorado differed between the two. The FQI is derived from the species list of each individual plot and represents the average “coefficient of conservatism” of the plot, corrected for the influence of area on species richness. The coefficient of conservatism is a measure of the degree to which a plant species will decline or disappear according to the degree of human disturbance (Wilhelm and Masters 1995). Species that have high conservatism values show strong fidelity to high-quality, undisturbed habitats. We used the DistI value at the point associated with each plot location to relate landscape-scale disturbance to floristic quality. Details are provided in Appendix S2.

We used simple linear regression for the Wetland-Riparian analyses because the data were collected from across the state. We used linear mixed models for the NPS data with Site as a random categorical predictor to account for heterogeneity in FQI scores (and the underlying vegetation communities used to calculate those scores) among NPS units across Colorado. The DistI disturbance index was the sole fixed-effect predictor variable in both vegetation analyses. We present standard adjusted R² and model results for the Wetland-Riparian analysis. For the mixed model NPS analysis, we calculated marginal (DistI effect only) and conditional (both DistI and Site effects) pseudo-R² values in R package “piecewiseSEM” using the methods of Nakagawa and Schielzeth (2013) and Johnson (2014). We used the conservative Kenward-Roger degree-of-freedom adjustment to calculate P-values using R package “pbkrtest” (Schaalje et al. 2002).

Greater sage-grouse disturbance models.—We evaluated the ability of each spatial disturbance model to represent GRSG response to disturbance by testing the relationship between modeled disturbance and two aspects of GRSG lek dynamics: lek persistence (activity status) and male abundance. Lek data were obtained from Colorado Parks and Wildlife (CPW), which maintains a comprehensive long-term GRSG database. We applied the CPW definitions of active and historic leks to represent lek persistence. Active leks were those at which at least one GRSG has been observed in at least one of the past 10 yr (2006–2015) and historic leks were those that have not been active in the last 10 yr (2006–2015). Leks where at least one GRSG had been observed in at least one of the last 10 yr, but which do not meet the qualification of an active lek, are categorized as inactive and were not included in this analysis. For male abundance, we used the highest maximum male count recorded over the past five years at active leks. We used the SG-DenI value at the point associated with a lek to relate landscape-scale disturbance to each lek. We used the mean SG-DistI value within a 6-km circular buffer surrounding each lek location to represent the portion of the
landscape in which we expect to encounter the most GRSG. The majority of females breeding on a given lek nest within 6 km of that lek (Holloran and Anderson 2005, Colorado Greater Sage-grouse Steering Committee 2008).

For the lek persistence test, we fit logistic regression models of active vs. historic leks, with SG-DistI and SG-DenI as dependent variables in separate models. The male count data included a large number of zero or low count observations and had a poor fit with a Poisson distribution. Therefore, we used negative binomial regression to model the number of males as a function of SG-DistI or SG-DenI (Venables and Ripley 2002). To assess model fit, we calculated the dispersion parameter \( \phi \) (residual deviance/degrees of freedom), which should be close to 1.0 for an appropriately fit model, and a simple pseudo-\( \text{R}^2 \) \((1 – (\text{residual deviance}/\text{null deviance}))\) (Cameron and Windmeijer 1996, Nakagawa and Schielzeth 2013). To describe effect size, we reported the odds ratios (exp(\( \beta \))) for lek persistence models and the proportional change in peak male abundance (exp(\( \beta \))) for the count models, along with asymptotic 95% confidence intervals.

**RESULTS**

**General distance-based disturbance model**

Floristic indicators of ecological integrity showed a small, but consistent negative relationship with anthropogenic disturbance, as indexed by DistI. We found that on average, across the State of Colorado, quality of vegetation plots on NPS units declined as anthropogenic disturbance increased. NPS FQI values decreased on average by 0.610 (95% CI: \((-0.861, -0.359); P\text{-value } < 0.001\)) for every 100-unit increase in DistI (raw DistI range: 0.0–1491.32). The marginal pseudo-\( \text{R}^2 \) value for DistI was 0.085. The conditional pseudo-\( \text{R}^2 \) value for both fixed DistI and random Site effects combined was 0.349. Observed FQI values for the NPS plots ranged from 1.15 to 46.97. Wetland-Riparian vegetation community quality was also negatively related to general anthropogenic disturbance. The FQI index for Wetland-Riparian plots decreased by \(-0.880 \) (95% CI: \((-1.207, -0.553); P\text{-value } < 0.001\)) for every 100-unit increase in DistI. The adjusted \( \text{R}^2 \) for DistI on Wetland-Riparian plots was 0.118. Observed FQI values for the Wetland-Riparian samples ranged from 1.79 to 37.64.

