

Chapter 2

Image Resolution: Habitat Selection Scale in a Remote Sensing Context

2.1 Scale of Habitat Selection

Researchers have long sought to understand what cues are used by animals to select those subsets of the landscape that maximize their reproductive fitness (MacArthur and MacArthur 1961; Hilden 1965; James 1971; Fretwell and Lucas 1972; Johnson 1980; Cody 1981; Morris 1987; Wiens et al. 1987; Wiens 1989b; Martin 1992; Pribil and Picman 1997; Thompson and McGarigal 2002; Ahlring and Faaborg 2006). Historically, habitat selection studies focused on local structure of the environment and identified selection mechanisms linked to these local (high resolution) conditions. Many studies still employ this ground-based approach. In their review of the influence of variables measured at different scales, Mazerolle and Villard (1999:119) noted, “*One would intuitively expect that patch (local) conditions would be better predictors of species presence or abundance than landscape context (i.e., habitat must be favourable in order for the species to be present).*” Results of the 61 studies they reviewed at that time supported this view. More recently, however, studies employing GIS metrics have expanded in spatial extent well beyond plots to include regional scale attributes (e.g., McGarigal and McComb 1995; Saab 1999; Cushman and McGarigal 2002; Drapeau et al. 2002; MacFaden and Capen 2002; Pearman 2002; Lawlor et al. 2004; Miller et al. 2004; Bakermans and Rodewald 2006; Rioux et al. 2009; Cornell and Donovan 2010; Kennedy et al. 2011; LeBrun et al. 2012). Studies examining behavioral influences on habitat selection such as conspecific attraction (e.g., Campomizzi et al. 2008) also have been added to this mix (reviewed by Ahlring and Faaborg 2006).

A growing number of these more recent studies, while often finding correlations with plot- or local-scale variables (e.g., Lichstein et al. 2002a, MacFaden and Capen 2002), have convincingly argued that consideration of effects at one or several geographically more extensive scales, particularly in anthropogenically

influenced landscapes, is important in developing conservation strategies (e.g., Saab 1999; Howell et al. 2000; Johnson et al. 2002; Lee et al. 2002; Thompson et al. 2002; Bakermans and Rodewald 2006; Kennedy et al. 2011; Thompson et al. 2012). Thus, inclusion of GIS metrics in development of species–habitat models has become the norm. This trend notwithstanding, analyses that include spatially more extensive areas have frequently produced models with only modest predictive power (McGarigal and McCombs 1995; Dettmers and Bart 1999; Cushman and McGarigal 2002; Drapeau et al. 2002; Lichstein et al. 2002a; McFaden and Capen 2002; Miller et al. 2004; Thogmartin et al. 2004b; Betts et al. 2006; Howell et al. 2008; LeBrun et al. 2012; Garvey et al. 2013; Lapin et al. 2013). In this and the following chapter, respectively, we discuss (1) issues related to image resolution and (2) the types of metrics employed as potential causes for this outcome.

2.2 Image Resolution and Minimum Mapping Unit Size

First, in describing the attributes of raster-based GIS's, Keller et al. (1979a) and Turner (1989) noted that such programs used cells (minimum size delineation) of a fixed size for the chosen scale of imagery, thus producing variables (metrics) that are relative rather than absolute measures of landscape heterogeneity. Keller et al. (1979a) noted, however, that the value of these metrics is not diminished as long as the resulting cell size, and the underlying image resolution associated with that cell size, has biological relevance to the species or taxon of interest. Although this observation was made originally in describing raster-based programs, all GISs, raster- or vector-based, have minimum size delineation units or minimum mapping units, and associated classification systems (see next section) that are subject to these constraints.

More recently, in analyzing the influence of pixel (or more correctly, *cell*) size variation on landscape pattern metrics, Trani (2002) demonstrated that application of increasingly coarser resolutions (Table 11.2, op. cit.) routinely led to measurement errors of landscape predictor variables (e.g., edge length, interspersion), which reduced species occurrence prediction rates and resulted in misinterpretations of species–habitat relationships (see also Wu 2004; Ostapowicz et al. 2008). She concluded (Trani 2002:151) that “*Only at the proper spatial scale* (sic—resolution and minimum mapping unit size) *do metrics have potential meaning for resource managers.*” She went on to note (op. cit.:153) “*Pattern analysis is most useful when the scale of analysis matches the scale at which species use the landscape.*” Thus, for any study involving wildlife habitat analysis, the choices of image resolution, minimum mapping unit, and the associated classification system are critical to one's ability to identify and map features/components of potential importance to habitat selection by the organism (Huston 2002; Arponen et al. 2012) and should be based on some understanding of the focal taxon's mechanism(s) of habitat selection and use (see Morrison et al. 1998 for discussion).

Consider, for example, the application of Trani's findings to migratory birds, which are widely agreed to exhibit broad-level selection at geographic scales much larger than an individual territory or home range. Avian visual acuity, however, suggests birds likely accomplish this at much higher levels of *resolution* than the imagery employed in studies designed to test for such assessment (cf. Lawler et al. 2004 in Sect. 2.3).

Migrants associated with shrub-scrub plant communities, for example, have the ability, whether within areas of extensive forest or other unsuitable biotopes, to locate small and ephemeral parcels of such early successional habitat (Confer and Knapp 1979; Titterton et al. 1979; DeGraaf 1991; Probst and Weinrich 1993; King et al. 2001; Keller et al. 2003; Martin et al. 2007; Schlossberg and King 2009). Yet, on 30 m or similarly lower resolution imagery such parcels are typically indiscernible and/or misclassified to more general forest types (Smith et al. 2001; Luoto et al. 2004; Thogmartin et al. 2004a). As a result, as noted by Huston (2002), although a species might be present only within a small subset of a larger sampling area, and thus counted as present within that area, measurement of habitat heterogeneity (i.e., the grain) at a low resolution would fail to differentiate the subset from the average conditions of the whole area, despite the likelihood that actual differences exist. This leads both to inaccurate predictions of species occurrence (Lebbin 2013) and to misunderstanding of the processes that resulted in the observed pattern of occurrence within the larger area (Van Horne 2002). Orians and Wittenberger (1989) summarized this problem, noting that if inappropriate scales of sampling and analysis are used, key factors in species-environment relations may be missed.

