Thank you for the constructive reviews of my manuscript. Below I provide a detail reply to each question raised during the review process and an explanation of how I have responded to your suggestions.

**Reviewer 1.**

*With respect to the discussion, no mention is made of the fact that expansions southward are somewhat counter-intuitive. This can be seen in elevational studies to (e.g., Mortiiz et al. 2008, see Montane Shrew). There is also nothing about historical range change in this species which over the last 10,000 years probably included many of the areas of the recent expansion. I think the author could also bring up the issues of climate change and what was predicted for Fox Sparrow (and possibly examining Blackpoll Warbler and Bicknell's Thrush) by recent broad analyses of North American birds that have suggested climate will drive most species northward.*

I agree that this was a shortcoming of the previous discussion. To address this gap, I have added several paragraphs to the discussion that 1) review the existing information on climate-driven range shifts, with a focus on breeding birds, 2) highlight specific predictions related to expected effects of climate-change on Fox Sparrow (both of which predict a northward, not southward, movement of the southern range limit), and 3) discuss some of the hypotheses for range extensions downslope or towards the equator. I have also added text pertaining to the possible northward expansion of the breeding range of Fox Sparrow, as I believe that this helps round out the picture of a bird undergoing a rapid range expansion at both its northern and southern limits.

*Line 160. This is a little bit of an overstatement. While there is documentation that the species occurs on the high mountains of the Adirondacks. This is based on a single record (so far).*

Agreed, this is not completely accurate. I amended the text to indicate that individuals have been sighted as far west as Vermont and the Adirondack Mountains of New York, but that their current breeding distribution is essentially limited to Maine and New Hampshire.

*Line 198. yet they are now widely reported in New Hampshire and Maine during June and July. This isn't really true. It is just a wording issue, but Fox sparrows are now reported from the high elevations in coniferous forest of northern and western Maine and northern New Hampshire.*

I’ve clarified here by adding the modifier “in both krummholz forest and in sites at lower elevations - presumably dense stands of young conifer - across New Hampshire and Maine during June and July”. Although many of the records are clearly mountaintop forests, some are from sites at lower elevations (as demonstrated by Figure 4), probably regenerating clearcuts given the reported habitat preferences of Fox Sparrows.

*Line 232. Change to: "Exapansion of breeding Fox sparrows"*

I’ve changed this accordingly.

*Line 236. "Banks (1970) suggested a similar explanation for the spread of Fox Sparrows onto the western slopes of the Cascade Mountains of Oregon (but see Marshall et al. (2003))."  
  
This should be expanded on, clearly Marshall disagreed with this hypothesis, why?*

Marshall argued that the apparent expansion was an artifact of increased sampling effort facilitated by the construction of logging roads. Although this could be true for the Cascades, it doesn’t explain the expansion of Fox Sparrow breeding range in the northeastern US and, as Reviewer 3 mentioned, isn’t especially relevant in this case. As Reviewer 3 also noted, Marshall et al. were simply speculating, so on further reflection I agreed that this was an unnecessary and possibly confusing sentence, and as such I’ve deleted it.

*Figure 3. I think this could be made better by adding in data that addresses the availability of suitable habitat across elevations in polygons related to the area of expansion. I assume the high frequency of lower elevation records in Maine could be related to latitude and/or habitat management.*

This is a great point, one that I wrestled with quite a bit during the analysis. Ultimately, I decided that it wasn’t practical to try to associate occurrence records with information on vegetation structure and composition. First, for many of the records, for example traveling counts, the exact location of the observation is uncertain. For those records that could be ascribed with precision to a location, recovering information on habitat conditions at the time of the observation is very difficult, except for krummholz forest. The challenge is that low-elevation habitat is highly ephemeral – it includes perhaps the first few decades of regeneration after a clearcut, where the dominant regrowth is balsam fir – and has a distribution very difficult to predict or identify remotely. In some cases, it will be present in small patches embedded in an otherwise unsuitable matrix of mature deciduous forest. To get at this question, I think that I would need to either manually search historic aerial imagery to match each occurrence to a temporally corresponding image or use a year-by-year analysis of Landsat imagery to generate a time-series of forest cover that would classify pixels by stand height and composition. The first approach is impractical given the lack of accessible historical imagery for most of the time period considered and I’m not even certain that the second approach is possible.