**Greater sage-grouse disturbance models**

Across GRSG range in Colorado, we found that lek persistence decreased as anthropogenic disturbance increased, as measured by mean SG-DistI within 6 km of leks (Table 1). On average, there was a 12.2 times increase in the odds of a lek being active at an SG-DistI of 1 (least disturbed, with highest potential value for GRSG) than at an SG-DistI of 0 (most disturbed, with no value for GRSG; Table 1), and mean SG-DistI was higher near active than historic leks (Fig. 4). There was a significant positive relationship between numbers of males and the mean SG-DistI within 6 km, with an average of 3.4 times higher peak male counts as SG-DistI increased from most disturbed (0) to least disturbed (1; Table 1, Fig. 5).

Greater sage-grouse abundance and the presence of active leks were also negatively related to the density of anthropogenic disturbance. SG-DenI was significantly higher near active than historic leks, with leks being 9.8 times more

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Table 1. Goodness of fit and effect size for logistic and negative binomial models of SG-DistI and SG-DenI in comparison with greater sage-grouse (GRSG) breeding lek data in Colorado, USA.

<table>
<thead>
<tr>
<th>Model</th>
<th>Lek sample size</th>
<th>Dispersion</th>
<th>Pseudo-( \text{R}^2 )</th>
<th>Mean effect size (95% confidence interval)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lek persistence ~ SG-DistI Active</td>
<td>195</td>
<td>1.25</td>
<td>0.04</td>
<td>A lek was 12.2 times (4.5–32.5) more likely to be active at SG-DistI of 1 than 0 (( P &lt; 0.001 ))</td>
</tr>
<tr>
<td>Historic = 366</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GRSG abundance ~ SG-DistI</td>
<td>296</td>
<td>1.14</td>
<td>0.03</td>
<td>Peak male count was 3.4 times (1.7–6.8) higher at SG-DistI of 1 than 0 (( P &lt; 0.001 ))</td>
</tr>
<tr>
<td>n = 296</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lek persistence ~ SG-DenI Active</td>
<td>195</td>
<td>1.25</td>
<td>0.03</td>
<td>A lek was 9.8 (3.6–26.7) times more likely to be active at SG-DenI of 1 than 0 (( P &lt; 0.001 ))</td>
</tr>
<tr>
<td>Historic = 366</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GRSG abundance ~ SG-DenI</td>
<td>296</td>
<td>1.14</td>
<td>0.02</td>
<td>Peak male count was 3.2 times (1.5–7.1) higher at SG-DenI of 1 than 0 (( P &lt; 0.01 ))</td>
</tr>
</tbody>
</table>

**Notes:** SG-DistI, GRSG distance-based disturbance model; SG-DenI, density-based disturbance model for GRSG habitat. Pseudo-\( \text{R}^2 \) was the proportional change in deviance from a null model to the fit model. Effect size is the odds ratio, calculated as exp(coefficient).
likely to be active at an SG-DenI of 1 (least disturbed) than at an SG-DenI of 0 (most disturbed; Table 1, Fig. 4). One influential point was identified, which was a high disturbance location where 34 males were counted. Removal of this point did not alter model conclusions. Numbers of males were on average 3.2 times higher as SG-DenI increased from most disturbed (0) to least disturbed (1; Table 1, Fig. 5).

**DISCUSSION**

Disturbance-sensitive plant species declined in frequency with increasing levels of anthropogenic disturbance as indexed by DistI. At first glance, the marginal pseudo- and adjusted $R^2$ values are low (0.085–0.118). However, there are two points to consider. First, the values were consistent across the two different types of vegetation communities. Second, given the level of variability associated with the sampled data, we did not

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**Fig. 4.** (A) Mean SG-DistI values corresponding with 6 km radius areas surrounding active or historic lek locations, and (B) SG-DenI values corresponding with active or historic lek locations. Error bars represent 95% confidence intervals around the mean.

**Fig. 5.** Numbers of greater sage-grouse males counted at active leks, in relation to mean SG-DistI values within 6 km of leks (A) and SG-DenI values at lek locations (B). Gray lines represent the negative binomial regression model fit.
expect direct explanatory power to be high and suggest that the consistency of the relationships establishes ecological relevance. The sample population came from a large geographic area (the entire State of Colorado, >269,000 km²) spanning a wide range of elevations and vegetation types. More than 200 different plant associations (about equally divided between upland and wetland/riparian types) were represented in the two datasets. Plots were a representative sample of Colorado’s vegetation, ranging in elevation from 1175 m on the eastern plains to alpine settings as high as 4076 m, and including herbaceous, shrubland, woodland, and forest types. This suggests that while factors such as climate, elevation, soil type, local disturbance, invasive weeds, and grazing regimes affect the composition and biotic integrity of vegetation communities, the general impact of anthropogenic disturbance consistently reduces ecological integrity.