While we acknowledge that the resolution of the remotely sensed imagery selected is frequently influenced by (1) the cost of data acquisition or transformation and (2) data availability (McDermid et al. 2009), using an image resolution and associated minimum mapping unit appropriate to address the research question of interest are essential to identify the potentially most insightful predictor variables for exploration of species-habitat or higher level relationships (see also Risser 1987; Wiens 1989a; Wiens and Milne 1989; Mazerolle and Villard 1999; Franklin et al. 2002; Young and Hutto 2002). As noted by Wagner and Fortin (2005), landscape metrics are highly sensitive to scale (sic—resolution and minimum mapping unit), and mapping errors increase if imagery scales are insensitive to the level of proposed classification systems. Ultimately, choice of image resolution and an associated minimum mapping unit are critical to strength, interpretability, and applicability of the results.

2.2.1 What About Mapping Scale?

The researcher's need to visualize and interpret image heterogeneity at an ecological scale thought to be relevant to the organism determines the importance of mapping scale. For example, viewing a remotely sensed image at a mapping scale, as

well as a resolution, that allows identification of components reasonably perceived and responded to by the organism can enable both selection and biological interpretation of potentially important predictor variables, points we discuss in Chap. 6. We submit these latter processes are both more difficult if one examines only (1) imagery at an overly small mapping scale or (2) landscape metric output (e.g., land-cover proportions) in isolation, regardless of the image resolution employed. Therefore, although resolution (GRD, NIIRS Level) is far more relevant, the ability of the researcher to observe it (mapping scale) also may be important to consider. Current GIS platforms allow for ready manipulation of mapping scale.

Given adequate image resolution, mapping (image) scale also determines (1) the ability of the researcher to develop a classification system or identify/modify an existing one to characterize landscape components of interest if the image is unclassified and (2) manually or through automated interpretation apply the classification to create the mapped data.

2.3 Landscape Component/Land-cover Classification

Knowing how animals use their habitat is critical to interpreting the results of GIS-based analyses (Van Horne 2002). However, this knowledge is equally critical at the outset of the investigation (cf. Farrell et al. 2013). This is because the values of all GIS-derived metrics will reflect the underlying image resolution and the corresponding level of detail in the chosen classification system. Therefore, both the image resolution and classification system should consider the minimum size landscape components thought to influence habitat choice by the focal taxon. Understanding the focal taxon's life history and habitat use are essential in this process.

For larger or wider ranging species (e.g., bears), landscape component classification may be more general and may be adequately represented by traditional broader cover types such as forest or grassland. For smaller species with typically more limited home ranges or territories and concomitantly finer scales of habitat selection and use, the classification may need to include more discrete elements such as individual shrubs, small canopy openings, or a narrow water feature only a few meters or less across. In either case, image resolution and the accompanying classification system should reflect the focal taxon's response to the subset of the landscape it uses in order to allow biologically meaningful interpretation of the results of GIS-based analyses. If employing a pre-classified image, one should evaluate whether the resolution and classification system of the image are appropriate to meet the objectives of the study (O'Neill et al. 1996; Gallant 2009; McDermid et al. 2009).

Many classification systems and taxonomies have been developed for interpreting and classifying remotely sensed imagery, often on an individual study basis. Among those classifications are a number of widely recognized systems in routine use, often applied to higher resolution imagery, such as aerial photography

or Landsat Thematic Mapper, with diverse land-cover or landscape component categories at a range of mapping scales. Some examples include the early land-cover classification suggested by Anderson et al. (1976), the national wetland classifications of Cowardin et al. (1979), ecological land types (ELTs) used primarily by the US Forest Service (Eyre 1980; MacFaden and Capen 2002), the National Land Cover Dataset (NLCD, Loveland et al. 1991), and the National Vegetation Classification Standard (NVCS) developed by the Federal Geographic Data Committee in close collaboration with the Vegetation Classification Panel of the Ecological Society of America (Federal Geographic Data Committee 2008).

In particular, the NVCS embodies a number of desirable attributes important for researchers working with species–habitat relationships to consider. In general, researchers and conservationists would do well to embrace and apply established standards such as the NVCS whenever possible rather than creating their own ad hoc classification schemes. If study-specific classifications of remotely sensed imagery are deemed necessary, they should be developed in close collaboration with remote sensing specialists and vegetation scientists (cf. McDermid et al. 2009).

Lawler et al. (2004) amply demonstrated the strikingly different results that can obtain by employing different land-cover classifications at a particular image resolution, in their case 160 land-cover types (fine grained) versus 14 land-cover types (coarse-grained). They also noted that, for many applications, classification systems should be designed to address species-specific habitat requirements and that *“determining the proper resolution of any classification needs to be incorporated into the design of studies with the same care that recent research has shown must be paid to the effects of scale”* (op. cit.:519). We agree, and note that, as stated in the previous section, the ability to classify cover types or more finely, individual landscape components, is ultimately limited by the *resolution of the image*. In the many GIS-based analyses we reviewed, neither the influence of the classification system chosen nor the limitations on classification accuracy due to image resolution are discussed by more than a few authors (e.g., Bart et al. 1995; Dussault et al. 2001; Smith et al. 2001; Thompson and McGarigal 2002; Hines et al. 2005; Thogmartin et al. 2004a; Davis et al. 2007; Habibzadeh et al. 2013), despite the fact that formal methods for addressing the latter issue exist (Congalton and Green 1998; cf. Bock et al. 2005). Gallant (2009) opined that most databases lack formal accuracy assessments because of the time and cost to complete them (see also McDermid et al. 2009).

As Smith et al. (2001) noted in applying Landsat-5 Thematic Mapper imagery at a nominal resolution of 10 ha for the New York Gap Analysis Project, although overall map accuracy was 74 %, producer accuracies for agricultural land-cover types and shrublands were consistently lower than the average. This is because at this resolution, agricultural cover types are highly dynamic in their spectral responses and shrublands can be confused with other forest types (McDermid et al. 2009; cf. Lapin et al. 2013 inability of Landsat to distinguish cutover from mature spruce). As a result, Smith et al. (2001) cautioned that any interpretations, conclusions, or management recommendations based on habitat associations of

(often declining) breeding bird species associated with these early successional cover types (Mitchell et al. 2000; Dettmers 2003) should take into account the mapping accuracies achieved. Thogmartin et al. (2004a) offered a similar caution on the use of the NLCD and McDermid et al. (2009) commented on the quality versus the *utility* for a particular wildlife study of different map sources available to researchers. These studies and the aforementioned lack of explicit consideration of mapping accuracy or other measures of quality in many studies we reviewed, suggest the need for field biologists and conservationists to possess a better understanding of the subtleties, strengths, and weaknesses inherent in the compilation, application, and interpretation of remotely sensed data (Glenn and Ripple 2004; Wulder et al. 2004; Gallant 2009).