Instead, what I’ve tried to do is explain more clearly how the increased frequency of low-elevation observations in Maine corresponds to the far greater extent of young fir forests in that state, and how the relative paucity of these forest types in New Hampshire may explain the preponderance of high-elevation records. Although this is speculative (a point that I’ve also added to the Discussion), I think it is reasonable given what we know of habitat use by Fox Sparrow and what we know about the distribution of young fir forest in the region.

**Reviewer 2.**

*I believe that this manuscript is missing the required dataset submission. The author indicates that all data are publicly available through eBird. However, additional records may come to light as existing, older field notes are added to the database, or as other records are re-reviewed when regional reviewers adjust filters, and this could potentially change the results of a repeated analysis. As it stands now, the reader cannot completely duplicate the analysis that the author undertook. I would suggest following the PRISM workflow that PeerJ requests for systematic reviews, and then upload the Excel files from the resulting eBird datasets.*

I have added a paragraph that provides the key information presented in the PRISM workflow (using a template in a paper[[1]](#footnote-1) suggested by Reviewer 1) and have provided a link to the raw data file used in analysis (thank you for pointing out that the continual updating of the eBird database would preclude replication of this analysis!). I opted not to use the PRISM workflow verbatim because it seemed that many sections in the checklist and flow diagram were not directly applicable to my effort to collect observations of Fox Sparrow. However, I believe that the changes I’ve made address the spirit of this comment.

Did the author check The Kingbird journal for additional New York records?

No, I did not, so I have gone back and manually searched the online archive. The only record noted in The Kingbird was the 2012 record that also occurred in the eBird data, but I added a citation to the Kingbird account of this sighting. Thank you for pointing this out.

*My concern, however, relates to the PeerJ expectations for this kind of manuscript. PeerJ states, "Manuscripts that report range extensions, life history information, or the description of new species or other taxa should address a biological question or hypothesis as the focus of the submission." While this submission does place the story of range expansion into the context of a hypothesized influence from increased habitat modification in the region, the manuscript does not explicitly test this. To do this, the author would need to quantify which areas have increased pressure and compare this to observed increases in breeding season records. I am not sure that this level of forestry data is available, so I wonder if there could be a rougher scale approach comparing areas with no logging pressure versus those with pressure (e.g. compare wilderness to non-wilderness mountains within State and National Forests)?*

I read this comment as being along the lines of some of the suggestions made by the other reviewers in which they sought additional context for my findings, and I agree that this was a weakness in the earlier version of the manuscript. What I’ve tried to do, in general and in response to the other reviewers, is to 1) highlight the unexpected nature of the range expansion given general and specific expectations of poleward range shifts among breeding birds in response to climate change and 2) consider more carefully the possible explanations for the observed shift. I hope that in doing so I can make clear that this work, although focused on a fairly simple description of a change in distribution, may offer some insights into contemporary changes in the distribution of animals and how they may or may not reflect climate change.

In response to the specific issue of testing more explicitly the role of habitat change as a driver of the observed range expansion, I appreciate the reviewer’s suggestion and have tried to address it by adding more detail about the spatial and temporal nature of the habitat changes, and how they might be connected to the expansion of Fox Sparrow breeding range. The reviewer is correct in assuming that fine-scale data on forest structure or timber harvest is not available, as forest statistics in this region are summarized at very large (i.e., multiple counties) spatial scales. As I noted in my reply to Reviewer 1, connecting any individual occurrence record with information on forest structure is exceedingly difficult, and perhaps impossible for many of the records, so I think that a fine-scale analysis of the correspondence between Fox Sparrow occurrence and the distribution of young spruce-fir forest is not practical. The key problems are that 1) eBird occurrences are not always recorded with high spatial precision (i.e., placing a particular observation in a particular forest stand is often impossible) and 2) corresponding data on forest structure at the location, even if it is recorded accurately, is not readily available. What I have tried to do instead is show, using published statistics from the USDA Forest Service Forest Inventory Analysis program, that the area of young spruce-fire forest increased dramatically between 1981 and 1995 and then continued to grow slowly thereafter, and that most of this gain occurred in the regions where Fox Sparrows were first discovered breeding. I recognize that this is not a strong test of the hypothesized causal link, and I have added a statement to this effect, but I do think it is probably the strongest argument that can be made at this point. Ultimately, I think that the best I can say with these data is that the increases in Fox Sparrow detections occurred in broad geographic regions where increases in the amount of young conifer forest occurred contemporaneously.