The SG-DistI and SG-DenI models were correlated with GRSG lek persistence and abundance, but it was clear that GRSG populations are influenced by factors in addition to disturbance. GRSG populations are affected by numerous natural and anthropogenic stressors with no two populations experiencing the same suite of conditions (Johnson et al. 2011). Trends in and persistence of populations are determined by the synergistic effects of these different stressors (Garton et al. 2011, Knick et al. 2013). The consistency in relationships between distance to and densities of anthropogenic disturbances and GRSG populations is in agreement with documented effects of human activity on GRSG and offers an approach to evaluate potential disturbance impacts to the species across large areas where it may not be possible to document specific effects on the ground. Our validation using lek-based data demonstrated that the SG-DistI and SG-DenI were each positively correlated with lek persistence and abundance, suggesting that one is not generally preferable over the other but that choice of scale depends on the application, such as representing impacts on individual GRSG vs. groups of breeding GRSG (leks). In a validation of a range-wide GRSG resistance model (i.e., model of habitat connectivity) incorporating human land-use patterns in addition to a variety of species-specific habitat requirements, overall habitat suitability declined with increasing anthropogenic disturbance levels (Knick et al. 2013). Although the inclusion of anthropogenic factors was not explicitly tested by Shirk et al. (2015), their validation of a GRSG resistance model in Washington was improved by the inclusion of transmission lines and other human land-use impacts.

Our results showed that modeled landscape disturbance was negatively correlated with habitat quality field measurements, for general and species-specific examples. These findings strengthen support for use of such disturbance indices to represent habitat quality, such as in conservation planning applications. Our models helped us to understand potential impacts to biodiversity generally or to one species of concern across a large landscape. Even for well-studied species like GRSG, detailed studies on disturbance have not been done everywhere and these methods may provide a means to understand habitat integrity in areas where site-specific research may be lacking.

Techniques of anthropogenic disturbance modeling are informed by the type of data available for a species, taxonomic group, or ecosystem. A generalized relative impact model based on distances may offer greater flexibility when specific thresholds in response to disturbance densities are not available. General distance-based disturbance indices similar to those presented here have been used in a variety of conservation applications to date, including as a cost layer input for site selection optimization and connectivity analysis (Kiesecker et al. 2009); as a composite anthropogenic disturbance score for biodiversity value (Copeland et al. 2007); or as part of climate change vulnerability analysis (Decker and Fink 2014, Pocewicz et al. 2014). Species disturbance modeling can be used to inform biological equivalency metrics in species compensatory mitigation frameworks. Such frameworks have been criticized for using inadequate or overly simplistic habitat quality measures (Quetier and Lavorel 2011, Bull et al. 2013). The GRSG models we developed were for application in Colorado as an estimate of habitat quality for prioritizing management actions. To apply such models in other locations, we recommend further validation with local data. In addition, an in-depth comparison of distance- and density-based model results could further clarify appropriate uses of these techniques.
Our models were static, but could be updated as disturbance changed over time. However, similar to other GIS-based models, the models are only as representative and accurate as the available spatial disturbance datasets. We also made the assumption that the impact of each disturbance type was fixed, but there is often variability in the impacts of disturbance by geographic area, variation in activities within disturbance type (e.g., noise levels associated with anthropogenic infrastructure; Blickley et al. 2012), or other factors. Although disturbance intensity levels may vary on a daily basis, our model cannot address that level of temporal variation. In many applications, however, the presence and effect of a particular disturbance over time can be considered reasonably constant in its long-term impact to the landscape (e.g., towns, industrial developments). These models might be further refined in the future by incorporating other important abiotic (e.g., ameliorating topography) and biotic (e.g., vegetative habitat quality) factors reflecting favorable conditions in addition to disturbance for a representation of the full spectrum of habitat quality.

Our tests of general and species-specific disturbances models against independent measures of habitat quality yielded results consistent with the expected decline of floristic quality scores and GRSG activity as anthropogenic disturbance increased. Although additional factors are obviously important drivers of species distribution and activity, our results show that geospatial models of disturbance impact did, in fact, capture disturbance effects that were negatively impacting individual plant and animal species. This suggests that a variety of spatially explicit disturbance models can be useful in explaining variability in different ecological indices. In general, geospatial disturbance models are highly customizable, scalable for a range of applications, and capture degrees of habitat degradation, not merely complete loss of habitat function, making them useful for a wide variety of ecological research and land management applications.

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Literature Cited


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**Supporting Information**

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