2.4 Image Resolution and Interpretability

Avery and Berlin (1985) discussed the interpretability of various mapping scales of remotely sensed imagery and noted that images at a scale of less than 1:10000 precluded identification of individual trees and shrubs, or estimation of their heights. In addition, they and Miller (1996) noted that for satellite imagery (typically 1:40000 at 30 m \times 30 m resolution), even classification systems and general mapping of forest cover are problematic due to the lower resolution of this imagery (see also Bart et al. 1995; Dussault et al. 2001; Glenn and Ripple 2004; Arponen et al. 2012).

Wulder et al. (2004) reviewed advancements in data acquisition technology (greater spatial, radiometric, temporal, and spectral resolution) for their utility in ecological studies. While they acknowledged the improved interpretive capabilities of modern sensors, they noted that only when there are many pixels per object rather than many objects in a single pixel can the object of interest (e.g., individual trees, and shrubs = grain size for our discussion) be meaningfully characterized (but see Bock et al. 2005). This H-resolution imagery (Strahler et al. 1986) allows identification of a high degree of local heterogeneity (i.e., multiple landscape components) and contains large amounts of spatial information (McDermid et al. 2010). In contrast, L-resolution images (e.g., a Landsat image that contains multiple trees within a single 30 m pixel) contain less spatial information about individual trees or other landscape components of potential interest but would provide an acceptable level of information about forest distribution at the scale of an entire stand (op. cit.). These are critical points in the investigation of species–habitat relationships using GIS, yet appear to be rarely considered explicitly.

The limitations of decreased image interpretability and increased misclassification at lower resolutions (Franklin et al. 2000; Fleming et al. 2004; Thogmartin et al. 2004a; Hines et al. 2005) are magnified when one considers the fundamental differences in the scales at which wildlife species select habitat (Wiens and Milne 1989; Pearson and Gardner 1997). Kerr and Ostrovsky (2003) observed there often is a perceived mismatch between the data sought by ecologists and the

data collected with remote sensing instruments. Turner et al. (2003) suggested this perception is declining due to the increasing availability of high-resolution data that can be directly linked to traditional field-based ecological measurements. Although we agree that imagery with appropriate resolution (measured as GRD or NIIRS Level) may be available, the resolution of imagery (or mmu) actually chosen for use in a particular analysis does not always account for differences in the scales at which wildlife select habitat (O'Neill et al. 1986; Gottschalk et al. 2005; cf. Donovan et al.'s (2012) use of the same L-resolution imagery for Bobcat [*Lynx rufus*] and Ovenbird [*Seiurus aurocapillus*]).

In contrast to this latter study, Hutto (2014) used H-resolution aerial photography (Fig. 1, 1:1560 scale, no resolution given) to identify “every visible shrub, tree, and downed log” (op. cit.:123) while mapping individual perch sites and territory boundaries of male Calliope Hummingbirds (*Selasphoris calliope*) on a dispersed lek within a 20-year-old seed tree cut in western Montana. Similarly, Farrell et al. (2013) combined LiDAR (resolution to less than 1 m) with H-resolution (0.35 m) color-infrared scanned image data (SID) to develop predictive occurrence models for two listed species of passerines. Conversely, using the same dependent data set, models they developed that included only traditional canopy cover estimates from L-resolution imagery were not plausible for either species.

Lawler et al. (2004) further illustrated this resolution/interpretability relationship. Using Breeding Bird Survey (BBS) data for six different species of birds, they compared models of species occurrence within the conterminous US built with fine-grained versus coarse-grained image classification data based on satellite imagery with 1.1-km² resolution. Most (8 of 12) models, whether employing the coarse- or the fine-grained cover type classification, included both cover type and climatological variables to explain the species distributions. However, none of the remaining four models, (2 each) for the House Wren (*Troglodytes aedon*) or Savannah Sparrow (*Passerculus sandwichensis*), included any of the available land-cover types or 24 pattern metrics as explanatory variables, only climate data.

The authors offered that the lack of inclusion of any land-cover variables in the House Wren or Savannah Sparrow models suggested a failure of the land-cover classification system to capture the habitat preferences [sic] of these species. They suggested (op. cit.:528) that “...*accurate models for some individual species will require the definition of species-specific land-cover classifications designed to address specific habitat requirements*”. We agree (see our sample analysis in Chap. 6 and associated landscape component classification in Appendix C). However, we also suggest that use of the landscape by these species was simply at too fine a resolution to be detected using the 1.1 km²-resolution satellite imagery employed (e.g., note the reference in the foregoing quote to “species specific *land cover classes*”, which connotes the mismatch of the imagery resolution employed to the scale at which small passerines actually use the landscape). Thus, although this type of range-level analysis can be useful in interpreting distributional patterns over large geographic scales (e.g., Collier et al. 2012; LeBrun et al. 2012; Lapin et al. 2013), it also may produce misleading or incomplete model results, as above; and appears

generally inappropriate for identification of local-scale management or conservation approaches due to the mismatch of image resolution and associated minimum mapping unit size with species' habitat-use scale, classification system notwithstanding (Farrell et al. 2013). We further discuss the use of BBS data and GIS sampling of BBS routes in Chap. 4.

Analytical scale disconnects as described above are not exclusive to vertebrate studies. For example, Rykken et al. (1997) attempted to correlate ground beetle distributions to the US Forest Service's Ecological Land Types (see McFaden and Capen 2002), whose minimum mapping unit is 10–100's of ha in size. Not surprisingly, based on the preceding discussion, no relationship was found (but see Luoto et al.'s 2002 use of satellite imagery to successfully model habitat for a more wide-ranging insect).

2.5 Matching Image Resolution to the Scale of Species Function

2.5.1 Domains of Scale

In a discussion of scales of analysis, Wiens (1989a) noted that patterns evident at a biogeographic scale reflect underlying patterns and processes at a local scale; and therefore, an understanding of local-scale events is necessary to properly interpret coarser scale patterns. Huston (2002:10) restated this observation in terms of resolution, describing how “...*patterns can be detected at resolutions far coarser than the resolution needed to understand the processes that produce the pattern, which is also the resolution needed to predict the pattern.*” So, what is the “appropriate” scale and (image) resolution of analysis to correctly infer process from observed pattern?

