1 Scaling-up camera traps: monitoring the planet's biodiversity with

2 networks of remote sensors

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29 Abstract

30 Countries committed to implementing the Convention on Biological Diversity's 2011-2020 strategic 31 plan need effective tools to monitor global trends in biodiversity. Remote cameras are a rapidly 32 growing technology that has great potential to transform global biodiversity monitoring and 33 contribute to the call for measuring Essential Biodiversity Variables. Recent advances in camera 34 technology and methods enable researchers to estimate changes in abundance and distribution for 35 entire communities of animals, and identify global drivers of biodiversity trends. We suggest that 36 interconnected networks of remote cameras will soon monitor biodiversity at a global scale and guide 37 conservation policy. This global network will require greater collaboration among camera studies and 38 citizen scientists, including standardized metadata, shared protocols, and security measures to protect 39 the records of sensitive species. With modest investment in infrastructure and continued innovation, 40 we envision a global network of remote cameras that will provide real-time biodiversity data while 41 connecting people with nature.

42 In a nutshell:

- Global biodiversity conservation needs a global standardized sensor system to monitor trends
 and drivers of biodiversity change to help achieve the needs of the Convention on Biological
 Diversity and the Intergovernmental Platform on Biodiversity and Ecosystem Services
- The rapid growth of remote-camera technology has the potential to provide this sensor
 network to effectively monitor biodiversity at global scales, akin to the global meteorological
 sensor network
- A growing number of case studies demonstrate the feasibility of large-scale camera networks
 to monitor biodiversity trends across 1000's of km² of diverse habitats, including tropical
 forests, alpine ecosystems, and beyond
- Modest investment in infrastructure combined with on-going collaborative efforts to
 standardize metadata, field protocols, and databases could harness the incredible power of
 remote camera technology
- Scientists alone need not bear the burden; there are many examples of viable ways to integrate
 the burgeoning interest of citizen scientists in remote camera monitoring

57 Introduction

58 Declining biodiversity is a reality of the Anthropocene, and society is lagging to meet international 59 biodiversity targets (Butchart et al., 2010; Secretariat of the Convention on Biological Diversity, 60 2014). From Carnivora to Coleoptera, biodiversity is declining across the globe due to human 61 activities (Butchart et al. 2010). Rare species are becoming rarer, geographic ranges are constricting, 62 and species are going extinct (Dirzo et al., 2014). Monitoring these changes to biodiversity is a 63 global priority required by international treaties (Secretariat of the Convention on Biological 64 Diversity, 2014) and coordinated by international networks like the Group on Earth Observations 65 Biodiversity Observation Network (GEO BON: earthobservations.org/geobon.shtml) which has made 66 a global call for the measurement of Essential Biodiversity Variables (EBVs; Pereira *et al.*, 2013). 67 With growing concern and funding for maintaining the health of our planet (Tittensor et al., 2014), 68 real-time biodiversity monitoring is key to identifying and addressing large-scale ecological threats. 69 The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) was created in 70 2012 with the unambiguous goal of strengthening the interface between science and policy to 71 improve biodiversity conservation outcomes, emulating the successful issue-specific policy focus of 72 the Intergovernmental Panel on Climate Change (IPCC; Mooney and Tallis, 2014). An important 73 distinction between IPBES and the IPCC, however, is that the latter has a global network of 74 standardized weather sensors to track changes and inform predictions about future climate. 75 Conversely, biodiversity data are typically collected to serve local objectives, and may not be 76 suitably standardized to provide effective measures of global change. An international biodiversity 77 network remains a major gap, and filling this gap is imperative to improve our understanding of 78 ecological patterns and processes at adequate spatial scales, and to quantify how human activities 79 affect them (Schmeller et al., 2015).