*The author cites a few instances of documented nesting, but most of these records do not have documentation of nesting. How many of these observations were of two individuals, and are there any data on females being present? Or are they all unpaired, singing males? There is a difference between unpaired males summering south of their range versus breeding there. Both are part of a single phenomenon, I would think; as a species expands, the vanguard would be unpaired males. But if almost all of these observations are of unpaired males, then this manuscript is documenting a changing behavior of unpaired (and presumably second calendar year individuals) rather than a difference in breeding distribution. We see this in lots of other species, where younger birds don't make it to the core breeding range for their first summer as an adult (particularly in shorebirds, but there are many, many reports of passerines doing this in the pages of North American Birds and in eBird).*

We don’t really have the data to speak directly to breeding. For example, most eBird checklists don’t contain information on sex or behavior. Even when the counts in a checklist indicate multiple birds, it was rarely possible to determine whether these birds were seen together or in different locales. I think about all we can say is that a) Fox Sparrow are far more common now than historically; and b) they are geographically widespread during the breeding season; and c) they nest in the region, at least occasionally. I’ve tried to be careful about this distinction in the text.

No references are cited to back up any statements about increased or changing forestry regimes. This is particularly needed in lines 233-234.

Indeed, this is a shortcoming, which I’ve addressed by providing a series of references that summarize and interpret data on changing forest structure and harvest levels during the period of analysis.

*Line 97 indicates that the choice of resolution for the grid was arbitrary. I agree that there is no true guideline for size to use, but I would like to see investigation of the effect of grid size on the results. 10 km^2 strikes me as being quite large for this study; does revisiting with 5 and 1 km^2 grids change your results? Your overall study covers very few grid cells at the 10 km^2 resolution.*

The median length of a traveling checklist analyzed in this report was 3.2 km, so I would rule out considering a 1-km2 grid on the grounds that many checklists will be ambiguously located relative to the grid. I did re-analyze the data against a 5-km2 grid, and found no qualitative difference in the results (which I’ve referenced as a set of supplemental results on Figshare). With a 5-km2 grid, the results for Fox Sparrow were: Byear = 0.17 (95% CI = 0.085 – 0.255). With a 10-km2 grid, Byear = 0.18 (95% CI = 0.097 – 0.275). Based on this, I believe it is safe to conclude that the results are not especially sensitive to the choice of a cell size.

*I have a minor note about scientific/common names here. The Red Fox Sparrow is an informally recognized common name (common names in North America are only assigned at the species level by the American Ornithological Society's Check-list Committee). In general usage, Red Fox Sparrow refers to a subspecies group, not a particular subspecies. That is, Red Fox Sparrow is P. i. iliaca and P. i. zaboria. This contribution focuses on P. i. iliaca, and the common name of Eastern Fox Sparrow is typically assigned to this one (see Rising 1996, for example). The manuscript's title is correct, but there are some additional uses within the text that should be corrected, particularly line 30.*

Thank you for this correction. I have updated the text accordingly.

*eBird is cited incorrectly; they prefer that you use this: Sullivan, B.L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142: 2282-2292. I would also suggest adding some text to explain that these are vetted observations by peers, not just acceptance of all observations from observers at all experience levels.*

The Fink et al. 2017 reference is the requested citation according to the README file that comes with the eBird Reference dataset, so I have left that citation as is. I did add the above citation to the first reference to eBird, however.