Cautioning against unrecognized bias in such choices, Wiens (1989a:391) then noted that “*scales chosen for analysis by researchers typically reflect hierarchies of spatial scales that are based on our own perceptions of nature. Just because particular scales seem ‘right’ to us, is no assurance that they are appropriate*” for the particular taxon of interest. Selection of image resolution in GIS-based analyses warrants a similar caution. This is because, as inferred by Huston's (2002) comment above, as image resolution decreases, there is a concurrent decrease in the ability to identify, classify, and quantify accurately species-specific landscape components (grain) and their spatial arrangement (habitat size, configuration, and distribution) (see Smith et al. 2002, 2003; Fleming et al. 2004). This leads to an increasing disconnect between actual occurrence of habitat on the landscape and one's ability to measure it, at any hierarchical scale.

Wiens (1989a, and Fig. 4 therein) then considered scale-dependency in ecological systems theoretically and argued that within the spectrum of potential analytical scales, there are “domains” (i.e., subsets of the scale continuum) of particular ecological phenomena within which process–pattern relationships are consistent, regardless of the scales of observation within that domain. He went on to note that proper analysis requires that the scale of researcher measurements and that of the

organism's responses fall within the *same* domain. We submit that viewed in this way, "domain" represents the range of image resolution and level of image classification at which GIS-based habitat analysis should occur. This is because in GIS, the ability to interpret an organism's responses to its environment (i.e., habitat selection and/or use) in a biologically meaningful way depends on adequately quantifying the composition, structure, and spatial arrangement of relevant elements composing that environment, which ultimately depends on image resolution and the associated classification system employed in the analysis.

Given this relationship, a good starting point for determination of appropriate image resolution would seem to be within territory core areas of activities such as foraging, singing, and nesting (e.g., Balbontin 2005; Barg et al. 2005, 2006; Moore et al. 2010; Hutto 2014). That is, one should ensure that the imagery, whether detected passively (e.g., photographs) or by propagated signals (e.g., LiDAR), provides the capability to characterize thoroughly **intraterritory spatial heterogeneity** (cf. Holland et al. 2004). As but one example, St-Louis et al. (2006), using a range of sampling window sizes (i.e., nested, increasingly larger, fixed-sized, typically square samples on a GIS map), found the strongest correlations of bird species richness with landscape heterogeneity (measured as image texture on high-resolution (1 m) aerial photographs) at sampling window sizes (21×21 m– 31×31 m = **441–961 pixels**) that represented subsets of territories for virtually all of the species being studied. Landsat (30×30 m = **1 pixel**) or other lower resolution imagery would not afford the same ability to quantify intraterritory heterogeneity. The results of this assemblage-level study illustrate the desirability of applying appropriately resolved imagery not only to individual species but also to higher organizational levels, as well.

With regard to broader geographic analyses, our literature review revealed that although understanding range-wide patterns of habitat occupancy is a desirable objective, attempts to elucidate such patterns for smaller animals using low resolution imagery have met with only limited success (but see Collier et al. 2012). Thus, although it can be argued that high-resolution imagery is not essential when examining context or for multi-scale studies of broad geographic areas, use of lower resolution imagery for smaller species can result in misinterpretations in both types of studies, and ultimately, in misinformed management recommendations.

The foregoing discussion suggests that although habitat selection may proceed in a top-down manor as described by Johnson (1980) and questions asked by researchers at biogeographic scales (e.g., population viability) may differ from those asked at local scales (e.g., presence / absence), the variables and image resolution used to address them should overlap broadly. As noted by Wiens (1989a:390), "*If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale. Because we are clever at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly.*" This astute observation points to the need for equally careful selection of the image resolution and classification system in GIS-based habitat analyses.

Only when image resolution (domain of scale) is appropriate for the species at all levels of analysis (local to biogeographic), can habitat occurrence, its spatial distribution, and hence, associated species distributions and populations, be accurately estimated using GIS-based models (cf. Farrell et al. 2013). Given the computational requirements and cost of using high-resolution imagery or LiDAR over biogeographic scales, sampling locations should be carefully considered when developing species–habitat models with the intent of estimating population distributions across range-wide levels of analysis (cf. Huston 2002; MacKenzie and Royle 2005).

Although it is beyond the scope of this paper to fully examine these issues, they do suggest potentially useful future research (e.g., are there differences in the apparent influence of the matrix when it is viewed at high versus low resolution, using classification schemes appropriate for both?).

2.5.2 *Less Arbitrary Selection of Image Resolution*

Wiens (1989a) noted that scales chosen for analysis of species–habitat associations are generally arbitrary but that what constitutes an “appropriate” scale is somewhat dependent on the questions asked by the researcher. He then noted that differences among organisms also affect the scale of investigation and suggested that these differences somewhat paralleled differences in body size, which raised the possibility of using allometric relationships to scale analyses. We agree and propose the use of a simple body-size-based rule to aid selection of a less arbitrary, more species-scaled image resolution for any GIS-based habitat analysis.

Considering the foregoing discussion and references cited, we suggest that, as a general rule, the remotely sensed imagery employed to elucidate species–habitat relationships should be capable of resolving landscape elements $\leq 5\times$ – $10\times$ the body length of the species of interest. For example, applying this criterion to a 13-cm warbler would result in a GRD range of 0.65–1.3 m, requiring imagery that could resolve small shrubs or saplings in the range of 1 m in width, a reasonable goal for a small, foliage-gleaning insectivore. However, as with all such generalities, there are exceptions. For example, due to their flexibility, snakes can take cover under landscape elements (e.g., rocks) that are considerably less than their body length, which again underscores the importance of understanding the natural history of the focal taxon. In this case, the smallest resolvable components of interest are likely *less than half* the length of the individual.

In general, we suggest researchers ask the following:

- Will the chosen remotely sensed imagery resolve **landscape components and potential intraterritory heterogeneity** that reflects the focal taxon’s scale of habitat use or association that is of interest to the researcher?
- If the scale of habitat use or association is unclear, are the smallest resolvable landscape components in the imagery more than $5\times$ – $10\times$ the body length of the species of interest? Are there morphological or physiological attributes of the species that suggest the need for resolution of even smaller landscape components?