80	To meet global challenges in monitoring and conserving biodiversity, we need to evaluate
81	changes in species composition, distribution, abundance, and response to anthropogenic impacts
82	(Pereira et al., 2013). Technological, financial and organizational constraints restrict most monitoring
83	initiatives to one or a few species of concern over relatively small areas, thereby incorporating only a
84	small selection of ecological processes. The result is a mismatch between the global scale of
85	conservation needs and the localized availability of ecological data (Fraser et al., 2012). Data on
86	ecological communities across multiple scales are needed to fully understand and anticipate
87	anthropogenic effects, establish baselines, identify mechanisms of species decline, and formulate
88	effective mitigation actions (Hampton et al., 2013). Remote sensing offers a promising means to
89	integrate local in situ biodiversity data with globally-available environmental data to test hypotheses
90	about the effects of changing environments on biodiversity (Turner, 2014).
91	Autonomously triggered cameras (also known as remote cameras, or camera traps) are effective
92	at sampling communities of medium and large sized birds and mammals, and we suggest that they
93	can help biodiversity monitoring initiatives expand to the necessary scales and meet these global
94	challenges. With recent advances in camera technology, reduction in cost, and increased interest in
95	wildlife images as an outreach and education tool, the use of remote cameras has grown
96	exponentially for the past 10-15 years, doubling every 2.9 years (Burton et al., 2015). Figure 1
97	scratches the surface of the magnitude of current camera trapping efforts, demonstrating the broad
98	geographic distribution, taxonomic diversity, and breadth of conservation issues addressed with
99	remote cameras. In this haphazard sample of global camera studies (only those conducted by
100	coauthors of this paper) there are on average 78 cameras deployed per study, totaling over 8,000
101	camera sites (WebTable 1). We estimate that this represents, at most, 5% of current global efforts and
102	Burton et al.'s (2015) 10-year review included 20,000 camera locations — meaning that tens of
103	thousands of cameras are already deployed across the planet.

104 Despite this increase and the concomitant accumulation of remote camera data, coordination of 105 multiple camera studies rarely occurs, and resultant datasets can be fragmented, unstandardized, and 106 difficult to integrate for broader biodiversity assessment and conservation (Meek et al., 2014). 107 However, we draw attention here to a growing number of examples that illustrate regional, 108 coordinated applications, and thereby demonstrate the truly global potential of remote cameras as a 109 standardized monitoring platform for terrestrial vertebrate biodiversity. The current emergence of 110 remote cameras and its coordination may, to some extent, mirror the coordination efforts of the world's earliest meteorological network in the late 19th and early 20th centuries. Progressing from 111 112 disparate hand-calculated local forecasts early on, to using new computers emerging after World War 113 II to provide medium-range forecasts, weather and climate forecasting data are now consolidated 114 globally by the World Meteorological Organization that combines data from ~20,000 weather 115 stations, including many satellite sensor networks (Smith and Roulston, 2002). 116 The complexity of ecosystem responses to human stressors, and the multiple spatial and temporal 117 scales at which ecological processes affect biological conservation require substantial amounts of 118 data to be collected, stored, and processed (Kelling et al., 2009). Ecology is rapidly becoming larger 119 scale in its collaborative networks, data intensification, and application (Peters *et al.*, 2008; 120 Reichman et al., 2011). Here, we review the current state of remote camera use in ecology and 121 conservation and provide a vision for expanding from individual, localized camera studies to 122 coordinated regional and global camera networks. Surmountable gaps remain in our ability to 123 effectively use these data to measure change to regional and global biodiversity. Extant regional 124 networks have worked through many of these challenges, which we review in part, and we suggest 125 strategies for overcoming other real and perceived barriers to further growth. We conclude with 126 recommendations on how to translate remote-camera science into effective tools for management and 127 conservation.

128 Current applications of remote cameras to biodiversity conservation

129 Given the pressing need for biodiversity monitoring, an increasing number of remote camera studies 130 are now focusing on multiple species (Figure 1). Studies now extend beyond the nuts and bolts 131 mensuration of biodiversity components (abundance, distribution, species richness) to applications 132 that address underlying causes of biodiversity change. For example, remote cameras are an ideal tool 133 to measure the effectiveness of highway crossing structures to improve multi-species landscape 134 connectivity (Barrueto et al., 2014), test corridor models (McShea et al., 2015), and evaluate the 135 effects of forest fragmentation on tropical species diversity and dominance (Ahumada et al., 2011). 136 Camera surveys can also highlight how different life-history stages respond differently to 137 disturbances; for example, cameras have identified key habitats linked to higher female grizzly bear 138 reproductive success (Fisher et al., 2014). Remote cameras are also increasingly used to address 139 complex ecological interactions between animal behavior and climate change. For example, cameras 140 were used to assess the impacts of climate change and trophic interactions on elk (Brodie et al., 141 2014), to measure plant phenology and climate (Morisette et al., 2008), and to determine how large-142 mammal food webs respond to forest fragmentation (Brodie et al., 2015). Furthermore, cameras can 143 measure the success of conservation actions (Dajun et al., 2006), including protected area 144 effectiveness (Burton et al., 2011), such that cameras are highlighted as tools to monitor local or 145 regional biodiversity (Tobler et al., 2015). For example, a camera-specific diversity metric, the 146 Wildlife Picture Index (WPI; O'Brien et al., 2010), has been used to measure trends in large-mammal 147 communities of Mongolia (Townsend et al., 2014), Costa Rica (Ahumada et al., 2013) and most 148 recently, on a entire network of forested tropical protected areas (Beaudrot *et al.*, 2016). 149 Remote camera projects usually target ground-dwelling vertebrates (mostly mammals), 150 although there are examples focused on arboreal mammals (Gregory et al., 2014), and "phenocams" 151 are an emerging technology for monitoring phenology, snow cover, and disturbance events (Brown