*Need a broader citation for North American Birds as a journal (list publisher, at minimum) and explain that the other titles are previous titles for the same journal. Maybe a phrase to explain that this is a vetted review of regional bird records for each season?*

I have made the requested change.

*Line 57: delete hyphen in "breeding-bird"  
  
Line 90-92: awkward sentence, could be rephrased or broken into two to explain why this decision was made.   
  
Lines 154, 165, and elsewhere: can remove the minus in front of the longitude, as indicating that the degrees are West makes the minus unnecessary.  
  
Line 167: extra parenthesis can be deleted.  
  
Line 200: delete hyphen in "breeding-range"  
  
Lines 204, 208, 217: delete hyphen in "breeding-season"*

Changed as requested.

*Lines 206-207: need to include some citations to back this up, I'm not sure which of these efforts would have been focused widely enough to describe rarities as opposed to the budworm-focused species.*

This is a good point, and on reflection I decided that my statement wasn’t really defensible. My initial point was that no published study that took place within the areas into which Fox Sparrows have been expanding provided any mention of the bird, suggesting that they were not present. However, as the reviewer notes, it is unlikely that these studies would have mentioned, even in passing, the presence of a handful of rare birds, and thus I have come to doubt whether the lack of mention provided strong inference about the absence of Fox Sparrow. In addition, I think that the other lines of evidence that I’ve provided about the historical absence of the species are adequately strong, and thus I’ve removed this sentence entirely.

*Line 212: need a citation for the Quebec trend.*

This was in reference to the results described in the literature review; I left this section as is because it all refers back to results presented earlier, but I could certainly repeat the citations if that would clarify.

*Figure 2: delete hyphen in "breeding-season". Figure legend should indicated what the solid and hyphenated lines mean.*

Changed as requested.

**Reviewer 3.**

*I personally would like to see more speculation or consideration of what this distributional change indicates by considering other bird species found in the same habitat in this range and other species that are expanding their range southward in this part of North America.*

In keeping with similar comments made by the other reviewers, I have added text to the discussion that places these findings in the context of the distributional shifts expected under climate change and that seeks to offer a more considered explanation of why the shift may be occurring, with a particular focus on the possibility that habitat changes are driving the observed southward extension of the breeding range.

*My main concern with this paper is that there is not a real attempt to place the changes in distribution of Fox Sparrow into context with other species in the region. The two groups of species, I’d like to see some consideration of would be species that are extending their breeding range south in the NE US, and those species that occupy the same sort of habitat as Fox Sparrow. In terms of species extending their range, I don’t know the specifics of the part of North America, but I know for example has Merlin has extended its breeding range south across much of its range in eastern North America. Are there others, perhaps species more focused in NE US, that might give insights into the changes happening in Fox Sparrow. Similarly, Fox Sparrow shares its habitat with some other species. I’m thinking particularly of species that occupy early successional clearings in coniferous forests. While Bicknell’s Thrush and Blackpoll Warbler are, I think, good species in terms of range and association with coniferous forest, neither are really tied to the specific habitat that Fox Sparrow uses. Gain, I don’t know the details of bird distributions in the northeast well enough to suggest a suite of species. The only one that occurs to me is Mourning Warbler. It has a much broader range and I wouldn’t expect them to be expanding their range, but you might see evidence of greater abundance or habitat occupancy if the Fox Sparrow response is not unique to that species. I don’t really expect a detailed analysis of other species, but at least some consideration of other species with analogous range changes or occupying habitat that might be responding to changes in forestry management in similar ways.*