- Regardless of whether the previous questions are answered affirmatively or negatively, what information might be lost at the chosen image resolution?
- Does the classification system employed reflect the component composition and heterogeneity described above?
- Will the chosen resolution allow meaningful characterization of **landscape attributes (i.e., spatial arrangement) of those components?**

Combining the body size–image resolution rule, we offer with an understanding of the species' natural history and core area, territory, or home range size, should suggest the appropriate image resolution and level of land-cover classification (e.g., physiognomic vs. floristic) to apply.

2.5.3 *Edges and Ecotones: Resolution Effects on Interpretation of Habitat Association*

As implied in the Working Definitions Chapter, the concept of edge has long interested ecologists and edge quantification has been facilitated by the advent of GIS. However, considering edges only at the scale of plant communities (i.e., *ecotones*), which is the typical case, implies that (1) there are relatively few types of edge in a landscape and (2) individually, those edges are relatively extensive spatially (cf. Fig. 1.1). As noted, the alternate view considers that myriad edges of numerous types are present at many scales (e.g., Fig. 1.2), both between and frequently, within plant communities (Risser 1987; Wiens 1989b). Under this latter concept, an ecotone such as that between a forest and a hayfield represents but one general type of interface or boundary, which itself contains multiple edge types (Gosz 1991) recognized by various species or guilds of wildlife. Along this extensive-to-local continuum of edge scale, increasingly smaller animals use progressively more fine-grained edge types (see Kotliar and Wiens 1990).

For example, White-tailed Deer (*Odocoileus virginianus*) and Red-tailed Hawk (*Buteo jamaicensis*), both of which have home ranges on the order of several hundred to >1,000 ha (e.g., Tierson et al. 1985; Andersen and Rongstad 1989), might be expected to select habitat generally at the scale of plant communities and ecotones [but see suggested finer resolution selection for deer by Fleming et al. (2004)], whereas passerines (breeding territory = 0.5–2 ha) appear to select at the scale of individual landscape components such as trees, shrubs, openings, and edges between them (cf. Suarez et al. 1997; Barg et al. 2006). Smaller or more sedentary animals (e.g., small mammals, salamanders, small fish, mollusks, gastropods, spiders, insects = home ranges of <0.5 ha) have been demonstrated to select at even finer scales of landscape components and associated edges (e.g., rocks, logs, individual plant parts; cf. Krawchuk and Taylor 2003; Stoddard and Hayes 2005; McKenny et al. 2006; Ewers et al. 2007; Matias et al. 2007; Macreadie et al. 2010; Matias et al. 2010; Moore et al. 2010; Vierling et al. 2011).

Failure to consider the resolution at which habitat selection occurs when attempting to categorize species as “edge,” “forest interior,” or other habitat association, has led to misinterpretation of these associations, and can have profound implications for conservation and management (Franklin et al. 2002). For example, the Cerulean Warbler (*Setophaga cerulea*) often has been characterized as a “forest interior” species. Yet, recent evidence suggests that it is frequently associated with closely spaced, variously sized canopy gaps (i.e., edge) (Weakland and Wood 2005; Perkins 2006; Bakermans and Rodewald 2009; McElhone et al. 2011; Boves et al. 2013; Perkins and Wood 2014) caused by tree deaths (more frequent in floodplains), blow-downs (more frequent on steep slopes and ridge tops), or deliberate forestry practices such as shelterwood harvest (Carpenter et al. 2011; S. Stoleson, USDA Forest Service personal communication). Thus, when viewed at the within-territory scale, it may actually be more of a forest interior-edge species, suggesting previously unconsidered management approaches (cf. Perkins and Wood 2014).

Imbeau et al. (2003) touched on the “labeling” issue, noting that categorizations of some bird species as early successional in one research context conflicted with classifications of the same species in another context, such as when defining so-called edge (=ecotone) species (see also Miller et al. 2004). They argued that early successional species are actually shrubland specialists and occur at mature forest edges (ecotones) only due to lack of appropriate shrubland habitat elsewhere in the immediate vicinity. They further argued (op. cit.:514) that “to be considered a true edge species, a species has to require the simultaneous availability of more than one habitat type” (i.e., habitat *sensu* plant community). As a result, they concluded that “real edge species” (i.e., ecotonal edge) are probably quite rare. We argue instead that edge species are only rare if the definition of edge is confined to the spatial scale of an ecotone. When considered at a species-specific scale and resolution (i.e., grain), the number of species dependent on edges between different habitat components (e.g., trees, shrubs, grass, and water) is, in fact, quite high. Using our Working Definition of edge habitat (Chap. 1), Red-tailed Hawk, Song Sparrow, Golden-winged Warbler (*Vermivora chrysoptera*), and Praying Mantis (*Stagmomantis carolina*) are all edge species, each associated with edges at spatial scales commensurate with their size and habits.

Additionally, some researchers have suggested that amount of edge is more influential on bird communities at the landscape scale (McGarigal and McComb 1995; Hagan et al. 1997). We suggest that when edge is measured at the plot (i.e., habitat) or biotope/community scale, it can be at least as predictive of community (assemblage) composition and potential ecotonal effects via correlations of more specific edge types with individual species or guilds. This has rarely been done to date (but see Keller 1990; Keller et al. 2003; Chapa Vargas and Robinson 2007; Rehm and Baldassarre 2006; Macreadie et al. 2010; Chap. 6 herein).

For example, as part of a study of the use of even-aged seres by breeding birds following cutting, Keller et al. (2003) analyzed edge effects using 1:5000 stereoscopic aerial photography at a mapping scale of 1:2000 with resolution of <0.75 m (NIIRS Level 6). They found that in addition to the perimeter edge (i.e., ecotone) between cutover areas and adjacent forests, which would be generally identifiable in Landsat imagery, clear-cuts initially (i.e., post-cut years 1–4) contained

high levels of internal edge (e.g., shrub-grass and sapling-grass). At an ecological scale relevant to habitat selection by passerines, the density of these latter edges was strongly associated with early successional species of terrestrial gleaners, primarily sparrows. As succession proceeded, regenerating sprouts and root suckers filled in the openings, thus eliminating the internal edges, and the sparrows were replaced by foliage-gleaning insectivores, primarily warblers. Viewed at a lower resolution Landsat scale, these internal edges would have been undetected. Only the clear-cut itself and surrounding forest would have been identified, and thus, only the plot perimeter edge (ecotone), which remained unchanged, would have been quantifiable (cf. Schlossberg and King 2008), setting up spurious correlations with edge-associated guilds such as the sparrows, which occurred primarily *within* the clear-cuts, not along the perimeters.