152 et al., 2016). Species commonly documented in remote camera surveys represent a critically 153 important group for biodiversity maintenance, including large carnivores and herbivores (Ripple et 154 al., 2014, 2015). Even small changes in vertebrate community composition can have large cascading 155 effects throughout lower trophic levels in food webs, including rates of primary productivity and 156 decomposition (Hooper et al., 2012). Early detection and mitigation of population declines may be 157 crucial to conservation. Moreover, actively engaging decision makers and citizen scientists in 158 conservation is enhanced by photographs of these charismatic mega-fauna, which can act as effective 159 conservation surrogates for large-scale conservation across taxa (Di Minin and Moilanen, 2014). 160 Many applications of camera data have yet to be fully exploited. Cameras are key to fill 161 knowledge gaps in mammal distributions. For example, Moriarty et al., (2009), used cameras to 162 document the first evidence of wolverine expansion in California. Cameras can potentially assess 163 range changes due to climate change. Cameras could also provide a skin coat database to assess the 164 origins of poached animals, similar to contemporary genetic analogues (Mondol et al., 2014), but 165 with the additional benefit of providing spatiotemporal data to help locate poachers. 166 As with museum specimens, the core data collected by remote cameras are spatiotemporally 167 referenced 'voucher' specimens documenting the occurrence of a species *in situ*. The Smithsonian 168 Institution has started archiving remote camera data similar to museum collections (McShea et al. 169 2015; eMammal, emammal.org) and the Global Biodiversity Information Facility (GBIF; 170 www.gbif.org) provides international open-access infrastructure to collect such data on all species, 171 including remote camera data. The digital specimen is a non-invasive documentation of an animal in 172 *situ*, in its habitat, with associated spatiotemporal data on behavior, temporal activity, heterospecifics, 173 and environmental covariates.

174 The public interest in remote camera imagery continues to grow, with coffee-table books now175 featuring remote camera photography (Kays, 2016). A frequent ancillary goal of remote camera

projects is the production of imagery for use in science communication and building support for
biodiversity conservation. Many studies have harnessed the keen interest of citizen scientists to help
maintain cameras (e.g., replacing batteries, memory cards; Barrueto *et al.*, 2014; McShea et al. 2015),
and to classify camera images (see below). Thus remote cameras significantly contribute to the first
goal of the Aichi biodiversity target of the Convention on Biological Diversity (CBD)'s 2011-2020
Strategic Plan: "Address the underlying causes of biodiversity loss by mainstreaming biodiversity
across government and society" (Secretariat of the Convention on Biological Diversity, 2014).

183 **Future vision: moving from local to global scales**

184 Global policy frameworks, like the CBD and IPBES, require equally ambitious and large-scale 185 monitoring tools to ensure progress toward meeting their goals. To meet this need, ecological 186 monitoring networks are striving to match the capacity of global weather monitoring through 187 deploying ecological sensors, building data infrastructures, and refining statistical models for 188 prediction (Keller *et al.*, 2008). The first step towards an equivalent standardized global network for 189 biodiversity is to link current in situ data streams with global-scale data, for example, satellite-based 190 remote sensing (Turner, 2014; Figure 2). Linking together and expanding current local remote 191 camera projects into nationally or internationally coordinated efforts, permits continental and global-192 scale questions to be asked from locally point-sampled data (Figure 2). This scaling up from local to 193 global requires not only the usual fuel of human endeavors—time and money—but also innovation 194 and cooperation. Obstacles to the formation of a truly global remote camera network are common to 195 many forms of large-scale monitoring; these include standardization of field protocols and metadata, 196 coordination among regional and international partners, and long-term funding for field and data 197 management (Lindenmayer and Likens, 2009). But with the number of existing networks growing as 198 reported below, the barriers to a truly global biodiversity network are falling away. By pulling from