Again, this is a good point also raised by the other reviewers. In general, I have tried to add discussion that places the findings in the context of climate change and changes to forest structure. In terms of other species showing similar patterns, the closest that I can find are the 6 species identified by Hitch and Leberg (2006) as having shown a southward extension of their range based on Breeding Bird Survey results. Three of these don’t seem to shed light on the case of the Fox Sparrow – one is a grassland bird, Bobolink, and two are nomadic granivores, Pine Siskin and White-winged Crossbill – but the other three – Yellow-rumped Warbler, Mourning Warbler, and Alder Flycatcher – may. I could find no studies that have addressed these distributional changes in detail, but the Birds of North America accounts for Mourning Warbler and Alder Flycatcher argue that the southward shift for both was a response to increased forest disturbance. From personal experience, Mourning Warbler tends to occur in very young clearcuts dominated by brushy hardwoods, but not in the stands of spruce-fir saplings in which Fox Sparrows seem to occur. As such Mourning Warblers may not be a perfect analog, but it is interesting that perhaps increased amounts of young forest are favoring similar changes in at least some species. To place my results in context, I have added a paragraph discussing these findings.

To the point regarding the extent to which Blackpoll Warbler and Bicknell’s Thrush overlap in habitat use with Fox Sparrows, I have added data showing rates of co-occurrence between observations of Fox Sparrows and observations of each of these species. As expected, co-occurrence rates are quite high, especially for Blackpoll Warblers, which frequently use younger stands of spruce and fir at low elevations.

*It would be really helpful to have a map that shows the range (or at least southern limit) of breeding Fox Sparrows in eastern Canada at some reference time period when the expansion begin. This would put the expansion into the NE US more in context*

I have added a map that shows the breeding range as estimated by BirdLife International, supplemented by points indicating all of the provincial records submitted to eBird as of 1990. I chose 1990 as the reference point because it approximates when records of Fox Sparrows in the U.S. during the breeding season appeared to have begun increasing in frequency.

*Line 100 People entering traveling counts into e-bird are supposed to place their point at the midpoint of the route they traveled, not the starting point as stated here. Doesn’t really change this issue, but might reduce the number of times that an observation came from the “wrong” grid cell, since the farthest the observer birded from the mapped point would be half the distance it would be if the starting point was mapped.*

I didn’t realize this was so (and a small survey of eBirders in my office revealed that no one else did, either!). Interestingly, the eBird app also seems to mark the starting point as the checklist location, which would run counter to the instructions given on the eBird web site. All of this is to say that the actual behavior of eBirders may result in checklists that are associated with a starting point, not a mid-point. In any case, I have edited the text so that it doesn’t suggest that the location of traveling checklists are to be recorded as the starting point. Also, in response to the request by Reviewer 2, I have conducted a sensitivity analysis of the choice of a size for the grid cells, and did not find any difference in the results when repeating the analysis on a finer grid.

*Line 129 States that Keith and Fox 2013 describe Fox Sparrow as common migrant in New Hampshire, but line 154 gives Keith and Fox as source for breeding record from New Hampshire. I think the seasonal status of Fox Sparrow in New Hampshire given by Keith and Fox needs to be better described.*

Keith and Fox (2013) note the existence of the breeding record, but seem to regard it as a one-off oddity, describing the status of Fox Sparrow as “Regular and moderately common spring and fall transient”. I’ve tried to update the text to explain this distinction.

*Line 151-152 This sentence provides information on occurrences in Maine in 1999 and 2000, but reference supporting this is a 1999 paper, which couldn’t possibly have information on a 2000 year.*

I’ve added the missing citation.

*Line 167-169 This is a run on sentence that should probably be broken up. I would put a period after “significance” and delete “but.” Also I think the ) following July 2016 should be a comma.*

I’ve changed this sentence accordingly.

*Lines 167-174 Can any sources be cited for the information in this paragraph?*

These statements were based on comments included with the associated eBird checklist. I’ve added text to clarify the source.