The preceding series of examples illustrates how edge-associated species may cue on ecotone-scale edges (e.g., Red-tailed Hawk and White-tailed Deer), intermediately scaled edges (e.g., flycatchers = canopy-opening or forest gap; song sparrow = shrub-grass) or much more localized subsets of edges [insects = edge between a leaf and adjacent air (Krawchuk and Taylor 2003) or small fish = edge between seagrass and adjacent open water (Macreadie et al. 2010)]. At the low resolution, large geographic scales typically employed in GIS analysis of species–habitat relationships (e.g., Landsat = 1:40000 with GSD 30 m, or widely available aerial photography databases = 1:24000), even intermediate scales of edge are generally not discernible and are thus, unmeasurable (Avery and Berlin 1985; Wulder et al. 2004).

Of the species mentioned above, lower resolution imagery (GRD <30 m, NIIRS Level 3 or higher) would appear reasonable for development and application of habitat models to only the larger-bodied, wider ranging species such as the deer and hawk (cf. Laymon and Reid 1986; Nixon et al. 1988; Poppelwell et al. 2003; Nielsen, et al. 2006; Davis et al. 2007; Kays et al. 2008; Rioux et al. 2009; but see Palmeirim 1985; Huber and Casler 1990; Thompson and McGarigal 2002; and Fleming et al. 2004; reviewed by Gottschalk et al. 2005). Higher resolution (e.g., GRD <1.2 m, NIIRS Level 5 or higher) imagery, and an associated larger mapping scale (e.g., 1:5000) to facilitate researcher interpretation, would be more appropriate for passerines (see our analysis in Chap. 6), and very high-resolution imagery (e.g., GRD <0.4 m, NIIRS Level 7 or higher) generally would seem necessary for small mammals, salamanders, and most arthropods, at least those associated with open-canopied habitats (e.g., Cronin 2009; see also scale of LiDAR imagery for spiders in Vierling et al. 2011).

As suggested by this discussion, failure to adequately match image resolution to the resolution at which species perceive and respond to edges (or solid patches) in the landscape can result in derived metric values that are artifacts of inappropriate image resolution (Wiens 1989a). Furthermore, even with higher resolution imagery that may more closely match landscape component composition and resolution with organism use of the landscape, GIS metrics (or researchers) frequently equate (i.e., lump together) all edge types or reduce specific edge types to “levels of contrast,” with a concomitant *a priori* loss of information (see Chap. 3).

Collectively, inappropriate resolution and overly simplified interpretations of edges can produce completely misleading correlations with metrics such as fractal dimension or edge density, which can result in incorrect inferences about species–habitat associations. Ultimately, these shortcomings can have important consequences for management and conservation.

2.6 Landsat Versus Higher Resolution Imagery

Many biotopes, despite their definition as being “more or less uniform,” are matrices of components containing substantial internal heterogeneity, quantification of which is entirely resolution dependent since an apparently solid habitat type, with problematic or unmeasurable edge at one resolution, reveals that edge (i.e., internal heterogeneity) at a higher resolution. In ecological terminology, this is the change in *grain* size, the smallest element used in habitat selection by the organism. This unresolved heterogeneity is very typical of Landsat imagery when considering open-canopy plant communities such as shrub-steppe, oldfields, early stage clear-cuts or shelterwood cuts, and some grasslands (cf. Bellis et al. 2008).

Figure 1.1, an image of central New York, illustrates the type of broad scale heterogeneity that has been quantified in many avian studies employing Landsat or other remote sensing data with similar resolution (e.g., Donovan and Flather 2002; MacFaden and Capen 2002; Betts et al. 2003; Thogmartin et al. 2004b; Howell, et al. 2008; Cornell and Donovan 2010; LeBrun et al. 2012). Such imagery and the resulting GIS data sets characterize many passerine territories with only a few pixels, each of which, with a sample area frequently of 900 m², may actually include diverse habitat components (“mixed pixels”) now reduced to a single, sometimes misclassified, cover type (Fig. 2.1, also see Sect. 2.4 and Appendix B) (Bart et al. 1995; Congalton and Green 1998).

As shown in Fig. 2.1, even a modest 10-m GSD mapping resolution using high-resolution (NIIRS Level 6) aerial photography produces 9x more information (81 cells vs. 9) than the 30-m GSD mapping resolution provided by Landsat for a nominal 0.81 ha passerine territory. Additionally, this resolution allows much more accurate classification of the landscape components actually present on the ground. Equally importantly, the 10-m versus 30-m cell size allows more accurate characterization of the spatial arrangement of now identifiable, and thus classifiable, individual landscape components such as trees, shrubs, and grass in an old-field or clear-cut (see Chap. 3).

The arrangement of these components dictates the presence or absence of declining early successional species such as Golden-winged Warbler (GWWA) and would be unquantifiable at a lower image resolution such as Landsat even if the oldfield or clear-cut itself were identifiable (Fig. 1.1). This is also true for the increasing number of studies employing widely available 1:24000 aerial photography. In the case of the GWWA and other Parulidae, some researchers have suggested their habitat selection cues are at even finer scales, on the order of 10 m² or