199	100+ years of combined remote camera experience among the authors, we supply some lessons in
200	overcoming these obstacles when starting regional-scale camera networks.
201	Getting on the same page: increasing sample size and standardizing protocols
202	Often, a perceived (or real) impediment to starting an individual camera study is the initial cost
203	associated with camera purchase. Improvements in camera technology continues to reduce their cost
204	(as low as \$100 US) giving this technology a low cost per unit of sampled area and per species.
205	Further, with proper protocols, relatively inexpensive local wildlife guides, park rangers, anti-
206	poaching patrollers or volunteer citizen scientists can be trained to service cameras, further reducing
207	costs per sample, and thus facilitating larger sample sizes. For example, the eMammal project enlists
208	more than 400 volunteers to run cameras in over 2000 locations across six US states (McShea et al.,
209	2015), and the Snapshot Wisconsin project makes effective use of citizen scientists to maintain
210	cameras across the state (www.snapshotwisconsin.org). Financial and logistical barriers for running
211	cameras at large scales, therefore, are becoming smaller and smaller.
212	Experimental design should be dictated by research objectives (Figure 3; Meek et al. 2014). Once
213	a design is chosen, metadata reporting is critical for compiling image data for larger-scale analyses
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214	(Meek et al. 2014, Burton et al. 2015). For example, project metadata should include camera model
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223 new tool to monitor biodiversity in the early 2000s, individual national parks began experimenting 224 with cameras for park-wide monitoring. With increased deployment came increased coordination and collaboration. Now, ten years later, 7 national parks covering $\sim 23,000 \text{ km}^2$ are using standardized 225 226 methods to systematically distribute 350 cameras for year-round multi-species monitoring (Steenweg 227 et al., 2016); the list of similarly coordinated networks grows (WebTable 1). Continuing towards 228 agreement on collecting matching metadata across camera studies is needed for global integration of 229 camera networks. Standards for metadata descriptions for camera studies are now available (Meek et 230 al. 2014; www.wildlifeinsights.org). 231 Statistical analyses and scaling up image classification 232

The first step in turning pictures into data is classifying the images, which can be labor intensive.

233 With proper management, large volumes of photographic data can be rapidly catalogued using

234 standard software, up to 1000 images per hour with minimally-trained technicians or volunteers

235 (Meek et al., 2014). eMammal capitalizes on its network of volunteers to help with this process and

236 has classified over 2.6 million images (McShea et al., 2015). The TEAM network uses specialized

237 software (Wild.ID), now available to any remote camera project, to classify images and provides a

238 project management framework for remote camera projects to keep track of sampling periods,

239 personnel, and even individual pieces of equipment (Fegraus et al., 2011;

240 https://github.com/ConservationInternational/Wild.ID/archive/master.zip). Further efficiencies come

241 with crowdsourcing image analysis, often with double classification techniques to reduce error;

242 examples including: www.chimpandsee.org, www.chicagowildlifewatch.org, and

243 www.snapshotwisconsin.org. One of the best-known projects is Snapshot Serengeti

244 (www.snapshotserengeti.org), which counts 28,000 registered online volunteers and 10.8 million

245 classified pictures from their park-wide camera project (Swanson et al., 2015). Software to allow

246 researchers to crowd source image processing is also freely available via www.zooniverse.org/lab.