*Lines 186-188 The difference in elevational distribution between Maine and New Hampshire is interesting and a figure (Figure 3) is used to support this difference. In the discussion, this difference is not talked about at all. The paragraph of lines 220-228 suggests to me that the lower elevation distribution in Maine and the fact that the summering records in Vermont and New York are in high elevation sites reflects habitat availability and not some other factor. However, the paragraph at 220-228 does not mention the elevational distribution of the summer records at all. One alternate possibility I have considered is that it is a reflection of time that the population has been established. The idea here is that Fox Sparrows expands range into high elevation krummholz habitat, and as the population expands is able to move into the structurally similar lowland early successional areas in logged spruce forest. I wonder if there would be any temporal pattern in the elevational distribution of birds in Maine and New Hampshire with earlier records being concentrated at high elevations.*

This is an interesting idea. I don’t see any evidence that this is the case, at least based on the elevations of the records of Fox Sparrow reported to eBird (Fig. 1). It is somewhat difficult to interpret these data, however, given the paucity of data and what is almost assuredly a strong spatial bias in the location of the early records. Nonetheless, mountaintops have been fairly well covered by birders in recent decades, because most of the mountains are accessible by trails, and thus I would expect that a signal would emerge if the colonization predictably began in the high country and then spread out into suitable habitat at lower elevations. Anecdotally, though, we see the opposite, in that the earliest records of Fox Sparrow in Maine all came from the relatively low, flat country along the northwestern border of Québec. The patterns in Vermont and New York would seem to support your hypothesis, as the only records are from mountaintops. However, I’m not sure what to make of this pattern, given that both states have relatively little young fir forest at low elevations. In contrast to Maine, and far northern New Hampshire, which have vast areas of potentially suitable habitat at low elevations, Vermont and New York simply may not have much suitable habitat for Fox Sparrows at lower elevations.

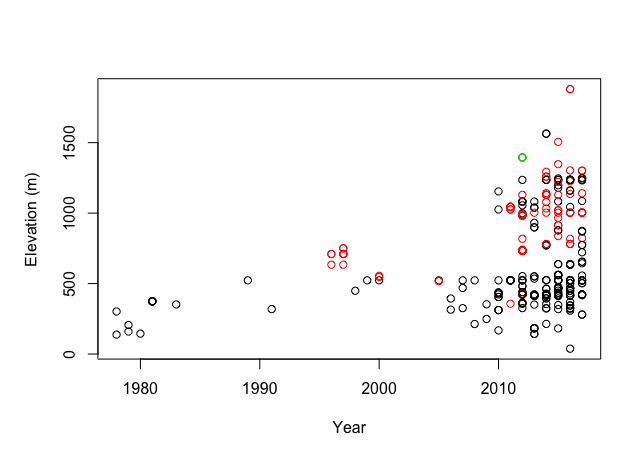


Figure 1. Elevation of records of Fox Sparrow in the U.S. reported to eBird from 1978-2017 (black circles represent records from Maine, red from New Hampshire, and green from New Hampshire).

*Lines 204-207 Can any sources be provided for “ornithological investigations” in the 1980s in this geography mentioned in this sentence.*

One of the other reviewers asked a similar question, and on reflection I decided that this statement wasn’t really defensible. My initial point was that no published study that took place within the current, expanded range of Fox Sparrow provided any mention of the bird, suggesting that they were not present. However, it is unlikely that these studies would have mentioned, even in passing, the presence of a handful of rare birds, and thus it did not seem like the lack of mention provided strong inference about the absence of Fox Sparrow. In addition, I think the other lines of evidence that I’ve provided about the historical absence of the species is adequately strong, and thus I’ve removed this sentence entirely.

*Line 236 – 238 I think it would be worth an additional line or 2 about the Oregon situation because the suggestion of Marshall et al is that the extension of the known range to the western Cascades might be a reflection of accessability rather than an actual range change. Given that they don’t provide any data, this is purely speculation, and given that this paper goes to some trouble to deal with this possibility in the NE US, I think it is worth being more explicit here about the parallels between the two cases.*

I agree that this was an unnecessary and possibly confusing sentence, and as such I’ve deleted it.

1. Page 2 in Ingenloff K, Hensz CM, Anamza T, Barve V, Campbell LP, Cooper JC, Komp E, Jimenez L, Olson KV, Osorio-Olvera L, Owens HL. Predictable invasion dynamics in North American populations of the Eurasian collared dove Streptopelia decaocto. Proc. R. Soc. B. 2017 Sep 13;284(1862):20171157. [↑](#footnote-ref-1)