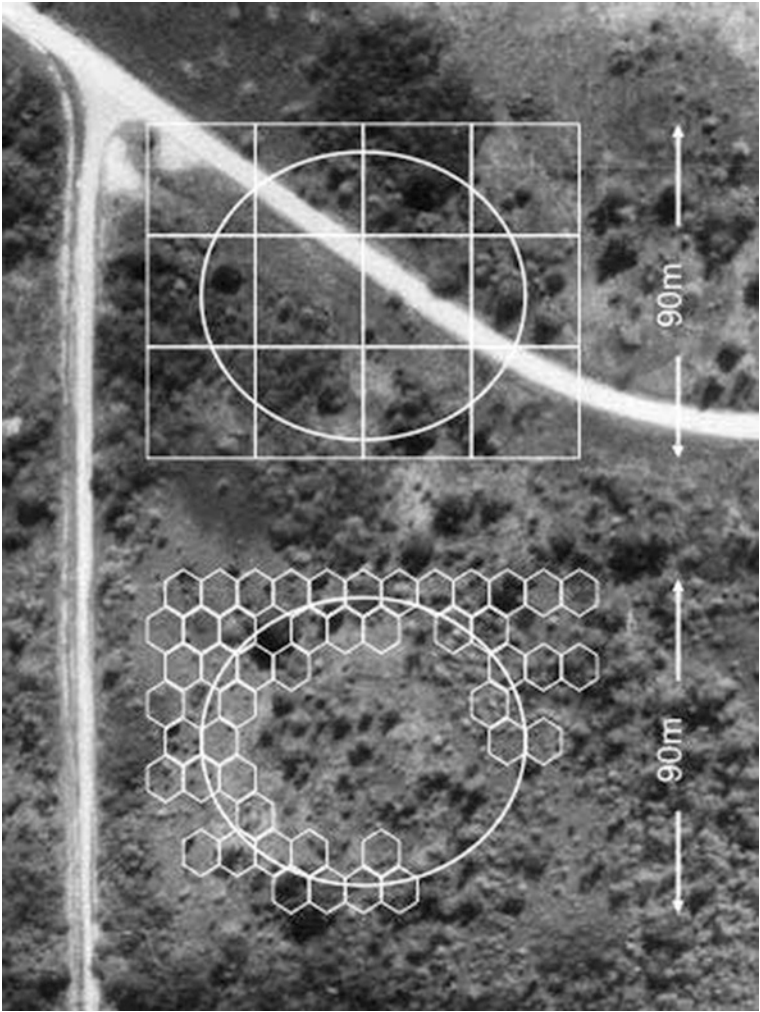


Fig. 2.1 Area of detail in Fig. 1.1 with grids of two cell sizes, 100 m² hexagons and 900 m² squares, superimposed over nominal 0.81 ha passerine territories (ovals) on 1:2000 aerial photography with <0.75 m (NIIRS Level 6) resolution. Notice in comparison with Fig. 1.1 how this much higher resolution image viewed at a larger scale allows identification of landscape components such as individual trees, shrubs, and small patches of open grass thought to be used in habitat selection by passerines. Note also the increased classification difficulties at the greater 30-m ground sampling distance (GSD = cell to cell center distance) of the Landsat-scale cells on high-resolution imagery due to increased inclusion of multiple identifiable component types (e.g., deciduous sawtimber, deciduous saplings, deciduous shrubs, coniferous trees, bare ground, and herbaceous cover) within a single 30 × 30-m (Landsat pixel equivalent) cell. *Source* 22 May 1977 aerial photography from an altitude of 1,100 m using a Hasselblad camera and 70-mm black and white film

less (Jeff Larkin, IUP, personal communication; Carpenter et al. 2011). Thus, mismatches of organism space use to image resolution will inevitably lead to lower correlations of species with landscape metrics intended to explain their occurrence (Trani 2002). This is exemplified in many of the studies we reviewed where Johnson's (1980) Third Order (habitat) analysis is attempted using Second Order (biotope) resolution imagery. This suggests the advisability of conducting exploratory analyses (James and McCulloch 2002) employing the highest resolution imagery available (compare Figs. 1.1 and 2.1). Lastly, as noted earlier, alternatives to the use of higher resolution imagery include textural analysis and LiDAR, both of which allow characterization of the heterogeneity within a given landuse class (e.g., Bellis et al. 2008; Graf et al. 2009; Seavy et al. 2009; Goetz et al. 2010; Vierling et al. 2011; Farrell et al. 2013).

Ultimately, interpretation of a species' habitat or patch association, or an assemblage's plant community as "solid" or "edge" is dependent on (1) the resolution at which the landscape is viewed by the researcher (i.e., resolution and mapping scale of imagery) and (2) the resolution-dependent explanatory variables used to test the association. Both should always attempt to match the focal taxon's use of that landscape (Keller et al. 1979a; Keller 1986; O'Neill et al. 1986; Turner 1989; Wiens 1989b; Noss 1991; Orians and Wittenberger 1991; Morrison et al. 1998; Dettmers and Bart 1999; Mazerolle and Villard 1999; Potvin et al. 2001; MacFaden and Capen 2002; Thompson and McGarigal 2002; Trani 2002; Barg et al. 2005; McGarigal and Cushman 2005; Moore et al. 2010; LeBrun et al. 2012; Farrell et al. 2013).

2.7 Gaps in Information: Scale Disconnects Between Local and Landscape-scale Metrics

Few studies measure landscape variables at a resolution that would allow quantification of intraterritory heterogeneity or, in the case of open-canopy communities, even within-biotope heterogeneity (but cf. Thompson and McGarigal 2002; Goetz et al. 2010; Farrell et al. 2013). Researchers frequently either (1) choose a minimum landscape component size (MMU), often a plant community, equivalent to the size of an *entire territory* used by the focal species (e.g., Magarigal and McComb 1995; Cushman and McGarigal 2003) regardless of whether the image resolution might allow a finer level of classification, or (2) use lower resolution imagery that limits the minimum resolvable landscape component to something more spatially extensive, again typically an entire plant community, than the scale of individual components (e.g., trees, shrubs, grassy openings = grain) used by the organism to select habitat (e.g., Rykken et al. 1997; Lee et al. 2002; Lichstein et al. 2002; Betts et al. 2003, 2006, 2007). In either case, the choice (mmu and/or image resolution) completely precludes GIS measurement of intraterritory heterogeneity or, at a minimum, restricts its characterization.

In addition, when hierarchical studies include on-the-ground measurements of habitat, the jump to a spatially more extensive and coarser-grained remotely sensed image may result in a GIS minimum mapping unit that is neither overlapping nor even contiguous with the scale of variables being measured on the ground (but see Saab 1999). This leads to a potential gap in information on the influence of local-scale spatial heterogeneity (cf. With 1994; Hagan and Meehan 2002; Lee et al. 2002; Betts et al. 2006; Dickson et al. 2009; Cornell and Donovan 2010), which, in turn, can lead to misinterpretation of the importance of landscape- versus local-scale variables (see discussion of scale disconnects in Kotliar and Wiens 1990).

In the case of passerines, other small vertebrates and most invertebrates, even most aerial photos are at resolutions too low (NIIRS Level 3) to allow accurate interpretation and thus, quantification, of the individual landscape components important to these species. As a result, if the scale of heterogeneity is not measured at the scale of the organism's response, it can be deemed unimportant to occurrence, even when it really is (With 1994; Mazerolle and Villard 1999; Huston 2002; Trani 2002).