247 Now there is a growing number of statistical approaches available to estimate abundance, 248 distribution (occupancy), or species diversity from camera data (Figure 3). A major milestone in the 249 development and application of camera data was the use of capture-recapture methodology to 250 estimate density and other demographic parameters of tigers (Karanth 1995). This advancement 251 contributed to the rapid and widespread adoption of remote cameras in population studies of species 252 with uniquely-identifiable individuals and has fueled the growth of spatially explicit capture-253 recapture methods (Royle et al. 2014). For all camera data, one key challenge is accounting for 254 occasions when species were present but not detected at a sampling site (Royle and Dorazio, 2008). 255 One approach applied to camera data is to discretize the continuous sample to mimic a repeated site 256 visit framework of abundance or occupancy estimation (Figure 3), though other methods using 257 continuous detection probabilities can be more appropriate (Guillera-Arroita et al., 2011). Using raw 258 detection rates as a measure of abundance is generally not recommended because it confounds true 259 absence and undetected presence, ignoring detection issues (Sollmann et al., 2013). Nonetheless, use 260 of these uncorrected relative abundance indices continues (Burton et al., 2015), perhaps because 261 more sophisticated approaches require the collection of ancillary movement data to estimate animal density (e.g. Random Encounter Model; Rowcliffe et al., 2008) or the use of complicated hierarchical 262 263 models. Hierarchical models are ideal for camera data analyses because they model biological and 264 imperfect observation processes that lead to observed data, nested within a model of the ecological 265 process of interest (e.g. how abundance changes over space; Figure 3). Hierarchical models have 266 been used to scale up regional estimates of species occupancy and relative abundance to large-scale 267 assessments of factors affecting species richness (Tobler et al. 2015, Sutherland et al., 2016). These 268 models are now becoming more available with the release of recent books (e.g. Kery and Royle, 269 2016), open source software (e.g. Fiske and Chandler, 2015; White and Burnham, 1999) and active

web forums for quick and friendly help (e.g. groups.google.com/forum/#!forum/unmarked and
 groups.google.com/forum/?hl=en#!forum/hmecology).

272 One challenge with camera data is communicating how the distribution and abundance of 273 multiple species change across numerous regions, over time. One proposed solution is the wildlife 274 picture index (WPI; Figure 3; O'Brien et al., 2010) a conceptually simple metric developed by 275 TEAM that summarizes the average proportional change in occupancy among species. Mechanisms 276 of change in WPI can be examined at multiple scales of interest to understand scale-specific causes 277 of decline. WPI is one of the indicators for CBD's Target 12 (preventing species extinctions), 278 fulfilling a critical need in tropical terrestrial biodiversity trend monitoring, but many logical 279 improvements in methodology are possible. For example, it is now possible to jointly model species 280 richness across study areas to share detection information (Sutherland et al., 2016) and some 281 diversity studies with cameras account for species that were never detected during the entire study 282 (Rovero et al. 2014). WPI is based on occupancy estimation from detection/non-detection data, but 283 recent work has estimated abundance from such data (Chandler and Royle, 2013) and thus, may 284 provide an avenue for moving beyond detection-corrected species richness to more sophisticated 285 abundance-based diversity measures (Chao et al., 2014).

286 Dealing with data: management, storage, sharing and access

A final challenge to scaling up remote camera data collection is improving data storage and
management, especially given the large storage requirements for images. Regional or global
biodiversity databases are needed that are tailored to camera data in an easy-to-use, accessible and
open-source format. Database platforms are already developed that host and facilitate the
management of large quantities of other types of shared ecological data. MOVEBANK
(www.movebank.org), for example, archives the ever-growing amount of animal movement data
(Kays *et al.*, 2015). A promising platform for camera data management, based upon the experience of

294 eMammal, the TEAM network, Smithsonian Institution, Wildlife Conservation Society and the North 295 Carolina Museum of Natural History, is the federated Wildlife Insights project (wildlifeinsights.org). 296 This latter database was developed to streamline data management and integrate camera data with 297 other *in situ* data streams such as forest carbon, gaseous flux, and other environmental monitoring 298 (McShea et al. 2015). This integration will allow scientists to better connect patterns in biodiversity 299 change with the ultimate causes of declines in biodiversity. If camera data descriptions begin to 300 follow biodiversity information standards for multimedia data (e.g. proposed by Meek et al. 2014; 301 Wildlife Insights) these data could make an important contribution to wider global networks of 302 biodiversity databanks such as GBIF, IUCN's Red list, and Map of Life (https://mol.org/). 303 A final consideration when combining data from globally disparate studies is addressing 304 intellectual property rights and privacy needs. Individual studies may be reluctant to contribute data 305 without such reassurances. For example, for privacy reasons, Parks Canada will never release image 306 data until it is certain it contains no images of any visitors to the parks. Similarly, some studies may 307 not want to release geographical locations of particular endangered species for fear of increasing 308 poaching; or researchers may want to maintain publishing rights to their data. MOVEBANK has a 309 tested model, offering several user-controlled levels of data security to collaborators wishing to store 310 data on the server. These options range from completely open access to completely invisible, where 311 the user controls who can see, use, access, or request collaboration on data contributed to the 312 database. Such flexibility provides a means to meet every user's intellectual property rights and 313 privacy needs, while still striving towards an open data philosophy. 314 Conclusions