2.8 Multi-scale Analyses

There has been much discussion about the need for examining species-habitat relationships at multiple scales (Pickett and White 1985; Urban et al. 1987; Wiens 1989a; Kotliar and Wiens 1990; Allen and Hoekstra 1992; Virkkala 1991; Forman 1995; Saab 1999; MacFaden and Capen 2002; Thompson and McGarigal 2002; Thompson et al. 2002; Van Horne 2002; Johnson et al. 2004); but what criteria determine the limits of the scales to be considered? Kotliar and Wiens (1990) suggested grain and extent as the lower and upper limits, respectively, of investigation but acknowledged the potential difficulty of identifying these limits. As noted earlier in this chapter, Wiens (1989a) suggested that they could be approximated and we suggested species-specific body-size criteria for establishing grain.

Among many authors commenting on scale effects and the need for analysis at multiple scales, Brennan and Schnell (2007:631) noted that analyses of species-habitat relationships at multiple scales *"allow the data to indicate the most appropriate scale or scales for a particular study, rather than depending entirely on a researcher's subjective perception of what scales are important to a given species."* We agree; however, this also implicitly assumes that both the resolution and range of scales (sampling areas) examined include the most appropriate ones to address the research question for the taxon of interest (see O'Neill et al. 1991; Wiens 2002). We are not sure this always is the case with GIS analyses, certainly for passerines and smaller animals, and refer the reader to Wiens' (1989a) quote in Sect. 2.5.1 regarding identifying patterns that are simply artifacts of scale, or per this discussion, artifacts of image resolution. We submit that frequently, low resolution of the imagery employed limits both identification of meaningful landscape components and quantification of their spatial arrangement (heterogeneity) for the species or assemblage being studied (e.g., Donovan and Flather 2002; MacFaden

and Capen 2002; Betts et al. 2003; Thogmartin et al. 2004b; Brennan and Schnell 2007; Howell et al. 2008; for discussions see Trani 2002 and Meyer 2007).

For all of the preceding studies, and many others we reviewed, one can legitimately ask whether the use of (1) higher resolution imagery, (2) smaller minimum size delineations, (3) a more detailed landscape component classification system, and (4) more explicit (i.e., taxon-specific) edge types (cf. Keller 1990 and Chap. 6 herein) might produce better correlations and more biologically interpretable results at both the local and regional scales? In general, there appears to be a field-wide lack of recognition of the potential effects of these issues on resulting management and conservation efforts.

To further emphasize the importance of the initial choices of image resolution, classification system and minimum size delineation, consider the following study of a much larger species than the passerines we have been discussing. Thompson and McGarigal 2002 examined habitat use for Bald Eagle (*Haliaeetus leucocephalus*), a species with a home range of well over 1 km² (op. cit.), using aerial photography at the relatively large mapping scale (for a bird of prey) of 1:7500. Image resolution was not mentioned, although the minimum mapping unit was 0.01 ha, implying a fairly high-resolution image. Although close to the scale we recommended as a minimum for passerines (1:5000 mapping, NIIRS 5 or higher) in Sect. 2.5, the authors' own analyses still demonstrated a loss of explanatory power for several aspects of habitat use when information on the photos was aggregated to larger minimum size delineations, in what amounted to use of lower resolution imagery. Given the eagle's large home range and, by inference, coarse-grained use of the landscape, this result emphasizes the need to start with the highest resolution imagery available to better assess local-scale relationships when examining GIS-based habitat associations (see also Fleming et al. 2004).

Although landscape-scale (i.e., large geographic extent) influences are clearly real, particularly for less mobile species, we suggest that more careful matching of image resolution and GIS analytical scales to the higher order habitat selection scales (*sensu* Johnson 1980) of the organisms of interest (Figs. 1.2 and 2.1) will lead to explanation of a greater amount of variance in species–habitat associations at local (habitat) and biotope (plant community) scales of analysis (cf. Farrell et al. 2013), particularly in less anthropogenically influenced landscapes (cf. Dickson et al.'s 2009 and LeBrun et al.'s 2012 cautions regarding application of regionally derived models (developed at low resolutions) to local areas).

2.9 Conclusions

- Species–habitat correlations improve significantly as the resolution of the imagery more closely matches the ecological scale at which the organism uses the landscape (Keller 1986; Huston 2002; Trani 2002; Chap. 6 herein). Therefore, use remotely sensed imagery that resolves, at a minimum, the smallest landscape component or component combination (edge) thought to be used

in habitat selection by the focal taxon. If the scale of habitat use is unclear, use imagery that can resolve landscape components as small as 5x–10x the body length of the species of interest, unless species morphology or physiology suggests even smaller objects are potentially important.

- We suggest the utility of at least exploring this body size–image resolution relationship, even for biogeographic scale questions of population viability. This is because the ability to identify, classify, and quantify accurately species-specific landscape components, component combinations, and spatial arrangements of these elements, which are often critical to species occurrence, decreases as imagery resolution decreases, resulting in an increasing disconnect between the actual and measurable amount of habitat on the landscape. Use of low resolution imagery, even for questions at large geographical scales, increases the risk of obtaining misleading species–habitat correlations and misinterpreting those relationships.
- When image resolution is adequate, but the classification system is overly general (i.e., similar but identifiable and potentially meaningful landscape components are lumped together within the classification), even geospatial variables may not capture threshold spatial distributions of habitat on the landscape.
- Use the highest resolution imagery available/affordable. One can always aggregate information (cf. Thompson and McGarigal 2002). One can never go back later and measure smaller components on resolution-limited imagery (cf. McElhone et al. 2011; Arponen et al. 2012).
- Landsat data (30 m resolution, square pixels) and smaller scale aerial photography are widely available in digital formats, and analysis software is optimized to deal with them (e.g., ARCINFO, GUIDOS).
- Based on the strength (i.e., % variance explained and predictive capability) of reviewed species-habitat models, Landsat may be adequate for large-bodied or wide-ranging mammals and many raptors; but unless landscapes are “simple” (i.e., relatively homogeneous) and/or the imagery employed has high classification accuracy, it appears generally inadequate for most passerines, small mammals, most herptiles, fish of lower order streams, and many invertebrates.
- The tradeoff in selecting higher resolution imagery and a more fine-grained classification system is one of increased cost and perhaps time versus the loss of information at lower resolutions and coarser classifications.

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