There is a pressing need for increased coordination of remote camera surveys to achieve effective global biodiversity monitoring. The non-invasive nature of remote cameras and their decreasing costs continues to hasten their adoption at every scale. Using concrete examples, we have demonstrated

how barriers to camera servicing, data classification, storage and management have been overcome to achieve synthesized coordinated regional networks. We suggest these efforts can be scaled up to create a global network of remote cameras that would provide a unique picture of our planet to complement other remote biodiversity sensing methods critical to documenting and mitigating the current biodiversity crisis.

323 Given these advancements in remote camera science, we have three recommendations for 324 further integration of camera data into biodiversity monitoring. First, we reiterate the need for 325 standardizing metadata collection and data storage. Agreeing to a global industry standard will 326 greatly facilitate the usefulness of the plethora of data being collected (Meek et al., 2014). Second, 327 greater support is required to provide a global infrastructure to improve collaborations among 328 existing projects and increase local buy-in for new camera projects that can be more explicitly linked 329 to regional and global camera networks. To do so, it would be important to tap into extant 330 collaborative networks to facilitate regional collaboration (e.g. TEAM, eMammal, Parks Canada). 331 With broad cross-institutional support, tremendous opportunities could be gained when capitalizing 332 on this framework for global biodiversity monitoring. Lastly, institutions like GEO BON and GBIF 333 could benefit from increasing their rate of adoption of camera data as one of the most standardizable 334 and expandable data types for biodiversity monitoring, as they can contribute to the generation of 335 Essential Biodiversity Variables (Pereira et al., 2013) for terrestrial vertebrates and complement other 336 indices like the Living Planet Index (livingplanetindex.org). The public appeal of remote camera 337 images and citizen-scientist participation will continue to scale-up biodiversity monitoring and excite 338 public support to ultimately help make successes in global conservation possible.

339

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509 Figure 1. Snapshot of recent global remote camera studies. All study area locations where authors

- 510 have used cameras to ask large-scale ecological questions are located on map (on average, 78
- 511 cameras at each point; range 11-600), providing a glimpse of the ubiquity and diversity of current
- efforts around the world to collect ecological data using remote cameras. Cameras studies used in
 eMammal and TEAM projects are included. (A) grizzly bear (*Ursus arctos*) (B) tragopan (*Tragopan*
- 515 eMammal and TEAM projects are included. (A) grizzly bear (*Ursus arctos*) (B) tragopan (*Tragopan* 514 *blythii*) (C) wolverine (*Gulo gulo*) (D) mule deer (*Odocoileus hemionus*) (E) coyote (*Canis latrans*)
- 515 (F) giant anteater (*Myrmecophaga tridactyla*) (G) African bush elephant (*Loxodonta africana*) (H)
- 516 clouded leopard (*Neofelis nebulosa*). See WebTable 1 for more details of each study included on
- 517 map.
- 518

519 **Figure 2.** How scaling up data collected from local *in situ* camera sites to higher levels of

- 520 organization results in changes in the interpretation of the data, the ecological and conservation
- 521 questions that can be asked, and the explanatory covariates required to answer these questions. The
- spatial scale of interest determines the meaning of data collected, availability of analyses, and the
- 523 needed explanatory variables, therefore, guiding the application of camera data. The smallest scale is
- the local *in situ* camera site that can be combined with other point data such as carbon metrics. Next,
- 525 cameras are often deployed relative to an idealized camera trap grid. These grids can be coordinated
- 526 across a network such as the Canadian mountain parks network, which have the potential to be
- 527 integrated across the globe with ever-increasing satellite data.
- 528

529 Figure 3. Common groups of statistical analyses performed on camera data. Data collected from the

same local camera grid can be easily analyzed to answer many different types of questions including

temporal and spatial behaviour patterns (subfigure modifed from Rowcliffe *et al.*, 2014); spatially

- 532 explicit abundance (Gopalaswamy *et al.*, 2012; reproduced by permission of John Wiley and Sons);
- 533 occupancy (Ahumada et al., 2013); and species richness (Ahumada et al., 2011; reproduced by
- 534 permission of the Royal Society).